with *CLAVATA3*. Plant Physiol. *126*, 939–942.
14. Fletcher, J.C., Brand, U., Running, M.P., Simon, R., and Meyerowitz, E.M. (1999). Signaling of cell fate decisions by CLAVATA3 in *Arabidopsis* shoot meristems. Science *283*, 1911–1914.
15. Kondo, T., Sawa, S., Kinoshita, A., Mizuno, S., Kakimoto, T., Fukuda, H., and Sakagami, Y. (2006). A plant peptide encoded by *CLV3* identified by *in situ* MALDI-TOF MS analysis. Science *313*, 845–848.
16. Sharma, V.K., Ramirez, J., and Fletcher, J.C. (2003). The Arabidopsis *CLV3-like (CLE)* genes are expressed in diverse tissues and encode secreted proteins. Plant Mol. Biol. *51*, 415–425.
17. Ito, Y., Nakanomyo, I., Motose, H., Iwamoto, K., Sawa, S., Dohmae, N., and Fukuda, H. (2006). Dodeca-CLE peptide as suppressors of plant stem cell differentiation. Science *313*, 842–845.
18. Matsubayashi, Y., and Sakagami, Y. (2006). Peptide hormones in plants. Annu. Rev. Plant Biol. *57*, 649–674.
19. Kinoshita, T., Caño-Delgado, A., Seto, H., Hiranuma, S., Fujioka, S., Yoshida, S., and an Chory, J. (2005). Binding of brassinosteroids to the extracellular domain of plant receptor kinase BRI1. Nature *433*, 167–171.
20. Scheres, B. (2001). Plant cell identity. The role of position and lineage. Plant Physiol. *125*, 112–114.

Department of Biology, University of Utah, 257 South,1400 East, Salt Lake City, Utah 84112, USA.
E-mail: Sieburth@biology.utah.edu

DOI: 10.1016/j.cub.2007.05.066

Behavioural Genetics: Evolutionary Fingerprint of the ‘Invisible Hand’

A recent study of the *foraging* gene in *Drosophila* illustrates a long-standing economic maxim that competition favors rare strategies. Two *foraging* alleles, rovers and sitters, each have higher fitness when rare — but only when competition is strong.

Daniel I. Bolnick

Adam Smith’s 1776 book *An Inquiry into the Nature and Causes of the Wealth of Nations* [1] laid the groundwork for much of modern economics. One of Smith’s insights was the view that competition can play a productive role in society. When too many individuals make a given product, their profits fall relative to other scarcer products for which consumer demand is high. Competition is thus an ‘invisible hand’ that maintains balance across multiple economic strategies.

Like any well-educated British intellectual of his era, Charles Darwin was familiar with Adam Smith’s work [2]. While Malthus’ political tract *An Essay on the Principle of Population* is generally credited with contributing to the development of Darwin’s theory of natural selection, one can also find echoes of Smith’s economic philosophy. For instance, in *The Origin of Species* [3], Darwin wrote:

> “*the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers… Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural power of increase be allowed to act, it can succeed in increasing… only by its varying descendants … being enabled to feed on new kinds of prey …inhabiting new stations, climbing trees, frequenting water, and some perhaps becoming less carnivorous*.”

In more modern terms, a population at its carrying capacity is subject to sufficiently strong competition that each individual is, on average, only capable of gathering enough resources to produce one offspring. However, if an individual is capable of using novel resources for which competition is less severe, it will gain a fitness advantage. This advantage will be transient, because once the phenotype in question becomes more common, competition for the new resource intensifies and fitness declines. Hence, competition has long been viewed as an innovative force favoring rare phenotypes (‘negative frequency-dependence’) [4–8]. Competition can thus drive evolutionary diversification — termed ‘annidation’ by Ludwig [7], though the moniker never caught on — has been of great interest to theoreticians for many years as a mechanism that can maintain genetic variation [6,7], drive disruptive selection [5], or maybe even promote speciation [9,10].

Despite the long-standing theoretical foundation, strong empirical evidence for frequency-dependent competition has been sparse. The reason for this lacuna is largely practical. To obtain unambiguous evidence for annidation, two challenging criteria must be met. First, one must demonstrate that rare phenotypes gain a fitness advantage [11–13]. For instance, in the polymorphic fish *Herichthys minckleyi*, individuals have either a fine-toothed (‘papilliform’) pharyngeal jaw suited to processing plant material, or a robust (‘molariform’) jaw for crushing snails. By experimentally manipulating morph frequencies, it was shown that each morph grew best when it was the less common form [13]. A second criterion to establish that competition drives diversification, is to prove that the rare-phenotype advantage only occurs when intraspecific competition is strong [14,15]. For example, selection favors rare phenotypes in another fish, the three-spine stickleback *Gasterosteus aculeatus*, but only when competition is strong [15].

While a number of studies have established frequency-dependence, and a few others have tested the diversifying effect of intraspecific competition, very few studies have done

Figure 1. Should I stay or should I go?

Fruit fly larvae are genetically programmed to either move extensively or very little in search of food. The alleles underlying these strategies are maintained by frequency-dependent selection: each confers higher fitness when it is the rarer strategy. (Photo credit: Mark Fitzpatrick.)

both. A recent experiment by Fitzpatrick *et al.* [16] tackled both lines of evidence together. These authors studied the *foraging* gene in the fruit fly *Drosophila melanogaster* (Figure 1). This gene has two widespread alleles, a 'rover' (for^R), and a 'sitter' (for^s), which affect the movement rate of larvae when they are feeding as well as movement rates between food patches [17,18]. The alleles both occur in natural populations, with rovers slightly outnumbering sitters [18]. To test whether frequency-dependent competition maintains this persistent balanced polymorphism, Fitzpatrick *et al.* [16] experimentally manipulated both genotype frequencies and nutrient abundance. Fly larvae were raised in groups with rover:sitter ratios of 3:1, 1:1 and 1:3, held at both low and high nutrient levels. Using survival to pupation as a measure of fitness, sitters had higher fitness when they were rare (sitter survival rate $\sim$ 0.8, rovers $\sim$ 0.7), but lower fitness when they were common (sitter survival rate $\sim$ 0.6, rovers $\sim$ 0.9). This rare-phenotype advantage was only observed when nutrients were scarce, otherwise both genotypes' fitness was independent of their frequency and rovers were consistently more fit (could this explain their higher frequency in nature?).

These results alone are notable, but the researchers were able to go one step further. Previous studies of frequency-dependent selection and competition have without exception studied the evolution of readily measurable morphological traits. The genetic basis of the trait is often not well known, raising the possible criticism that selection is actually operating on a different but genetically linked locus. Taking advantage of the genetic tools available in *Drosophila*, Fitzpatrick *et al.* [16] were able to clearly show that selection is acting specifically on the foraging gene. They did so using a strain of rover flies that had been irradiated to produce sitter mutants [19] on an otherwise for^R genome. These flies exhibited the same fitness as wild-type sitters, confirming that foraging is the target of selection. These results also highlight the potential for competition and selection to act on genetically determined behavioral, rather than morphological, variation.

The exact mechanism by which competition favors each genotype when rare is not yet clear. Do rovers incur greater energetic costs that are detrimental when they are common and nutrients are scarce? When sitters are common, do they create locally depleted resource patches that favor rovers who can find under exploited habitats? An even more challenging task is to determine how often competition in natural populations is severe enough to generate this frequency dependence, or weak enough to favor rovers. Nonetheless, Fitzpatrick *et al.*'s [16] experiment provides an exceptionally clear illustration of the principle that competition can promote genetic diversity by maintaining multiple alternative strategies in a balanced polymorphism. Adam Smith's 'invisible hand' seems to have left a fingerprint on the *Drosophila* genome. Interestingly, the influence is mutual: the economic idea that competition stimulates innovation and diversity is today often associated with a school of thought known as 'evolutionary economics' [20].

References

1. Smith, A. (1776). An Inquiry into the Nature and Causes of the Wealth of Nations.
2. Schweber, S.S. (1980). Darwin and the political economists: divergence of character. J. Hist. Biol. *13*, 195–289.
3. Darwin, C. (1859). On the Orign of Species (Cambridge, Massachusetts: Harvard University Press).
4. Maynard Smith, J. (1966). Sympatric speciation. Am. Nat. *100*, 637–650.
5. Bürger, R. (2005). A multilocus analysis of intraspecific competition and stabilizing selection on a quantitative trait. J. Math. Biol. *50*, 355–396.
6. Levene, H. (1953). Genetic equilibrium when more than one ecological niche is available. Am. Nat. *87*, 331–333.
7. Ludwig, W. (1950). Zur theorie der konkurrenz. Neue. Ergeb. Prob. Zool., Klatt-Festschrift, 516–537.
8. Rosenzweig, M.L. (1978). Competitive Speciation. Biol. J. Linnean Soc. *10*, 275–289.
9. Dieckmann, U., and Doebeli, M. (1999). On the origin of species by sympatric speciation. Nature *400*, 354–357.
10. Doebeli, M. (1996). A quantitative genetic competition model for sympatric speciation. J. Evol. Biol. *9*, 893–909.
11. Benkman, C.W. (1996). Are the ratios of bill crossing morphs in crossbills the result of frequency-dependent selection? Evol. Biol. *10*, 119–126.
12. Rainey, P.B., and Travisano, M. (1998). Adaptive radiation in a heterogeneous environment. Nature *394*, 69–72.
13. Swanson, B.O., Gibb, A.C., Marks, J.C., and Hendrickson, D.A. (2003). Trophic polymorphism and behavioral differences decrease intraspecific competition in a cichlid, *Herichthys minckleyi*. Ecology *84*, 1441–1446.
14. Bolnick, D.I. (2001). Intraspecific competition favours niche width expansion in Drosophila melanogaster. Nature *410*, 463–466.
15. Bolnick, D.I. (2004). Can intraspecific competition drive disruptive selection? an experimental test in natural populations of sticklebacks. Evolution *87*, 608–618.
16. Fitzpatrick, M.J., Feder, E., Rowe, L., and Sokolowski, M.B. (2007). Maintaining a behaviour polymorphism by frequency-dependent selection on a single gene. Nature *447*, 210–213.
17. Sokolowski, M.B. (2001). *Drosophila*: Genetics meets behaviour. Nat. Rev. Genet. *2*, 879–890.
18. Sokolowski, M.B. (1980). Foraging strategies of *Drosophila melanogaster*: a chromosomal analysis. Behav. Genet. *10*, 291–302.
19. Pereira, H.S., and Sokolowski, M.B. (1993). Mutations in the larval foraging gene affect adult locomotory behavior after feeding in Drosophila melanogaster. Proc. Natl. Acad. Sci. USA *90*, 5044–5046.
20. Schumpeter, J.A. (1934). The Theory of Economic Development (Cambridge, Massachusetts: Harvard University Press).

Section of Integrative Biology, University of Texas at Austin, One University Station C0930, Austin, Texas 78712, USA.
E-mail: danbolnick@mail.utexas.edu

DOI: 10.1016/j.cub.2007.05.056