



**Countergradient Selection for Rapid Growth in Pumpkinseed Sunfish:
Disentangling Ecological and Evolutionary Effects**

Jeffrey David Arendt; David Sloan Wilson

Ecology, Vol. 80, No. 8. (Dec., 1999), pp. 2793-2798.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199912%2980%3A8%3C2793%3ACSFIRGI%3E2.0.CO%3B2-K>

Ecology is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

COUNTERGRADIENT SELECTION FOR RAPID GROWTH IN PUMPKINSEED SUNFISH: DISENTANGLING ECOLOGICAL AND EVOLUTIONARY EFFECTS

JEFFREY DAVID ARENDT¹ AND DAVID SLOAN WILSON

Department of Biological Sciences, Binghamton University (SUNY), Binghamton, New York 13902-6000 USA

Abstract. Ecologists often assume that the evolutionary response to an environmental gradient will be the same as the phenotypic response. However, under some circumstances the evolutionary response to a gradient may be opposite of the ecological response, a phenomenon known as “countergradient variation.” We had previously predicted that countergradient selection has occurred in pumpkinseed sunfish in response to a resource gradient created by competition with bluegill sunfish. Because competition only occurs when pumpkinseed are small, rapid growth has evolved to allow passage through the competing size classes as quickly as possible. We performed a common-garden experiment using juvenile pumpkinseed derived from lakes with bluegill and from lakes without bluegill. Pumpkinseed were raised in cages without bluegill, or with a low density of bluegill, or with a high density of bluegill. Bluegill significantly decreased growth for all pumpkinseed, following the predicted ecological gradient. However, pumpkinseed derived from lakes with bluegill grew faster than those from lakes without bluegill under all treatments, following the predicted evolutionary response.

Key words: *bluegill; common-garden experiment; countergradient selection; ecological vs. evolutionary responses; interspecific competition; intrinsic growth rate; Lepomis gibbosus; Lepomis macrochirus; pumpkinseed sunfish.*

INTRODUCTION

Explaining phenotypic variation is one of the primary goals of ecologists. Variation in a trait among species or among populations within a species is usually associated with environmental gradients such as moisture, light, temperature, or nutrients. An interesting phenomenon that has the potential to complicate standard ecological interpretations of phenotypic variation is countergradient variation (defined by Levins [1969]; reviewed by Conover and Schultz [1995]). Countergradient variation appears when the evolutionary response to an environmental gradient is to compensate for the usual phenotypic effect of that gradient. For example, Levins (1969) described a case of countergradient variation in *Drosophila* body size with respect to an altitude/temperature gradient. In the wild, flies from a cool, high-altitude site were larger than those from a warmer, low-altitude site. This is the usual phenotypic response in *Drosophila* to temperature (e.g., Atkinson 1994, Partridge et al. 1994), and the typical genetic response across a *latitudinal* cline (Par-

tridge et al. 1994). However, when raised under common laboratory conditions, Levins found that flies from his warm site were larger than those from the cool site. Thus, genetic differentiation in body size was the opposite of the phenotypic gradient. Most subsequent examples of countergradient variation have also dealt directly or indirectly with temperature gradients, especially the effect of temperature on growth rate and adult body size (Conover and Schultz 1995).

Nutrient availability is another important gradient associated with phenotypic and genetic variation in growth rate. To date, most examples of genetic adaptation to nutrient levels have reflected cogradients. That is, organisms adapted to low nutrient levels evolve to grow slowly (but efficiently) even when nutrients are made abundant (Grime and Hunt 1975, Case 1978, Chapin 1980, Arendt 1997a). By contrast, Arendt and Wilson (1997) identified a situation in which low resource levels could select for a rapid intrinsic growth rate, provided there is a size-determined niche shift from a low-resource niche to a high-resource niche. This situation is illustrated by the competitive interaction between pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*). Pumpkinseed and bluegill are common in lakes and ponds

throughout the northern United States and southern Canada. During the last glaciation of North America, freshwater fish were confined to refugia that did not freeze. The refuge for pumpkinseed is thought to have been the Saint Lawrence River, while for bluegill it was the Mississippi River (Smith 1985, Schmidt 1986). Lakes between these two systems have an uneven distribution of pumpkinseed and bluegill as a result of historical variation in recolonization when the glaciers receded, with many lakes containing both species, while other lakes contain only one species or the other. By comparing pumpkinseed from lakes where bluegill are also present (sympatric populations) with pumpkinseed from lakes where bluegill are absent (allopatric populations), a number of studies have been able to examine the effects of interspecific competition on trophic morphology (Robinson et al. 1993), reproductive life-history traits (Fox 1994), and growth rate (Arendt and Wilson 1997).

Rapid growth is advantageous in pumpkinseed sympatric with bluegill because these species compete only when they are small. Below ~70 mm in length, both species are vulnerable to predation by largemouth bass (*Micropterus salmoides*). To avoid this predator, both species utilize the shallow, weedy habitats of lakes and ponds where they compete for soft-bodied macroinvertebrates. However, when they reach ~70 mm in length both pumpkinseed and bluegill have grown beyond the effective gape-limit of largemouth bass. Bluegill move into the open water and feed predominantly on zooplankton. At about the same size, pumpkinseed are first able to effectively crush the shells of gastropods, their primary adult resource (Mittelbach 1984, Osenberg and Mittelbach 1989). Estimates of growth rates in the wild by measuring growth annuli on scales show that small pumpkinseed sympatric with bluegill grow more slowly than pumpkinseed allopatric with bluegill (Osenberg et al. 1992), a result we have replicated in local ponds (Fig. 1; from previously unpublished data), suggesting this pattern is typical for pumpkinseed. This is probably a phenotypic response to the decreased resource availability in the presence of bluegill (Mittelbach 1984, 1988). In fact, once pumpkinseed reach the size at which they begin to incorporate snails in their diet, sympatric pumpkinseed grow faster than allopatric pumpkinseed (Fig. 1; Osenberg et al. 1992), as predicted theoretically by Mittelbach and Chesson (1987). Arendt and Wilson (1997) suggested that rapid growth should evolve in sympatric pumpkinseed so that fish may pass through the competitive size classes and reach the size refuge from competition as quickly as possible. They tested this model by comparing the growth rates of pumpkinseed derived from several populations sympatric with bluegill to those of pumpkinseed allopatric to bluegill. Under identical lab-

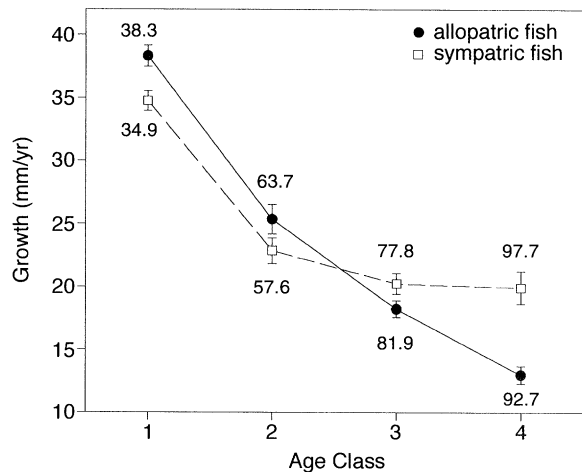


FIG. 1. Growth increments for different age classes of pumpkinseed sunfish in the wild, some from a lake without bluegill (allopatric condition, ●; $n = 42$ fish) and some from a lake where bluegill are present (sympatric condition, □; $n = 36$ fish). Age class represents growth in the previous year; e.g., age class 1 denotes growth from hatching through the first year of life. Numbers above or below symbols are mean sizes (in millimeters) of fish for that age. Note that the lines cross between ages 2 and 3. It is during this year that pumpkinseed reach a size where they begin to feed predominantly on snails. Prior to this, growth is significantly lower in the sympatric population due to competition with bluegill. After the niche shift, when resources are no longer constrained by interspecific competition, growth is actually better in the sympatric population. See Osenberg et al. (1992) for similar results.

oratory conditions, small sympatric pumpkinseed consistently grew faster than allopatric pumpkinseed.

The experiment described by Arendt and Wilson (1997) took place under artificial conditions. Fish were semi-isolated (visual contact, but were not allowed to interact) and raised on artificial diet under constant conditions. In order for a faster intrinsic growth rate to benefit sympatric pumpkinseed, they must be able to grow faster than allopatric fish when actually competing with bluegill, not just in the laboratory. As noted by Irving and Magurran (1997), experimental results under laboratory conditions may be very different from those obtained under more natural conditions. The following study was designed to test the differences in growth rate between sympatric and allopatric pumpkinseed under more natural conditions including a natural food source, fluctuating environmental conditions, and the presence of bluegill. If countergradient selection for rapid growth has occurred in this system, pumpkinseed growth rates should decrease as bluegill density increases (the ecological effect), but sympatric pumpkinseed should grow faster than allopatric pumpkinseed under all conditions (the evolutionary effect).

TABLE 1. Bluegill density treatments.

Bluegill density	No. of enclosures per population	No. of bluegill per enclosure	Initial bluegill length (mm)†	Initial pumpkinseed length (mm)†	Relative biomass (bluegill/pumpkinseed)	Date stocked
None	4	0	...	37.8 (37–39)	0	...
Low	3	4	42.6 (36–48)	38.1 (37–39)	1.5	2–4 July
High	3	7	46.6 (36–57)	38.4 (37–40)	3.2	5–7 July

Notes: Length and mass of bluegill are means for all replicates combined. Enclosures did not differ significantly within treatment for bluegill lengths or pumpkinseed lengths. Across treatments, however, pumpkinseed were significantly longer in the high-density treatment according to a Tukey post hoc test.

† Data are means, with the range in parentheses.

METHODS

Experiments took place in 30 × 30 m experimental ponds located at the Cornell Experimental Pond Facility in Ithaca, New York, USA. Adult pumpkinseed from six lakes, three sympatric with bluegill and three allopatric with bluegill, were stocked into six fishless ponds in June 1995 and allowed to breed. Five of these source lakes are located in southeastern Ontario, Canada; the sixth is located in Susquehanna County, Pennsylvania, USA (see Arendt and Wilson [1997] for details about lakes). A seventh pond was selected for the common-garden experiment. This pond contained resident pumpkinseed, bluntnose minnow (*Pimephales notatus*), golden shiner (*Notemigonus crysoleucus*), and brown bullhead (*Ictalurus nebulosus*).

From 27 through 30 June 1996, young-of-year were collected from the six breeding ponds using a seine net. Pumpkinseed ranging from 37.0 to 40.0 mm standard length were transferred to the experimental enclosures, four fish per enclosure. All fish in a given enclosure were from the same population. Pumpkinseed were selected to minimize the range in initial length, and did not differ significantly in size among populations or competition type, but were significantly larger in the high-density treatment (Table 1), although this difference was small and should not alter the general conclusions about evolution of growth rates. Enclosures were cylinders 1 m in diameter and 1 m high constructed of 6-mm mesh hardware cloth. Bottoms were sealed with hardware cloth, which allowed macrophytes, primarily Eurasian milfoil (*Myriophyllum spicatum*), to grow through. The top of each enclosure was covered by two lengths of twine stretched at right angles. The twine helped the cylinders maintain shape and served as a visual barrier for predatory birds. Fifteen enclosures were placed along each of the four sides of the pond for a total of 60 enclosures. Pumpkinseed were stocked so that a sympatric enclosure alternated with an allopatric enclosure. Prior to stocking into the enclosures, each fish was individually marked by clipping one of its dorsal spines and its standard length was measured to the nearest 0.5 mm.

Enclosures were assigned to one of three treatments: (1) no bluegill, (2) a low density of bluegill, or (3) a high density of bluegill (Table 1)—a design meant to be comparable to that of Mittelbach (1988). Ideally, bluegill sizes would have matched pumpkinseed sizes in the low- and high-density treatments. However, because of limited availability of bluegill on site, those used were significantly larger than pumpkinseed in a given enclosure. In addition, we had to supplement bluegill in the high-density treatment with fish from Nanticoke pond 13 located in Broome County, New York. Based on total biomass in enclosures, bluegill averaged 1.54 times pumpkinseed biomass in the low-density treatment and 3.20 times in the high-density treatment. Because our intention was to compare sympatric and allopatric pumpkinseed, the greater size of bluegill should not effect the general conclusions of this experiment.

Half of the enclosures were harvested on 11 September 1996. The second half were harvested the following day. Fish were collected, chilled in ice water, and sacrificed in methanosulfonate-222. The fish were then preserved in 10% neutral buffered formalin for 2 mo before being transferred to 90% ethanol.

The standard length of preserved fish was measured to the nearest 0.5 mm and growth rate calculated as instantaneous growth rate: $100 \times \ln(\text{final length}/\text{initial length})/\text{time in cage}$. Fish were then blotted dry and weighed to the nearest 0.001 mg. Condition factor was calculated as mass divided by the cube of the length (homogeneity of slopes for mass regressed on length was confirmed for all populations prior to full analysis). Data were analyzed using a two-factor analysis of variance with bluegill density as one factor and competition type (sympatric or allopatric) as the other factor. Population of origin was nested within competition type and treated as a random factor. To avoid sacrificial pseudoreplication (Hurlbert 1984), statistical analysis was conducted on mean values for each enclosure.

RESULTS

Growth rates for all populations showed a significant decrease as bluegill density increased (Table 2, Fig. 2a)

TABLE 2. Results of analysis of variance for pumpkinseed sunfish (A) growth rate and (B) condition factor. Population is nested within competition type (sympatric vs. allopatric origin).

Source of variation	Error term	ss	df	F	P
A) Growth rate					
Bluegill density	5	0.0231	2	42.385	0.000
Competition	3	0.00337	1	8.987	0.040
Population(competition)	5	0.0015	4	1.376	0.324
Density × Competition	5	0.00038	2	0.697	0.526
Density × Pop.(competition)	6	0.00218	8	0.520	0.835
Error		0.0215	41		
B) Condition factor					
Bluegill density	5	2.404×10^{-10}	2	185.673	0.000
Competition	3	2.303×10^{-12}	1	1.910	0.239
Population(competition)	5	4.824×10^{-12}	4	1.863	0.210
Density × Competition	5	1.326×10^{-12}	2	1.024	0.402
Density × Pop.(competition)	6	5.179×10^{-12}	8	0.289	0.966
Error		9.17654×10^{-11}	41		

† Numbers in the error-term column refer to quantity in "Source" column used as denominator to calculate *F* statistic.

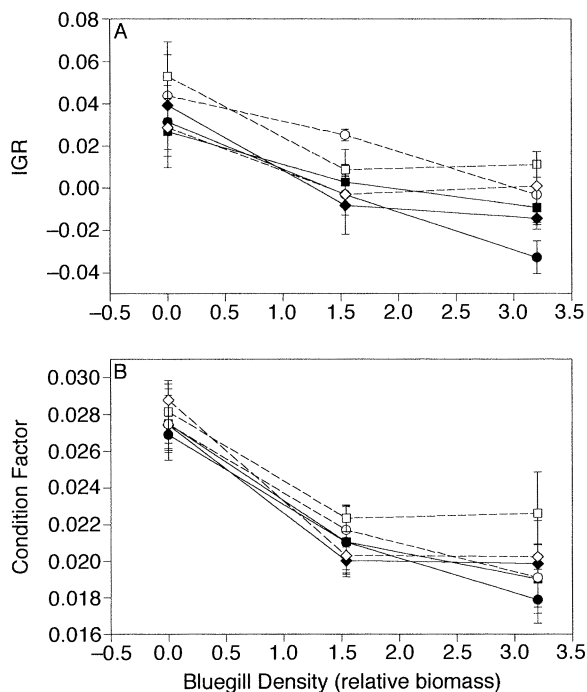


FIG. 2. Enclosure means for (A) instantaneous growth rate (IGR) and (B) condition factor (mass/length³) for the six pumpkinseed sunfish populations. Solid symbols and solid lines represent the allopatric populations; open symbols and dashed lines represent the sympatric populations. There is a significant decrease in both growth rate and condition as the density of bluegill increases. In addition, the sympatric pumpkinseed grow significantly faster than allopatric pumpkinseed under all densities of bluegill. Condition factor was not significantly different between sympatric and allopatric pumpkinseed.

in agreement with previously described phenotypic effects of bluegill competition (Mittelbach 1988). However, when we look at each population, the sympatric pumpkinseed grew significantly faster than allopatric pumpkinseed (Table 2, Fig. 2a). All of the allopatric fish showed negative growth rates (i.e., they appeared to decrease in length, although this may reflect measurement error rather than actual shrinking) in the presence of bluegill. In contrast, the sympatric populations were typically able to maintain positive growth even at the highest density of bluegill. Variation among populations within competition type was not significant. There were also no significant interaction effects between bluegill density and either population or competition type. Thus bluegill density appears to have the same relative effect on the growth rates of sympatric pumpkinseed as it does on allopatric pumpkinseed. In contrast to growth rates, only bluegill density had a significant effect on condition factor (Table 2, Fig. 2b). This means that sympatric pumpkinseed are able to maintain faster growth rates (as measured by change in length) in the presence of bluegill while suffering no additional loss in relative weight.

DISCUSSION

This study confirms that countergradient selection for rapid growth has occurred in pumpkinseed sunfish under competition with bluegill sunfish. These results parallel those found by Arendt and Wilson (1997), but under more natural conditions and with bluegill incorporated directly into the experimental design. In agreement with Mittelbach (1988), bluegill density had a clear negative effect on realized growth rate. However, this only reflects the ecological response to competition with bluegill. The evolutionary effect has been an increase in growth rate in pumpkinseed from populations where bluegill are present. Thus the ecological and the

evolutionary responses to competition are in opposite directions; countergradient selection for rapid growth has occurred.

Many ecological studies that compare populations across gradients assume the species being tested is genetically uniform. However adaptation to local conditions is common, and can occur very rapidly (e.g., Reznick and Bryga 1987, Reznick et al. 1990). Failure to recognize local adaptive variation can lead to erroneous conclusions about both the ecological and the evolutionary nature of a system. This is especially true for a trait like growth rate, which, as an important component of fitness, is usually assumed to be maximized. There is, however, abundant evidence that growth rates are carefully regulated by organisms (Case 1982) and optimized to local conditions (Case 1978, Arendt 1997a). Had we assumed that growth rate is always at its physiological maximum, we would have expected growth rates measured in the field to reflect the true relative growth rates of sympatric and allopatric fish. Note that this would have been qualitatively equivalent to comparing allopatric fish under the no-bluegill condition to sympatric fish measured under the high-bluegill-density condition. This is clearly only a small component of what is going on. Such a simplification would not be a serious problem to ecologists if the evolutionary response to a gradient always (or even typically) paralleled the ecological response, i.e., if cogradient variation were common. In fact, a cogradient response to nutrient level is common with respect to growth rate (Grime and Hunt 1975, Chapin 1980, Arendt 1997a). Had we only considered the juvenile stage we might have expected competition with bluegill to select for a slow intrinsic growth rate in sympatric pumpkinseed. However, as Werner (1986) has made clear, it is important to consider the entire life cycle of an organism when developing an optimality model. Because competition between bluegill and pumpkinseed only occurs when they are small, resource levels increase after a threshold size is reached. Taking into account the full life cycle, sympatric pumpkinseed should evolve—and have evolved—a rapid growth rate (Arendt and Wilson 1997) despite the reduced resource level caused by the presence of bluegill.

Countergradient variation has only rarely been recognized, and can easily be overlooked (Conover and Schultz 1995). We therefore cannot currently estimate how prevalent countergradient variation is relative to cogradient variation. We can, however, ask what conditions are likely to select for countergradient variation. One possibility is that selection is responding to an unidentified gradient, one that is actually driving cogradient variation in growth rate. Levins (1969) suggested that desiccation resistance may select for a large body size in opposition to the effects of temperature.

For many cases, the length of the growing season appears to override the effects of temperature on growth rate (Berven and Gill 1983, Present and Conover 1992). Most cases, unfortunately, simply have not been studied in enough detail to know what other factors may be important. The current study shows that there need not be a second gradient. It is the fact that resources become more abundant once a certain size is reached (Arendt and Wilson 1997) that produces countergradient variation. This suggests that countergradient variation may not be simply due to misidentification of the relevant gradient.

This study confirms the assumptions made by Arendt and Wilson (1997) that sympatric pumpkinseed will grow faster than allopatric pumpkinseed in the presence of bluegill. Rapid growth provides many advantages for pumpkinseed including decreased vulnerability to predators, increased overwinter survival, size advantages over both inter- and intraspecific competitors, and rapid passage through competitive size classes. That sympatric pumpkinseed maintain a faster growth rate, and without sacrificing condition, in the presence of bluegill suggests that fast growth has evolved in response to competition. However, an important question emerges from this study. Given the benefits of rapid growth, why don't allopatric pumpkinseed grow as fast as possible? Clearly, there must be a cost to rapid growth, as predicted by the model of Arendt and Wilson (1997; see also Case 1978, Sibly et al. 1985), and the presence of bluegill increases the relative benefit of growing faster for sympatric pumpkinseed. Costs of rapid growth may be developmental (e.g., Ricklefs et al. 1994), behavioral (e.g., greater risk taking to obtain food; Werner and Anholt 1993, Skelly 1996), or physiological (e.g., starvation resistance; Gotthard et al. 1994). Which cost occurs is probably dependent upon the system under study. For example, we have found evidence for a trade-off between growth rate and skeletal development as well as growth rate and capacity to regenerate damaged fins in pumpkinseed (both developmental costs). However, we have found no evidence for difference in boldness in the presence of a predator (a behavioral cost) or fasting endurance (a physiological cost) (Arendt 1997b).

ACKNOWLEDGMENTS

Thanks to Mike Fox for help in our initial collections of fish, and Ed and Florence Warrrens for allowing us to sample on their property. Thanks also to A. Clark, K. Coleman, T. DeWitt, B. Robinson, and C. Wilczynski for insight and discussion on this paper. Thanks to Bob Johnson for maintenance of ponds. Thanks also to two anonymous reviewers and D. Reznick whose comments helped clarify several issues in this paper. This work was supported by an NSF dissertation improvement grant (DEB-9423718).

LITERATURE CITED

- Arendt, J. D. 1997a. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* **72**:149–177.
- . 1997b. The optimistic growth strategy: evolution and costs of rapid growth in pumpkinseed sunfish. Dissertation. Department of Biology, Binghamton University, Binghamton, New York, USA.
- Arendt, J. D., and D. S. Wilson. 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution* **51**:1946–1954.
- Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms. *Advances in Ecological Research* **25**:1–58.
- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variations in life-history traits. *American Zoologist* **23**:85–97.
- Calow, P. 1982. Homeostasis and fitness. *American Naturalist* **120**:416–419.
- Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* **53**:243–282.
- Chapin, F. S., III 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233–260.
- Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient selection. *Trends in Ecology & Evolution* **10**:248–252.
- Fox, M. G. 1994. Growth, density, and interspecific influences on pumpkinseed sunfish life histories. *Ecology* **75**:1157–1171.
- Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* **99**:281–289.
- Grime, J. P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**:393–422.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187–211.
- Irving, P. W., and A. E. Magurran. 1997. Context-dependent fright reactions in captive European minnows: the importance of naturalness in laboratory experiments. *Animal Behaviour* **53**:1193–1201.
- Levins, R. 1969. Thermal acclimation and heat resistance in *Drosophila* species. *American Naturalist* **103**:483–499.
- Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**:499–513.
- . 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* **69**:614–623.
- Mittelbach, G. G., and P. L. Chesson. 1987. Predation risk: indirect effects on fish populations. Pages 315–332 in W. C. Kerfoot and A. Sih, Editors. *Predation*. University Press of New England, Hanover, New Hampshire, USA.
- Osenberg, C. W., and G. G. Mittelbach. 1989. Effects of body size on the predator–prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs* **59**:405–432.
- Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* **73**:255–267.
- Partridge, L., B. Barrie, K. Fowler, and V. French. 1994. Evolution and development of body size and cell size in *Drosophila melanogaster* in response to temperature. *Evolution* **48**:1269–1276.
- Present, T. M., and D. O. Conover. 1992. Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? *Functional Ecology* **6**:23–31.
- Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41**:1370–1385.
- Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**:357–359.
- Ricklefs, R. E., R. E. Shea, and I. Choi. 1994. Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: a constraint on evolutionary response. *Evolution* **48**:1080–1088.
- Robinson, B. W., D. S. Wilson, A. S. Margosian, and P. T. Lotito. 1993. Ecological and morphological differentiation by pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology* **7**:451–464.
- Schmidt, R. E. 1986. Zoogeography of the Northern Appalachians. Pages 137–159 in C. H. Hocutt and E. O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley & Sons, New York, New York, USA.
- Sibly, R., P. Calow, and N. Nichols. 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* **112**:553–574.
- Skelly, D. K. 1996. Tadpole communities. *American Scientist* **85**:36–45.
- Smith, C. L. 1985. *The inland fishes of New York State*. New York State Department of Environmental Conservation, Albany, New York, USA.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* **128**:319–341.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* **142**:242–272.