nificant increase in the probability of spawning observed for populations of females with males of the other ecomorph from different lakes versus males of the other ecomorph from the same lake was significant in the absence of the phylogenetic correction (paired *t* test, t_s = 3.37, *P* = 0.020) (Fig. 2, comparison C).

28. No significant difference in microsatellite or mtDNA divergence is detected between pairs of populations (conspecific pairs excluded) from the same versus a different environment [microsatellite, analysis of variance (ANOVA), $F_{1,10}$ = 0.22, *P* = 0.65; mtDNA, ANOVA, $F_{1,10}$ = 0.76, *P* = 0.40].

29. D. J. Funk, *Evolution* 52, 1744 (1998); J. S. McKinnon, S. Mori, D. Schluter, unpublished data.

30. Two other cases exist in which the traits that form the proximate basis of reproductive isolation have known adaptive significance. These are beak and body size in Darwin's finches in the Galápagos Islands [P. T. Boag and P. R. Grant, *Science* 214, 82 (1981); L. M. Ratcliffe and P. R. Grant, *Anim. Behav.* 31, 1139 (1983); T. D. Price, P. R. Grant, H. L. Gibbs, P. T. Boag, *Nature* 309, 787 (1984)] and copper tolerance in *Mimulus* [M. R. MacNair and P. Christie, *Heredity* 50, 295 (1983); P. Christie and M. R. MacNair, *J. Hered.* 75, 510 (1984)].

31. W. J. Rowland, *Behav. Ecol. Sociobiol.* 24, 433 (1989); W. J. Rowland, *Anim. Behav.* 38, 112 (1989); M. Borland, thesis (University of British Columbia, Vancouver, 1986).

Rapid Evolution of a Geographic Cline in Size in an Introduced Fly

Raymond B. Huey,[1]*† George W. Gilchrist,[1]*‡
Margen L. Carlson,[1] David Berrigan,[1]§ Luís Serra[2]

The introduction and rapid spread of *Drosophila subobscura* in the New World two decades ago provide an opportunity to determine the predictability and rate of evolution of a geographic cline. In ancestral Old World populations, wing length increases clinally with latitude. In North American populations, no wing length cline was detected one decade after the introduction. After two decades, however, a cline has evolved and largely converged on the ancestral cline. The rate of morphological evolution on a continental scale is very fast, relative even to rates measured within local populations. Nevertheless, different wing sections dominate the New versus Old World clines. Thus, the evolution of geographic variation in wing length has been predictable, but the means by which the cline is achieved is contingent.

How fast can evolution occur in nature (*1, 2*)? Are evolutionary trajectories predictable or idiosyncratic (*3, 4*)? Answers to these two questions are fundamental to attempts to forecast evolutionary responses to natural or anthropogenic perturbations (*5*). Rates of evolution are usually estimated by monitoring phenotypic shifts within local populations over time (*2, 4, 6–8*) and are rarely evaluated on a continental scale (*9*). The predictability of evolution is evaluated by determining whether replicate populations show convergent responses (*4, 10*).

Recently introduced species that quickly colonize large areas offer special opportunities to address both the speed and predictability of evolution on a geographic scale (*11*): Rapid and predictable evolution would be demonstrated if

[1]Department of Zoology, University of Washington, Box 351800, Seattle, WA 98195–1800, USA. [2]Departament de Genètica, Universitat de Barcelona, 08071 Barcelona, Spain.

*These authors contributed equally to this work.
†To whom correspondence should be addressed. E-mail: hueyrb@u.washington.edu
‡Present address: Department of Biology, Clarkson University, Box 5805, Potsdam, NY 13699–5805, USA.
§Present address: National Cancer Institute, Division of Cancer Prevention and Control, Bethesda, MD 20852, USA.

introduced populations quickly evolved clines that converge on clines among ancestral populations (*12, 13*). A candidate species is *Drosophila subobscura*. This fly is native to the Old World (*12, 13*), where it exhibits a clinal increase in body size with latitude (*14–16*). It was accidentally introduced into western North and South America about two decades ago (*17*) and spread rapidly in temperate regions (*12, 13*). No latitudinal cline in wing size was evident on either continent about one decade after the introduction (*15, 16*). Here we reexamine the North American populations to determine whether a cline has evolved after two decades and whether it has converged on the Old World cline.

We collected introduced flies from 11 localities in western North America (NA) (April and May 1997) and native flies from 10 localities in continental Europe (May 1998) (*18*). We established stocks for each (10 per sex from each of 15 to 25 isofemale lines) and maintained them (20°C, low density) for five to six generations in a common garden to ensure that any observed differences between populations would be genetic. We then set up four vials per population (50 eggs per vial) and reared flies to adulthood. Shortly after the flies eclosed, we mounted the left wing from flies selected haphazardly (~20

per sex per population) and measured wing length as the combined length of the basal and distal segments of vein IV (*15*).

Wing length of native European females increased significantly with latitude (Fig. 1A), as in previous studies (*14–16*). Wing length of introduced North American females also increased significantly with latitude (Fig. 1A) (*19*), and the slope of the regression was not significantly different from that of European females (comparison of slopes, *P* = 0.834). Wing length of males also increased significantly with latitude in both native and introduced populations (Fig. 1A), but the slope for North American males was less steep than that for European males (*P* < 0.001) or that for North American females (*P* < 0.001) (*20*).

The striking convergence of clinal variation in wing size (Fig. 1A) has been achieved through analogous, not homologous, changes in the relative lengths of different parts of the wing (Fig. 1B). The increase in wing length with latitude in Europe is caused by a relative lengthening of the basal portion of vein IV, whereas the increase in NA is caused by a relative lengthening of the distal portion of vein IV (*21*). These differences in slopes between continents are significant for both females (Fig. 1B, *P* < 0.001) and males (*22*) (*P* < 0.001).

How fast can evolution occur on a continental scale? Although no cline in wing length was evident in samples collected about one decade after the introduction in NA (*15*), a cline is conspicuous after two decades (Fig. 1A). Thus, this cline evolved in only one to two decades (*23*). The rate of size divergence on a continental scale for *D. subobscura* females is rapid [~1700 darwins, ~0.22 haldanes (*2, 24*)] and is faster than almost all previously measured rates in nature, even within local populations (*2, 24*). For morphological traits in natural populations, only rates of Galápagos finches during the 1978 drought are faster [0.37 to 0.71 haldanes (*2, 6*)].

Is evolution predictable or historically contingent (*3, 4*)? Convergent latitudinal clines in wing length of North American *D. subobscura* (especially of females) and ancestral European *D. subobscura* (Fig. 1A), as well as those of many other drosophilids (*15, 25*), demonstrate that the evolution of wing

Fig. 1. The latitudinal cline in wing size of introduced North American *D. subobscura* is converging on that for native [European (EU)] flies. (**A**) Female wing length (logarithmically transformed, mean slope ± SE) of introduced North American flies increases with latitude ($b = 0.0020 \pm 0.0004$, $P < 0.001$, $R^2 = 0.1393$) in a pattern virtually identical to that of European flies ($b = 0.0018 \pm 0.0004$, $P < 0.001$, $R^2 = 0.0749$). Male wing size also increases positively with latitude in NA ($b = 0.0007 \pm 0.0004$, $P = 0.0265$, $R^2 = 0.0191$) and Europe ($b = 0.0024 \pm 0.0005$, $P < 0.001$, $R^2 = 0.1119$). (**B**) The relative length of the basal portion of vein IV (the arc sine–square root–transformed proportion of the total wing length) versus latitude for *D. subobscura* (only the females are graphed; the pattern for males is similar). In the native European populations, the relative length of the basal portion increases with latitude (females: $b = 0.0005 \pm 0.0002$, $P <$

0.001, $R^2 = 0.0482$; males: $b = 0.0005 \pm 0.0001$, $P < 0.001$, $R^2 = 0.0680$), whereas in NA, it decreases with latitude (females: $b = -0.0005 \pm 0.0001$, $P < 0.001$, $R^2 = 0.0618$; males: $b = -0.0005 \pm 0.0002$, $P < 0.001$, $R^2 = 0.0555$). Thus, the wing section controlling the cline in wing length (A) differs between North American and European populations.
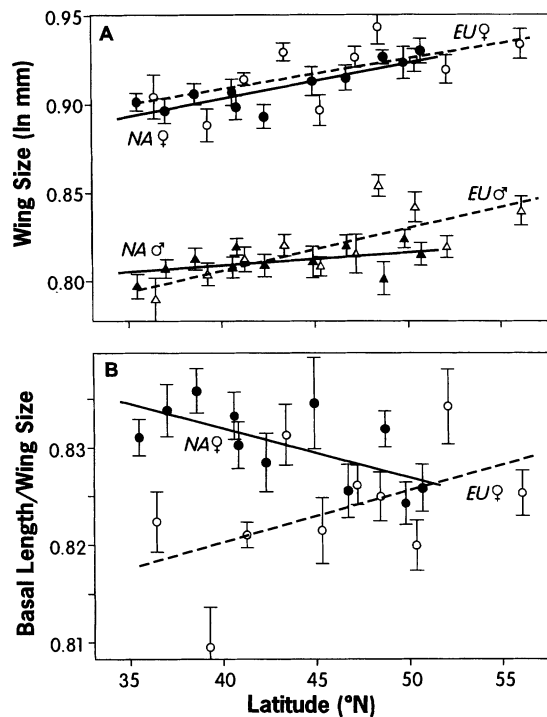
length with latitude is predictable and likely adaptive (*4, 10, 25, 26*). Nevertheless, males have evolved more slowly than females in NA (Fig. 1A), and the clines in NA and in Europe involve changes in the relative lengths of different sections of the wing (Fig. 1B). Thus, even though the overall evolutionary response (increased wing length with latitude) is predictable, the underlying details are not. In this system, evolution is thus simultaneously predictable and contingent.

References and Notes

1. C. D. Darwin, *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (J. Murray, London, 1859); G. G. Simpson, *Tempo and Mode in Evolution* (Columbia Univ. Press, New York, 1944); P. D. Gingerich, *Science* **222**, 159 (1983); S. J. Gould, *Science* **226**, 994 (1984); P. D. Gingerich, *Science* **226**, 995 (1984).
2. A. P. Hendry and M. T. Kinnison, *Evolution* **53**, 1637 (1999).
3. If the forces of natural selection are strong and deterministic, evolutionary trajectories can be predicted. If, however, unique past events play an overriding role, evolutionary trajectories can be idiosyncratic or "contingent." [S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (Norton, New York, 1989); M. Travisano, J. A. Mongold, A. F. Bennett, R. E. Lenski, *Science* **267**, 87 (1995); (*4*).]
4. J. B. Losos, T. R. Jackman, A. Larson, K. de Queiroz, L. Rodriquez-Schettino, *Science* **279**, 2115 (1998).
5. P. W. Ewald, *Evolution of Infectious Disease* (Oxford Univ. Press, Oxford, UK, 1994); M. Lynch and R. Lande, in *Biotic Interactions and Global Change*, P. M. Kareiva, J. G. Kingsolver, R. B. Huey, Eds. (Sinauer, Sunderland, MA, 1993), pp. 234–250.
6. P. R. Grant and B. R. Grant, *Evolution* **49**, 241 (1995).
7. J. B. Losos, K. I. Warheit, T. W. Schoener, *Nature* **387**, 70 (1997).

8. D. N. Reznick, F. H. Shaw, F. H. Rodd, R. G. Shaw, *Science* **275**, 1934 (1997).
9. C. K. Williams and R. J. Moore, *J. Anim. Ecol.* **58**, 495 (1989); S. P. Carroll, H. Dingle, S. P. Klassen, *Evolution* **51**, 1182 (1997).
10. Repeated or replicated convergent evolution is often interpreted as strong evidence that evolution is predictable, not contingent [(*3, 4*); J. A. Endler, *Natural Selection in the Wild* (Princeton Univ. Press, Princeton, NJ, 1986); J. B. Mitton, *Selection in Natural Populations* (Oxford Univ. Press, Oxford, UK, 1997)]. Convergent phenotypes can, however, be achieved through different mechanisms and thus are predictable on one level, but contingent on another [R. E. Lenski, *Evolution* **42**, 425 (1983); (*4*)].
11. R. F. Johnston and R. K. Selander, *Science* **144**, 548 (1964); H. G. Baker and G. L. Stebbins, Eds., *The Genetics of Colonizing Species* (Academic Press, New York, 1965); P. A. Parsons, *The Evolutionary Biology of Colonizing Species* (Cambridge Univ. Press, Cambridge, 1983).
12. A. Prevosti *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **85**, 5597 (1988); D. Brncic, in *Genetics of Natural Populations: The Continuing Importance of Theodosius Dobzhansky*, L. Levine, Ed. (Columbia Univ. Press, New York, 1995), pp. 154–169.
13. F. J. Ayala, L. Serra, A. Prevosti, *Genome* **31**, 246 (1989).
14. A. Prevosti, *Cold Spring Harbor Symp. Quant. Biol.* **20**, 294 (1955); R. K. Misra and E. C. R. Reeve, *Genet. Res.* **5**, 240 (1964).
15. G. Pegueroles *et al.*, *Evol. Ecol.* **9**, 453 (1995).
16. M. Budnik, L. Cifuentes, D. Brncic, *Heredity* **67**, 29 (1991).
17. Flies were first discovered in South America in 1978 [D. Brncic and M. Budnik, *Drosophila Inf. Serv.* **55**, 20 (1980)] and in NA in 1982 [A. T. Beckenbach and A. Prevosti, *Am. Midl. Nat.* **115**, 10 (1986)]. Discussions in (*12, 13*) establish that the North and South American introductions came from the same founder stock and are unlikely to have occurred much before 1978. This system has been called a "grand experiment in evolution" (*13*) because the introduction is replicated

and evolutionary responses can be compared directly against the Old World evolutionary baseline.
18. European localities—Spain: Malaga (36.5°N), Valencia (39.3°N), and Barcelona (41.3°N); France: Montpellier (43.4°N), Lyon (45.3°N), Dijon (47.2°N), Gif-sur-Yvette (48.4°N), and Lille (50.4°N); Leiden, Netherlands (52.1°N); and Århus, Denmark (56.1°N). North American localities—California: Atascadero (35.5°N), Gilroy (37.0°N), Davis (38.6°N), Redding (40.6°N), and Eureka (40.8°N); Oregon: Medford (42.3°N) and Salem (44.9°N); Washington: Centralia (46.7°N) and Bellingham (48.7°N); and British Columbia: Peachland (49.8°N) and Port Hardy (50.7°N).
19. Because a directional hypothesis (size increases with latitude) is at risk, we used one-tailed tests for evaluating the significance of clines.
20. In Europe, the slope of the size increase does not differ statistically for males and females ($P = 0.130$), whereas the North American sexes are significantly different ($P = 0.001$). The difference in the clinal pattern of males and females in NA suggests that either males are under less stringent selection pressure (and that genetic correlations between male and female wing size are weak) or that some component of selection is retarding the evolution of male wing size. For example, if female preferences for male wing size exist and evolve more slowly than female wing size, sexual selection might constrain the evolution of male wing size.
21. This contrast might reflect between-continent differences in genetic variation for developmental domains determining the basal-distal wing axis or in selective regimes.
22. R. B. Huey, G. W. Gilchrist, M. L. Carlson, D. Berrigan, L. Serra, data not shown.
23. Clines in chromosomal markers of introduced *D. subobscura* evolved even faster and were detected within a few years of the introduction [D. Brncic, A. Prevosti, M. Budnik, M. Monclús, J. Ocaña, *Genetica* **56**, 3 (1981); (*12, 13*)].
24. J. B. S. Haldane, *Evolution* **3**, 51 (1949). "Haldanes" were estimated by comparing fitted values of the latitudinally extreme populations and by assuming five generations per year. The values for males are lower (699 darwins and 0.0784 haldanes).
25. Positive latitudinal clines in size are documented in many other drosophilids as well [J. R. David and C. Bocquet, *Nature* **257**, 588 (1975); A. C. James, R. B. R. Azevedo, L. Partridge, *Genetics* **140**, 659 (1995); D. Karan *et al.*, *Genet. Res.* **71**, 31 (1998); but see A. D. Long and R. S. Sing, *Heredity* **74**, 569 (1995)], although not in all insects [T. Mousseau, *Evolution* **51**, 630 (1997)].
26. Although convergent clines strongly suggest that clines are adaptive (*10*), the possible adaptive basis of latitudinal size clines is unclear [C. Ray, *J. Morphol.* **106**, 85 (1960); R. Sibly and D. Atkinson, *Funct. Ecol.* **8**, 486 (1994); D. Atkinson, in *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, I. A. Johnston and A. F. Bennett, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 183–204; L. Partridge and V. French, in *Animals and Temperature: Phenotypic and Evolutionary Adaptation*, I. A. Johnston and A. F. Bennett, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 265–292]. Although many environmental factors change with latitude, temperature is generally considered the most likely selective agent for several reasons [for details, see L. Partridge and J. A. Coyne, *Evolution* **51**, 632 (1997)]. For example, drosophilids maintained by laboratory natural selection at low temperature quickly evolve larger size [W. W. Anderson, *Genet Res.* **7**, 255 (1966); S. Cavicchi, D. Guerra, G. Giorgi, C. Pezzoli, *Genetics* **109**, 655 (1985); L. Partridge, B. Barrie, K. Fowler, V. K. French, *Evolution* **48**, 1269 (1994)]. Nevertheless, a nonadaptive explanation has been proposed [T. M. van der Have and G. de Jong, *J. Theor. Biol.* **183**, 329 (1996)].