

## DETECTING ECOLOGICAL TRADE-OFFS USING SELECTION EXPERIMENTS

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**Abstract.** Theories of the evolution of niche breadth usually depend on the assumption that genotypes that are well adapted to exploit one habitat or resource are not well adapted to others. Such “trade-offs” are often apparent in interspecific comparisons, but have been harder to document at the within-population level. Selection experiments provide a promising means for detecting within-population trade-offs: if selection for adaptation to one environment (e.g., diet, host, temperature) reproducibly lowers fitness in another, trade-offs are the likeliest explanation. Here, I describe strategies for using selection experiments to detect ecological trade-offs and discuss some of the ambiguities that can arise in interpreting the results of such experiments. I also review two sets of studies that found evidence for trade-offs using selection experiments.

**Key words:** *adaptation; artificial selection; ecological specialization; genotype–environment interaction; negative genetic correlation; niche breadth; trade-offs.*

### INTRODUCTION

Theories of the evolution of niche breadth have traditionally depended on the assumption that a “jack of all trades is a master of none” (Levins 1968, MacArthur 1972, Futuyma and Moreno 1988, Rausher 1988). According to this view, no genotype can have maximal fitness in each of a set of environments (e.g., habitats or hosts), so that a population’s improvement in fitness in one environment comes at the expense of its fitness in others. I refer to the situation where no genotype has maximal fitness in each of two environments as a “trade-off” (see Fry 1996 for a somewhat more subtle definition). Trade-offs in fitness between environments can both favor restriction of niche breadth in generalist species, and prevent expansion of niche breadth in specialist species (Holt and Gaines 1992). They can also maintain genetic variation in ecologically important traits within and among populations (Levene 1953, Hedrick 1986, Gillespie and Turelli 1989).

Negative correlations between fitness in one environment and fitness in another are often observed in comparisons among species or populations, but these do not give definitive evidence for trade-offs (e.g., Kasen 2002). The traditional approach to detecting trade-offs has been to perform a “split-family” experiment, in which individuals from each of a set of full-sib, half-sib, or clonal broods are reared in two or more environments (reviewed in Fry 1996, Roff 1997). If a negative correlation is observed between a family’s fitness in one environment and its fitness in another, a trade-

off is concluded to be present. Although relatively easy to perform, split-family experiments have the serious drawback that several factors can cause positive correlations to be observed, even when a trade-off is present (Rausher 1988, Jaenike 1990, Fry 1993, 1996, Shaw et al. 1995). This may help explain why trade-offs have not frequently been detected using split-family designs (see Via 1991, Shaw et al. 1995 for exceptions).

Selection experiments are a powerful but underutilized method that can potentially detect trade-offs not revealed by split-family designs. The purpose of this paper is to describe the uses and limitations of selection experiments for detecting ecological trade-offs. I will discuss practical considerations in the design and execution of selection experiments, and point out some commonly encountered pitfalls and how they can be avoided. I will also discuss two examples of sets of selection experiments that revealed ecological trade-offs. The emphasis will be on selection experiments with sexually reproducing outbreeding species. Experiments with clonal or self-fertilizing organisms impose a different set of challenges and will not be considered.

### DESIGN OF SELECTION EXPERIMENTS

The goal of the experimental designs considered here is to determine whether allowing a population to adapt to one habitat, host, or environment reproducibly lowers its fitness in another habitat, host, or environment. If this is the case, then it will usually be safe to conclude that a trade-off is present, i.e., that there is no (homozygous) genotype with maximal fitness in both environments.

It is important to distinguish between two types of selection experiments. In traditional artificial selection experiments, individuals are measured for one or more traits each generation, and the investigator uses the trait

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values to determine which individuals are allowed to contribute to the next generation. There is a considerable body of literature on the design and interpretation of such experiments (Hill 1971, 1972*a, b*, Hill and Caballero 1992, Falconer and Mackay 1996, Roff 1997). The type of selection experiment most useful for ecologists, however, is a “quasinnatural” (Kassen 2002) selection experiment. In this type of experiment, differences in contribution to the next generation result from inherent differences in adaptedness to the environment; there is no need for phenotypic scoring by the investigator. An example of such an experiment would be to maintain a population of a phytophagous arthropod on a plant species on which its survival and reproduction are initially low, in order to select for genotypes with higher fitness on the host. After some number of generations, individuals descended from the selected population are compared to individuals from a control population in fitness on the initially unfavorable host. In this type of experiment, unless lifetime fitness of each individual is measured each generation, it is not possible to calculate selection intensities, realized heritabilities, and realized genetic correlations—quantities that are standard in the artificial selection literature (Falconer and Mackay 1996). Nonetheless, quasinnatural selection experiments can give important qualitative evidence for or against the existence of trade-offs. This paper will emphasize experiments of the quasinnatural type.

The usual quasinnatural selection experiment to detect trade-offs will consist of at least two selection regimes, and two assay regimes. “Selection regime” refers to the environment or set of conditions under which a population is maintained. One of the selection regimes should be a control treatment designed to preserve the characteristics of the base population as much as possible. The experiment begins by subdividing the base population into a set of populations; one or more replicate populations is then maintained in each of the different selection regimes. “Assay regime” refers to the environment or conditions under which fitness, or one or more surrogates for fitness, is measured. At intervals (or perhaps just once), a sample of individuals descended from each replicate population is measured in each assay regime. Several decisions therefore need to be made by the investigator. These include (1) how to maintain the control populations; (2) the base population to use; (3) the number of replicate populations to maintain in each selection regime; (4) the size of the populations and the intensity of selection; (5) the fitness traits to assay and the details of the assay procedure; (6) the frequency with which to perform assays; (7) how to analyze the data; and (8) how to interpret the results. These issues will be discussed in turn.

#### *Control populations*

Control populations should be derived from the same base population as the selected populations, and main-

tained in a manner that minimizes evolutionary change. How this can best be achieved will depend in part on the nature of the base population (see *Design of Selection Experiments: The base population*), so only a few general comments will be made here. Ideally, a set of individuals from the base population can be cryopreserved or maintained as seeds, or in another dormant stage. If this option is not available, the best option is to maintain the control population(s) in an environment to which it is already well adapted. For example, for an experiment on the effects of adaptation to cold in *Drosophila*, the control population might be a laboratory population that has been maintained at 25°C for many generations. Alternatively, for selection experiments initiated with individuals directly collected from the wild, one could use one or more collections made from the same site at a later date as controls, but unfortunately there is no guarantee that such a repeat collection would have the same genetic characteristics as the base population.

#### *The base population*

One of the first choices faced by the investigator will be to decide on a base population to use for the selection experiment. For the sake of illustration, I will return to the example of an investigator who wishes to maintain a phytophagous arthropod population on a toxic or “challenging” host species (call this host B). The investigator has two choices. He or she could make a fresh collection of individuals from a wild population, perhaps from a diversity of host species, to form the base population. Alternatively, he or she could initiate the selection experiment with individuals from a long-established laboratory population, for example, one maintained on host A for 50 generations. These approaches both have advantages and disadvantages.

The newly collected base population would best represent the genetic diversity in a wild population. Unfortunately, there are two disadvantages to using such a population. First, if it is not possible to maintain a dormant or cryopreserved control, the control population is likely to adapt to its environment, and hence depart from the characteristics of the base population. Adaptation of the control can be minimized, but not eliminated, by maintaining it under conditions that are as “benign” as possible (e.g., on a nontoxic host), and by restricting the experiment to a small number of generations. Second, even if it is possible to use a cryopreserved or dormant control, laboratory adaptation in the selected population(s) could confound interpretation of the results. After multiple generations evolving in the laboratory, individuals derived from the populations maintained on host B might outperform individuals from the control populations in laboratory assays of fitness on any host, simply because they are better adapted to laboratory conditions. Such a result could mask underlying trade-offs.

A long-established laboratory population has the advantage of stability: if the population has been kept at a large size and in a constant environment for many generations, its rate of further evolution should be low. (In practice, of course, no environment is completely constant; but the environment can be held relatively constant with respect to the attribute of interest, such as temperature.) Therefore one or more replicate populations continued in the same regime can serve as controls. One might expect long-established laboratory populations to be depauperate in genetic variation, but as long as they are started with multiple founders and maintained at a large size, high levels of quantitative genetic variation should be maintained (Briscoe et al. 1992, Falconer and Mackay 1996). Many selection experiments started from large long-established laboratory populations have given strong responses (e.g., Gould 1979, Chippindale et al. 1997, Borash et al. 2000).

There are, nonetheless, plausible scenarios under which using a base population that has been maintained in a constant environment for many generations could either bias against detecting trade-offs that exist in wild populations, or create the spurious appearance of trade-offs where none exist. To understand the first possibility, imagine that most natural populations of the hypothetical arthropod segregate for two alleles,  $M^A$  and  $M^B$ ; on host A, the fitness ranking of these alleles is  $M^A > M^B$ , while on host B the inequality is reversed. A population that has been maintained on host A for many generations would be expected to be fixed for the  $M^A$  allele; thus if a derivative of this population were transferred on host B, the  $M$  locus could not cause reduction in fitness on host A. To understand the second possibility, consider another biallelic locus ( $N$ ) that shows overdominance (heterozygote superiority) on host A, but is neutral on host B. In a population maintained on host A, locus  $N$  will reach a stable polymorphic equilibrium, with allele frequencies that maximize mean fitness on A. If a derivative of the population were then transferred to host B, the locus would no longer be under selection, and changes of allele frequencies would be free to occur due to random drift or (especially) hitchhiking with linked alleles favored on host B. Because any change in allele frequencies at the  $N$  locus would lower mean fitness on host A, a spurious appearance of a trade-off would be created. A quantitative trait under stabilizing selection on host A but neutral on host B could similarly give rise to the spurious appearance of a trade-off. In addition to being prone to changes in the mean due to drift and hitchhiking after selection is relaxed, such a trait would be expected to increase in variance as linkage disequilibrium built up by stabilizing selection (Bulmer 1985, Hill and Caballero 1992) decays. This would be expected to deterministically reduce fitness on host A. (Mutations that are deleterious on host B but neutral on A could also deterministically reduce fitness on B

in a population maintained on A, but would probably not do so significantly in under 100 generations.)

A solution that could minimize the above problems would be to use a base population that had been maintained on a combination of the two hosts for many generations (e.g., by alternating hosts every generation or two). Such a population would be more likely to remain segregating at the  $M$  locus than a population maintained on either host alone. If a derivative of this population were established on host B alone, allele frequencies at the  $N$  locus could still change due to drift, but hitchhiking would be much less important, because the population would already be relatively well adapted to host B.

#### *Number of replicate populations*

If at all possible, each selection regime (including the controls) should be replicated. Replication allows the effects of selection to be separated from those of random drift. Furthermore, crossing replicate populations within a selection regime permits one to check for inbreeding depression (see below). If replication is not possible, each population should be assayed at frequent intervals. Changes due to drift in successive time intervals are expected to be independent; therefore changes that are consistent in direction over time are likely to be due to selection.

#### *Population size*

The smaller the population size of each replicate population, the more limited the response to selection is likely to be, and the greater the chance that inbreeding depression will occur (Weber and Diggins 1990, Falconer and Mackay 1996, Chippindale et al. 1997). Investigators should strive to maintain population sizes of at least 50 breeding adults (cf. Weber and Diggins 1990). The need to maintain a reasonable population size will often affect the decision of how harsh the selection regime should be. Harsher regimes (e.g., host plants that are more toxic) result in stronger selection, but also increase inbreeding and genetic drift by reducing the number of individuals that successfully reproduce.

#### *Fitness assays*

Because the goal is to determine whether populations from different selection regimes differ in total fitness in a given assay regime, as many components of fitness as possible should be assayed. In addition, to exclude nongenetic causes of fitness differences, samples from each population should be reared in a common environment for at least one full generation (preferably two) before the assays. Even with this precaution, microbial infection (including infection of the food medium) could mimic genetic differences. The likelihood of this possibility and the precautions needed to exclude it will depend on the study organism.

Assays of populations from different selection regimes should be carried out simultaneously with proper randomization. If there are multiple replicate populations within each selection regime, comparing pairs of populations at different times may make the fitness assays more manageable (e.g., Joshi and Mueller 1996).

If populations within a given selection regime (say B) are found to have evolved lower fitness in another regime (say A), then it is a good idea to repeat the fitness assays after crossing replicate populations within regimes. If the same difference is found, inbreeding depression can be ruled out as a cause of the fitness declines (e.g., Chippindale et al. 1997).

#### *Frequency of assays*

Long intervals between fitness assays allow greater differences between populations to accumulate, but have a potential disadvantage. It is possible that populations maintained in selection regime B will initially decline in fitness in assay regime A, but that this decline will be erased in subsequent generations by the accumulation of modifier alleles that mitigate the trade-off (e.g., McKenzie and Game 1987). Relatively frequent fitness assays (say every 10–15 generations) allow a check for this possibility.

#### *Data analysis*

If all populations are assayed simultaneously, the appropriate analysis will be an analysis of variance with replicate populations (a random effect) nested within selection regime (a fixed effect). If a paired design is used, the appropriate analysis is a two-way ANOVA with selection regime crossed to population pair (a random effect); alternatively, a paired *t* test can be used.

#### *Interpreting the results*

If adaptation to one regime is not accompanied by a detectable reduction in fitness in a second regime, there are at least three possible interpretations. First, it is possible that a reduction in fitness occurred, but was not detected due to insufficient statistical power. Calculating a 95% confidence limit for the difference between regimes (e.g., Fry 1990, 1992) can help clarify whether a biologically important fitness difference might still be present. Second, it is possible that trade-offs exist in nature, but are not detectable under the laboratory assay regimes used. For example, a phytophagous insect population selected to survive and grow well on host B in the laboratory may suffer no reduction in survival and growth on host A. In nature, however, the two host species might have different predator faunas that select for different attributes in the herbivore. Detailed knowledge of the biology of one's study organism might suggest appropriate hypotheses to test regarding the nature of possible trade-offs. A third possibility is that trade-offs are truly absent. It is

important to consider whether alternative hypotheses for niche limitation and specialization could apply to one's study organism (Colwell 1986, Kawecki 1994, Holt 1995, Fry 1996, Whitlock 1996, Kawecki et al. 1997, Bernays 2001).

Alternatively, adaptation to one regime may result in reduced fitness in a second regime. If the reduction in fitness is rapid and reproducible across replicates, it is not likely to be due to drift, hitchhiking, or decay of linkage disequilibrium. In this case, and if inbreeding depression can be ruled out, one can safely conclude that trade-offs are present.

#### EXAMPLES

I discuss here two sets of experiments whose goal was to determine whether trade-offs were present between pairs of ecologically relevant environments. The studies discussed took a diversity of approaches; although they were relatively successful, they illustrate some of the ambiguities that can arise in interpreting the results of selection experiments. I make no attempt to review the literature on ecologically motivated selection experiments; in particular, I ignore the many experiments on costs of resistance to pesticides (Roush and McKenzie 1987), on selection for early or late reproduction (Partridge and Barton 1993), and on density-dependent selection (Mueller 1997).

#### *Trade-offs in fitness on different hosts in the phytophagous mite Tetranychus urticae*

The two-spotted spider mite *T. urticae* Koch is a ubiquitous pest of house plants, greenhouse plants, and field crops in warmer regions. The species is an extreme generalist, having been recorded from hundreds of host species (Jeppson et al. 1975). Nonetheless, there are many hosts on which *T. urticae* has low reproductive success. This raises the questions of whether *T. urticae* populations could adapt to such hosts, and if so, whether the adaptation would involve a loss of fitness on initially more favorable hosts. A "yes" answer to both questions would give evidence that the host range of *T. urticae* is ultimately hindered from expanding by trade-offs.

The short generation time of the mites and the ease with which they can be reared make *T. urticae* a good candidate for the selection experiment approach. Gould (1979), Fry (1990, 1999), and Agrawal (2000) each established a base population of *T. urticae* in the laboratory on an initially favorable host, lima bean (Gould 1979, Fry 1990, 1999) or cotton (Agrawal 2000); egg-to-adult survival on these hosts was high. A second ("selected") population was later established from the base population on a host that initially caused high juvenile mortality, cultivars of cucumber (Gould 1979, Agrawal 2000) or tomato (Fry 1990, 1999). The other population continued to be maintained on the favorable host and was used as a control. Each experimenter periodically compared viability or reproductive rate of

the selected and control populations on the host of the selected population. Adaptation of the selected population to its host occurred rapidly in each case. To test the possibility that a trade-off was present, each investigator created one or two "reversion" lines by re-establishing mites from the selected population on the control host. If alleles favored on the host of the selected population were selected against on the control host, reversion lines would be expected to decline in fitness on the host of the selected population. This was precisely what was observed. The reversion was especially rapid in the two experiments using cucumber; in fact, in Agrawal's experiment, the reversion line had slightly lower fitness on cucumber than the control population after only five generations of reversion.

A puzzling feature of these experiments is that, when the selected and control populations were compared in oviposition rate (Gould 1979, Fry 1990) or a measure of reproductive rate (Agrawal 2000) on the host of the control population, no differences were observed. This would seem to contradict the evidence for trade-offs provided by the reversion lines. Recent results of Yano et al. (2001) suggest a possible resolution to this paradox. These authors selected a *T. urticae* population for higher fecundity on *Commelina communis*, a poor host. After four generations, the selected line had significantly higher fecundity than the control line on *C. communis* and several other host species. In tests of male ability to compete for mates, however, the selected line was inferior. This suggests that the reversion in the previous experiments may have been caused by selection for higher mating success, rather than by selection on female components of fitness.

In contrast to the rapid reversion observed by Gould (1979) and Agrawal (2000), the reversion lines in Fry's (1990) experiment declined relatively slowly in fitness on tomato, and never returned to the survival level of the base population, even though one was maintained for over 30 generations. Fry (1999) considered two explanations for this result; both are based on the observation that the selected line had reached an apparent plateau or equilibrium by the time the reversion lines were established (Fry 1990). The first possibility is that the reversion lines did not contain the necessary genetic variation to revert to the survival level of the control population. Alternatively, the declines in fitness on tomato in the reversion lines may have been caused by random drift or hitchhiking rather than by trade-offs. To distinguish between these hypotheses, Fry (1999) established a "hybrid reversion line" by crossing mites from the selected and control populations. This population was necessarily polymorphic for alleles favored on tomato, and therefore should have reverted rapidly under the first hypothesis. Contrary to this prediction, after ~15 generations on bean, the hybrid reversion line had similar survival on tomato as a fresh set of hybrids between the selected and control populations.

This led Fry (1999) to conclude that drift or hitchhiking might have been responsible for the original reversion.

All of these experiments had shortcomings. The selection and control populations, although large, were unreplicated. Although genetic drift or hitchhiking seem less likely than selection as an explanation for the rapid reversion of adaptation to cucumber observed by Gould (1979) and Agrawal (2000), the type of selection responsible was not demonstrated. A new set of experiments with replicate populations and measurements of more components of fitness, including male mating success, are necessary to confirm the presence of trade-offs in fitness on different hosts in *T. urticae* and to elucidate their nature.

*Trade-offs between parasitoid resistance and competitive ability in Drosophila melanogaster*

*Drosophila melanogaster*, like many insects, is attacked by several species of parasitic Hymenoptera. Larvae can defend themselves against parasitoids by an encapsulation response, in which cells in the haemocoel form a melanic capsule around a parasitoid egg, eventually killing it. Natural populations of *D. melanogaster* vary in their ability to encapsulate eggs of two common parasitoids, *Asobara tabida* and *Leptopilina boulardi*. Kraaijeveld and Godfray (1997) and Fellowes et al. (1998) used selection experiments to investigate whether trade-offs exist between encapsulation ability and fitness in the absence of parasitoids. Such trade-offs could explain why encapsulation ability in natural populations does not evolve to 100%.

Kraaijeveld and Godfray (1997) selected a susceptible *D. melanogaster* population for resistance to *A. tabida*, while Fellowes et al. (1998) selected a different population for resistance to *L. boulardi*. Selection was carried out by exposing larvae to heavy parasitoid attack and breeding the survivors. Four selection and control lines were established in each experiment, and selection was carried out for eight to nine generations. To minimize inbreeding, population sizes of at least 100 were used. In both experiments, encapsulation ability increased rapidly, from less than 10% to over 40%. Furthermore, in each experiment, larvae from the selected lines showed lower survival under conditions of intraspecific competition for food than larvae of the control lines. In both cases, this lower competitive ability was accompanied, and possibly caused, by a lower feeding rate (Fellowes et al. 1999). Fitness under non-competitive conditions did not differ between the selected and control lines. Kraaijeveld et al. (2001) investigated the mechanistic basis of the response in the lines selected for resistance to *A. tabida*, and found that larvae of the selected lines had approximately twice the density of haemocytes, a type of cell involved in encapsulation, than the controls. They hypothesized that the increased haemocyte levels may have diverted resources away from trophic functions, accounting for the lower feeding rate.

These studies provide an excellent demonstration of the power of selection experiment in documenting ecologically important trade-offs. Because *D. melanogaster* larvae often develop under competitive competitions in the wild (Atkinson 1979), the trade-off between parasitoid resistance and competitive ability might explain why some *D. melanogaster* populations that are regularly attacked by parasitoids have low encapsulation ability (Kraaijeveld and Godfray 1999). This hypothesis could be explored further by documenting levels of larval competition and parasitoid attack in wild populations.

#### CONCLUSION

Selection experiments provide a powerful method for testing for trade-offs that could be important in the evolution of niche breadth and in the maintenance of genetic variation in ecologically important traits. This paper has explored only a subset of the ways in which selection experiments can be used to answer questions in evolutionary ecology; selection experiments can also be used to investigate the evolution of phenotypic plasticity (Scheiner 2002), the roles of intraspecific competition (Bolnick 2001) and environmental heterogeneity (Kassen 2002) in the evolution of niche breadth, and mechanisms of speciation (Rice and Hostert 1993). Although the selection experiment literature has a heavy bias towards *Drosophila*, this bias exists more for historical than for practical reasons. Selection experiments are feasible with any species that can be reared in the laboratory or greenhouse, and which has a generation time of a few weeks to a few months. Therefore, evolutionary ecologists should more often consider using selection experiments as part of their research program.

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