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LIFE-HISTORICAL CONSEQUENCES OF DENSITY-DEPENDENT
SELECTION IN THE PITCHER-PLANT MOSQUITO,
WYEOMYIA SMITHII

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The concept of density-dependent selection affecting the evolution of demographic traits is not new. The concept was apparent to Salisbury (1942), Dobzhansky (1950), and Fisher (1958). MacArthur provided genetic models of how density-dependent selection should act and concluded that in equilibrium populations, "the carrying capacity, K , replaces fitness (r) as the agent controlling the action of natural selection" (1962, p. 1897). Later, MacArthur and Wilson (1967) formulated the ancillary theory of r - and K -selection based on contrasting strategies of offspring productivity or efficient utilization of resources, respectively. Competitive ability, independent of resource-conversion efficiency, was envisioned by MacArthur as a confounding factor and not part of K -selection: "unless one type of competitor can pollute the resource so that the other type cannot use it, natural selection seems always to decrease the density of the limiting resource required to maintain the population at a constant level" (1962, p. 1897). These considerations are the fundamental tenets of r - and K -selection that need verification or refutation from among natural populations. The most basic predictions following from r - and K -selection are, then, (1) that selection at low densities or high resource levels should result in populations with a higher capacity for increase when resources are abundant; and (2) that selection at high densities near or at equilibrium levels should result in populations that require less resource to maintain a constant population.

Despite early caveats (Hairston et al. 1970; Wilbur et al. 1974), subsequent theoretical and conceptual offspring of r - and K -selection theory spawned myriad a posteriori "confirmations" (Pianka 1970; Giesel 1976; Stearns 1976, 1977; Gould 1977). Direct experiments designed specifically to discriminate between these theories or to test them have been slower to emerge. Some attempts in the laboratory have been undertaken with bacteria (Luckinbill 1978, 1984), protozoans (Luckinbill 1979), copepods (Bergmans 1984), and *Drosophila* (Giesel and Zettler 1980; C. Taylor and Condra 1980; Barclay and Gregory 1981; Mueller and Ayala 1981). The experiments with bacteria, protozoans, and copepods conform more to the predictions from stage-specific mortality or bet hedging (Istock 1967;

Murphy 1968; Emlen 1970; Schaffer 1974 a,b ; Stearns 1976) than to those from density alone. In *Drosophila*, it is clear that heritable variation exists for carrying capacity (Buzzati-Traverso 1955; Ayala 1965, 1968; Mueller and Ayala 1981; Marks 1982); and in one unambiguous study (Mueller and Ayala), carrying capacity did respond to selection regimes based on density. The results of other studies are ambiguous. C. Taylor and Condra (1980) based their selection on age at reproduction, not density per se (see Mueller 1985; Bradshaw and Holzapfel 1986). Barclay and Gregory (1981) confounded selection at variable juvenile and adult densities with selection to tolerate and survive putrid conditions (see Mueller 1985). Giesel and Zettler (1980) used inbred lines that are biased toward producing positive genetic correlations among fitness traits (see Rose 1984).

Even the unambiguous approaches above all applied selection to laboratory populations. Mueller and Ayala (1981) found that *Drosophila* lines reared at high and low densities clearly diverged in their life-history traits. High-density-selected lines realized increased viability and higher rates of population growth at high densities than did low-density-selected lines. Larvae of the high-density-selected line crawl farther out of the medium and pupate higher on the wall of the vial (Mueller and Sweet 1986). This behavior, not a greater efficiency in resource use or metabolite tolerance, may be responsible for the increased fitness of the higher-density-selected line. Although pupation height is a heritable trait (Markow 1979; Sokolowski and Hansell 1983; Bauer and Sokolowski 1985), so too is density tolerance (Buzzati-Traverso 1955; Ayala 1965, 1968; Mueller and Ayala 1981; Marks 1982), and it is not clear which trait, if either, would be selected for under natural conditions of increased density. Well-designed laboratory selection studies constitute a desirable, more rigorous test of theory than did earlier, mainly a posteriori, comparisons of isolated life-history traits between two or a few field populations. Yet, laboratory selection reveals only the ways in which natural populations might respond to selection; testing the ways in which natural populations do respond to selection requires comparisons among populations that have undergone selection in nature.

The problem with testing predictions with field-selected populations is that, under natural conditions, it is difficult to isolate density dependence from other selective factors. Even when differences in density-dependent selection between local or distant populations can be demonstrated or reasonably inferred, differences in local microhabitat coupled with a low number of test populations can obscure the true agents of selection.

In this paper, we review density-dependent selection in the mosquito *Wyeomyia smithii* (Coq.), which completes its entire pre-adult development only in the water-filled leaves of a single species of pitcher plant, *Sarracenia purpurea* L., which ranges from the Gulf of Mexico (30°N) to northern Canada (54°N). Other than for parasitism or phoresy, it is difficult to imagine a microhabitat that varies so little over so wide a geographical range. Finally, we show that populations having undergone varying degrees of density-dependent selection in nature do not vary in capacity for increase at either low or limiting densities when grown under uniform conditions in the laboratory. We then discuss life-history traits that do vary over geographical distances and potential causes for these variations.

DENSITY-DEPENDENT DEVELOPMENT IN *WYEOMYIA SMITHII*

The foundation for this study is contained primarily in four previous papers (Istock et al. 1976a; Bradshaw 1983; Bradshaw and Holzapfel 1983, 1986) and is summarized below.

Pitcher-plant insects rely upon the prey captured by their host leaf as a resource base. When a leaf first opens, it is maximally attractive to *Wyeomyia smithii*, and this attraction falls exponentially with leaf age. Prey attraction is at first low, peaks 2–4 wk after the leaf opens, and declines exponentially thereafter. Mosquitoes hatch as prey capture begins, and peak resource demand by developing mosquitoes coincides with peak prey capture by the host leaf. This process from leaf opening to decline in prey capture takes place over about a 6–8-wk period. Prey capture can be quantified as the number of disarticulated head capsules remaining in the leaf from prey captured either over the lifetime of a leaf or during the first few months after leaf opening. Mosquito density, expressed as mosquito larvae per prey captured, is a good predictor of the mosquito biomass sustained by a leaf, the probability that a leaf will produce any pupae, and the pupation success among leaves that produce at least one pupa. In northern Florida, at the southern end of *W. smithii*'s range (30°N), mosquitoes encounter density-dependent constraints on growth and pupation success all year, even during the winter, when density-dependent resource limitations prevent most of the overwintering generation from attaining the diapause instar. Density-dependent constraints abate with increasing latitude and altitude, and in the sparsest populations, density-dependent development is low or absent even in the spring. Mosquito density per unit of resource varies 20-fold over the range of *W. smithii* and correlates negatively with latitude or altitude from the Gulf of Mexico (30°N) to north-central Manitoba (54°N). *Wyeomyia smithii* populations therefore encounter a gradient of decreasing density-dependent developmental constraints over this range. Evidence from the geography, morphology, behavior, development, and physiology of *W. smithii* lead to the conclusion that this species has evolved from south to north (Bradshaw and Lounibos 1977; Bradshaw 1986). In this paper, we assume that densities currently encountered in nature have persisted through recent evolutionary time and that, consequently, the gradient in density-dependent development also reflects a gradient in density-dependent selection. By comparing variation in life-history traits in the laboratory among populations of *W. smithii* collected from 30° to 49°N (table 1), we are then determining to what extent populations have responded to this selection.

RATIONALE

Our basic rationale was to compare the response to increasing density in the laboratory among populations that had experienced varying degrees of density-dependent selection in nature. We employed mosquitoes from 12 localities over a range of 19° latitude, 25° longitude, and 900 m in altitude (table 1). These localities were chosen to provide replicate samples from each of six general zones: Gulf Coast, low-elevation North Carolina, high-elevation North Carolina, New Jersey,

TABLE 1
LOCALITIES AND ZONES OF ORIGIN FOR *WYEOMYIA SMITHII*

Location	Latitude, °N	Longitude, °W	Altitude, m	Zone
WI, Florida	30	85	10	Gulf Coast (30° N)
CR, Florida	31	87	30	
GS, No. Carolina	34	78	20	low-elevation North Carolina
EW, No. Carolina	35	80	150	
HK, No. Carolina	35	83	890	high-elevation North Carolina
DB, No. Carolina	35	83	900	
MM, New Jersey	40	75	10	New Jersey (40° N)
PB, New Jersey	40	74	10	
FV, Massachusetts	43	72	60	moderate north (43° N)
HL, Michigan	43	84	260	
KC, Maine	46	68	110	far north (46°–49° N)
DL, Ontario	49	94	366	

moderate north, and far north. In our analyses, then, our samples provided truly independent estimates from separate localities within general zones rather than repeated measures of the same population. Thus, in each analysis of variance (ANOVA) we tested for the effect of geography (the degree of density-dependent selection in nature), varying density imposed in the laboratory (to assess the response to density-dependent selection), and their interaction.

As a composite index of fitness, we calculated Laughlin's (1965) capacity for increase: $r_c = \ln R_0/T$, where R_0 is the replacement rate, that is, the eggs produced by a cohort throughout its lifetime divided by the number of freshly hatched first instars that the original cohort comprised; and T is the mean generation time, $\Sigma(xE_x)/\Sigma E_x$, where E_x is the number of eggs oviposited by a cohort of uniform age at time x , the number of days since oviposition of the cohort. Using this approach with the above geographical rationale, we ask whether and at what level life-history evolution reflects the degree of density-dependent selection experienced in nature.

METHODS

Standard Regimens

Details of stock maintenance and experimental regimen are provided elsewhere (Bradshaw 1986) and are summarized briefly below.

Stock maintenance.—We collected all the populations from the 1978–1979 overwintering generation when 100% of the population was present as diapausing larvae in pitcher-plant leaves. Each founding colony consisted of 800–2200 mosquitoes; each subsequent generation in the laboratory was perpetuated with 200–800 mosquitoes. Assuming the minimum breeding population of 200 adults with an effective population size of 100 to allow for differing sex ratios and unequal contributions by parents, the amount of inbreeding after 10 generations should be

no more than $1 - (1 - 1/200)^{10} = 4.9\%$ (Falconer 1981). When we ran stocks through a generation to build up a population or to initiate an experiment, we always maintained the adult cage and collected eggs until all adults had died. We then thinned stocks or removed experimental animals to maintain a constant proportion from each date of oviposition. In this way, we sought to preserve as much of the original variability within populations as possible. Stock populations were all maintained at the same density of 35–50 larvae per petri dish (150 × 25 mm). The stock was maintained continuously; the progeny of experimental subpopulations were discarded and never added back to the stock. To avoid maternal and/or environmental effects from field-collected larvae, the stock population from each locality was run through two generations in the laboratory before the experiments began. Thus, all experimental populations were 2–8 generations old by the conclusion of the experiments. Experiments were run sequentially, yielding different laboratory ages in generations for each experiment: (1) for the capacity for increase at warmer temperature (Bradshaw and Holzapfel 1983), 2 generations; (2) for density tolerance (figs. 1, 2), 3–5 generations; (3) for competition (fig. 5), 5 or 6 generations; (4) for blood feeding (Bradshaw 1986), 6 or 7 generations; (5) for hybrid phenotypes (fig. 4), 7 or 8 generations.

Experimental regimen.—Our basic goal was to provide natural conditions of water, photoperiod, temperature, and food. Unless otherwise stated, we conducted all experiments in 15 ml of distilled water added to leaves of intact pitcher plants in a controlled-environment room. To approximate temperature conditions in nature (Bradshaw 1980b), we imposed a daily sine-wave thermoperiod of 12°–28°C (mean, 21°C) that lagged the photoperiod by 3 h. To approximate the natural prey capture by pitcher plants in nature (Fish and Hall 1978; Bradshaw 1983; Bradshaw and Holzapfel 1983), we fed the *Wyeomyia smithii* in each leaf 25 freeze-dried adults of *Drosophila melanogaster* on the day that the larvae hatched and we started an experiment. We then provided 100 more flies after 1 wk, 50 more after 2 wk, and 25 more after 3 wk.

We placed individual, intact pitcher plants in polystyrene terraria below two 48-watt cool-white fluorescent lamps programmed for a photoperiod of 17 h light and 7 h dark. Three sets of plant lights plus two overhead 48-watt cool-white fluorescent lamps provided bright “daytime.” We approximated a transitory twilight with 0.5 h of the two overhead lights preceding and following the main photophase. This regimen provided unambiguously long days for all populations over the range studied (Bradshaw and Lounibos 1977).

We placed pupae in 100 ml of distilled water in plastic dessert dishes in humidified adult cages. From the day of first adult eclosion until the last adult death, we provided weekly a freshly cut leaf of *Sarracenia purpurea* for oviposition.

Experimental procedures.—To start an experiment, we removed eggs daily from the adult cage, washed them with distilled water into petri dishes, and maintained them in the thermoperiod room until they hatched. On the day of hatching, we placed experimental cohorts into plant leaves and fed them according to the regimen given above. To produce similar-sized adult populations at each density, we used 10 leaves at 10 larvae per leaf, 5 leaves at 20 larvae per leaf, 4 leaves at 40 larvae per leaf, and 3 or 4 leaves at 60 larvae per leaf. Starting 22–25

days after oviposition, we checked for and removed pupae 3 times per week (on Monday, Wednesday, Friday). On the same day, we (1) scored adult ecdysis by counting the number of exuviae of each sex, (2) removed and counted all eggs, and (3) removed, sexed, and counted all dead adults. We continued to census leaves for 90 days after oviposition; thereafter, we continued to monitor adult cages 3 times per week until all adults had died.

' r ,' ' K ,' and Density

To compare r and K determined in the laboratory with the degree of density-dependent selection in nature, we estimated r as $\max r_c$, the maximum value of r_c obtained for a given population at low density in the laboratory, and K as the density at which $r_c = 0$ from the regression of r_c on laboratory density for a given population.

As a measurement of density-dependent selection in nature, we used mean crowding (in the sense of Lloyd 1967) of *W. smithii* per head capsule of prey in pitcher-plant leaves at the locality of origin. The mean crowding of *W. smithii* per head capsule expresses the density per unit of resource and closely correlates (1) with pupation success during the summer and the developmental age among overwintering larvae at southern latitudes and (2) with the developmental progress of post-diapause larvae and pupae during the spring at higher latitudes and altitudes (Bradshaw and Holzapfel 1986), especially at moderately northern latitudes, where Istock et al. (1976a) have shown density-dependent vernal bottlenecks (Bradshaw and Holzapfel 1986). As a basis of reference, we therefore used the mean crowding of *W. smithii* larvae per head capsule of prey of the overwintering generation when, at northern latitudes and higher altitudes, we are assessing density that affects density-dependent vernal development (Bradshaw and Holzapfel 1986). Estimates of the mean crowding of *W. smithii* per head capsule of prey are available for 11 of the 12 localities considered in this paper (table 1, all but CR).

Hybridization

In creating hybrids, we chose populations that were arranged along geographical gradients (table 1) and that exhibited maximal differences in r_c , R_0 , and T by crossing: one southern (WI) population times 6 others along a latitudinal gradient (CR, GS, MM, FV, KC, DL); one low-elevation North Carolina population (GS) with a high-elevation North Carolina population (HK) including local controls (GS \times EW) and latitudinal controls (GS \times MM; WI \times GS); two nearby populations (MM \times PB), two moderately displaced populations (WI \times CR), and two widely separated populations (FV \times HL); and latitudinally and longitudinally displaced populations (MM \times DL and KC \times DL). We chose an experimental density of 20 larvae per leaf, since this density resulted in the consistently highest percentage of eclosion.

We first reared parental populations to adulthood in the thermoperiod room. At pupation, we separated the sexes and made reciprocal crosses to create hybrids by permitting males of one population to undergo ecdysis in adult cages with

females from another population, and vice versa in a separate cage. We collected eggs 3 times per week as above, allowed them to hatch, and, on the day of hatching, initiated an experiment by recombining equal proportions of freshly hatched first instars from both reciprocally crossed populations.

Competitive Ability

To test for differences in competitive ability, we took advantage of the observations (Bradshaw and Lounibos 1977) that southern and northern *W. smithii* populations differ in the morphology of the larval anal papillae and that each is distinct from its F_1 hybrid. We reared *W. smithii* larvae from 30°N (WI, CR) with larvae from 40°N (MM, PB), 42.5°N (FV, HL), or 46°–49°N (KC, DL) at a ratio of 5:5 or 20:20 (10 or 40 larvae per leaf, respectively) under the standard regimen. The resulting adults were allowed to mate and oviposit at random. We allowed eggs to hatch and maintained larvae on short days (8 h light, 16 h dark) at 21°C ± 0.5° until 3 wk after the last egg was oviposited. We then examined each larva under the microscope, scored it as southern, northern, or hybrid, and calculated r_c , R_0 , and T for each parental population separately:

$$R_0 = \Sigma[(P_x + 0.5H_x)/N_0],$$

$$T = \Sigma[x(P_x + 0.5H_x)]/\Sigma(P_x + 0.5H_x),$$

$$r_c = \ln R_0/T,$$

where N_0 is the total number of first instars of that population in the original mixed parental cohort, P_x is the number of parental-phenotype larvae of a given population from eggs oviposited on day x (days since eggs of the parental cohort were oviposited), and H_x is the number of hybrid-phenotype larvae from eggs oviposited on day x .

We calculated R_0 and T for each parental cohort independently. Finally, we compared, for each northern and southern pair, the difference between the r_c of larvae reared together and that of larvae reared separately. Since the comparisons were planned a priori, we used a t -test for paired comparisons to test for differences between southern and northern populations.

RESULTS

Capacity for Increase and Its Components

Capacity for increase declined continuously with density in the laboratory, although neither zone of origin nor its interaction with density significantly affected r_c (fig. 1). Similarly, replacement rate ($\ln R_0$) declined with density, but neither zone of origin nor its interaction with density had a significant effect on R_0 . Mean generation time (T) increased with density, and, again, neither zone of origin nor its interaction with density significantly affected T . Capacity for increase at either low density was not significantly correlated with capacity for increase at either high density (fig. 2).

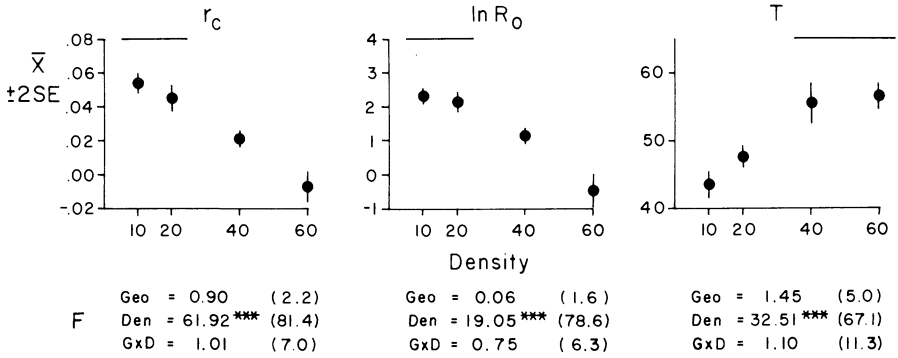


FIG. 1.—Effects of density in the laboratory and of the geographical zone of origin on capacity for increase (r_c), replacement rate ($\ln R_0$), and mean generation time (T). The table below each graph shows the F values from the two-way ANOVA for effects of geographical zone of origin (Geo), density in the lab (Den), and their interaction ($G \times D$). The horizontal line at the top of each graph lies over points not significantly different according to Duncan's multiple-range test (***) $P < 0.001$.

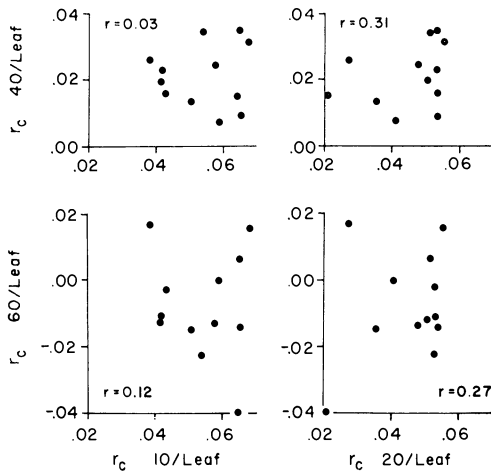


FIG. 2.—Correlation between capacity for increase (r_c) at high (40 or 60 larvae per leaf) and at low (10 or 20 larvae per leaf) densities in the laboratory. None of the correlations is significant.

Neither max r_c nor K in the laboratory correlated with the density per unit of resource in nature (fig. 3). The nonsignificant correlation of max r_c with density was positive and that of K with density was negative. The northern and high-altitude localities at which we observed no density-dependent vernal development in nature exhibited the seventh and eighth highest max r_c and the seventh and eighth lowest K of 11 populations.

As controls for the competition experiments (below), we determined r_c , R_0 , and T at a later, separate time for 8 of the 12 populations. With the above results, we

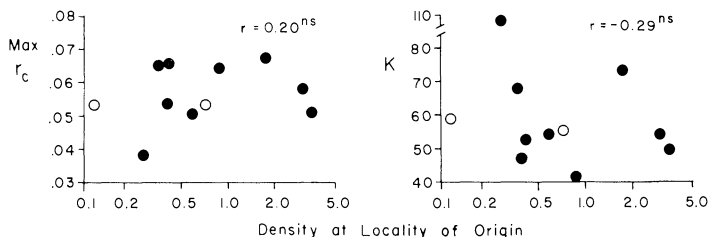


FIG. 3.—Relationship between max r_c or K determined under uniform conditions in the laboratory and the density per unit of resource in nature. Density was measured as the mean crowding of *W. smithii* per head capsule of prey in leaves of the overwintering generation (Bradshaw and Holzapfel 1986). Observations are limited to the 11 populations for which density is known. *Open circles*, Populations with no significant density-dependent effects on vernal development; *solid circles*, populations with at least some significant density-dependent effects on development in the winter, spring, and/or summer.

had duplicate estimates of r_c , R_0 , and T for both localities within each of four zones (table 1): Gulf Coast, 40°N, 43°N, and high-elevation North Carolina. Nested ANOVA (table 2) for r_c and its components, R_0 and T , revealed highly significant differences between densities, no significant differences among zones, and significant differences between localities within zones.

Hybrid populations exhibited significantly higher capacity for increase, shorter generation times, and greater replacement rates than predicted from mid-parent population values (fig. 4).

Competitive Ability

Differences in competitive ability between southern and northern populations depended on density (fig. 5). At a total density of 10 larvae per leaf, the differences in r_c between southern and northern populations were not significant, regardless of whether the populations were reared together or separately. At a total density of 40 larvae per leaf, the differences in the capacity for increase were significant but only when the two populations were reared together. When the populations of larvae were reared separately at a density of 40 larvae per leaf, there was no significant difference in mean generation time between southern and northern populations (fig. 5). When reared together, southern populations realized significantly shorter generation times than northern populations. Although the values of t for the two tests are close, with one just significant and the other barely nonsignificant, it is clear from figure 5 that each difference in T between southern and northern populations either declined or reversed in sign in the two comparisons (separate vs. together). R_0 presented little ambiguity: southern populations realized a significantly and substantially greater replacement rate than northern populations when they were reared together than when they were reared separately.

These results show that differences between southern and northern populations are expressed only at higher, limiting densities and only when the two populations are reared together. Thus, southern and northern populations differ in competitive ability but not in density tolerance.

TABLE 2

NESTED ANOVA OF r_c , R_0 , AND T TO SHOW THE EFFECTS OF LOCALITIES OF ORIGIN WITHIN FOUR REGIONS AMONG EIGHT POPULATIONS AT TWO DENSITIES IN THE LABORATORY

Treatment	Sum of Squares	df	Mean Square	<i>F</i>
r_c , capacity for increase				
Between densities	1,264,448	1	1,264,448	77.75***
Among regions	97,694	6	16,262	0.88
Among localities within regions	148,118	8	18,515	3.27*
Within localities between generations	90,657	16	5,666	
Total	1,600,915	31		
R_0 , replacement rate				
Between densities	15.166	1	15.166	60.39***
Among regions	1.507	6	0.251	0.53
Among localities within regions	3.773	8	0.472	3.43*
Within localities between generations	2.201	16	0.138	
Total	22.648	31		
T , mean generation time				
Between densities	1,743.5	1	1,743.5	44.94***
Among regions	232.8	6	38.8	0.95
Among localities within regions	326.3	8	40.8	2.89*
Within localities between generations	225.6	16	14.1	
Total	2,528.1	31		

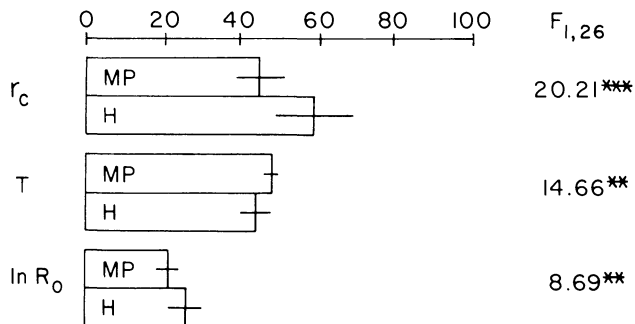
* $P < 0.05$.*** $P < 0.001$.

FIG. 4.—Comparison of hybrid and mid-parent population values for capacity for increase (r_c), mean generation time (T), and replacement rate ($\ln R_0$) in the laboratory. Each parameter has been scaled for better comparison: $r_c \times 10^3$, $T \times 1$, $R_0 \times 10$ (one-way ANOVA comparing hybrid with mid-parent values: ** $P < 0.01$; *** $P < 0.001$).

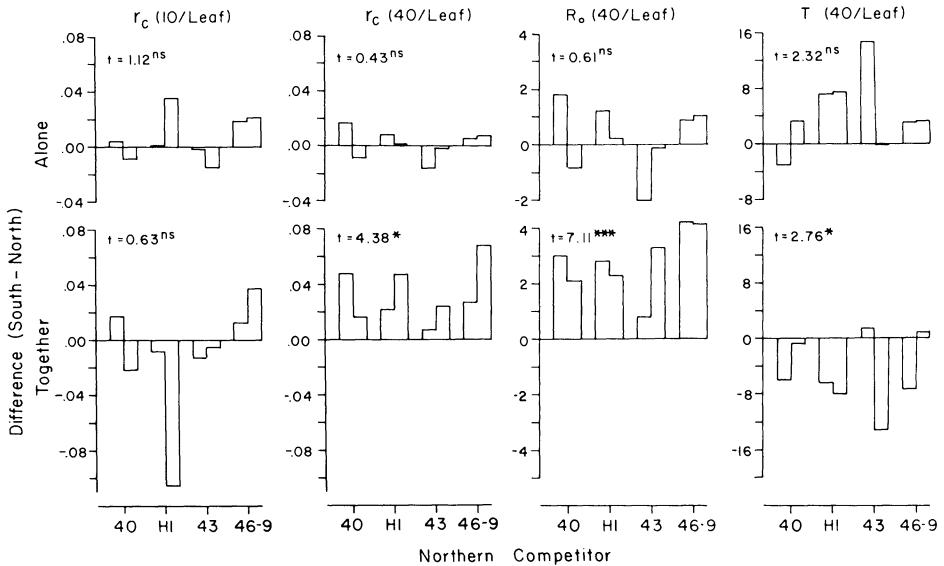


FIG. 5.—Intraspecific competitive ability expressed as the difference between one southern (WI or CR) and one of eight northern localities for capacity for increase (r_c), replacement rate (R_0), or mean generation time (T), all determined in the laboratory. Northern competitors are designated by zone of origin (table 1), with HI coming from high-elevation North Carolina. Populations were reared at either 10 or 40 larvae per leaf and either in separate leaves (Alone) or mixed 1:1 within the same leaf (Together). A positive value indicates a larger value for the southern than for the northern population (t -test for paired comparisons: ^{ns} not significant; * $P < 0.05$; *** $P < 0.001$).

DISCUSSION

Evolution of 'r_c' and Its Components

Capacity for increase (r_c) and its components, replacement rate (R_0) and generation time (T), have diverged phenotypically as well as genetically among populations of *Wyeomyia smithii*. A nested ANOVA (table 2) shows significant differences for these traits between localities within zones independent of laboratory-density effects. Hybrid phenotypes (fig. 4) are all in the direction of improved hybrid fitness over mid-parent values. Such heterotic effects are indicative (Endler 1977; Falconer 1981; Dingle et al. 1982) of genetic divergence since separation of the parental populations. This heterosis is not likely attributable to inbreeding in the laboratory within 10 generations for two reasons. First, the sizes of the founding and subsequent populations should have limited inbreeding to no more than 5% (see “*Stock maintenance*” in the Methods section, above). Second, the change in capacity for increase in successive determinations (table 2) spanning 1–3 generations was not significantly different at densities of either 10 or 40 larvae per leaf (t -test for paired comparisons; r_c of younger – r_c of older generation: $D_{10} = -0.0013$, $t = 0.16$, NS; $D_{40} = -0.0055$, $t = 0.845$, NS), and in each case, the sign

of the difference is opposite that expected for inbreeding depression. Thus, both significant differences among localities (table 2) and heterosis exhibited in hybrid characters (fig. 4) indicate that populations of *W. smithii* have diverged phenotypically as well as genetically in capacity for increase, replacement rate, and generation time.

Divergence of demographic traits in *W. smithii* is a local phenomenon. Despite the differences in climate and field density (Bradshaw and Holzapfel 1986) among geographical zones, zone of origin has no effect on capacity for increase or its components under uniform conditions in the laboratory (fig. 1). Yet, as discussed above, populations of *W. smithii* have diverged phenotypically as well as genetically. Significant differences in r_c , R_0 , and T exist between populations within zones but not among zones (table 2). It would thus appear that, despite the great microhabitat consistency of pitcher-plant leaves, local conditions within bogs have been more important for the divergence of demographic traits in *W. smithii* than have been regional differences in climate or degree of density-dependent selection in nature. Significant local life-history adaptation is not restricted to a weak-flying species in a specialized habitat such as *W. smithii*. In the widely dispersing and migratory milkweed bug, *Oncopeltus fasciatus*, Groeters and Dingle (1987) found differences in life-history traits and in the genetic substructure underlying these traits between local populations 120 km apart. Unless positive evidence is found to the contrary, variation among habitats within regions should then be suspected as a significant factor affecting life-history evolution.

Competitive Ability

The data in figure 1 show that all populations of *W. smithii* have similar abilities to exploit abundant resources and to tolerate high densities. High-density tolerance may or may not hide variation in competitive ability. Thus, if two populations varied with respect to their competitive abilities, high intrapopulation density would match strong with strong and weak with weak competitors. Each population might then exhibit the same response to increased density but for different reasons. Only interpopulation encounters would reveal these differences.

Competitive ability in *W. smithii* exhibits regional variation. Southern populations undergoing intense density-dependent development are more competitive in head-to-head encounters at high density than are more-northern populations. Although we do not know the mechanism of competitive dominance by southern over northern *W. smithii*, there is apparently a cost to this dominance because the northern (derived) populations have lowered competitive ability. Variation in intraspecific competitive ability is clearly present and was totally unpredictable from examination of density tolerance. This result supports Gill's (Gill 1972, 1974; Hairston 1983) concept that competitive ability may evolve independently of other demographic traits and, especially, of the " r - K continuum." We therefore reiterate the warning that competitive ability may not be inferred from a response to density by independent strains, populations, or species; it must be tested for directly with head-to-head encounters of the groups involved.

Life-History Evolution in 'W. smithii'

The differences in r_c and its components among populations (table 2) are not great relative to the homeostatic abilities within populations (fig. 1). Although this apparent constancy might imply evolutionary stasis of life-history traits in *W. smithii*, a variety of other life-history traits exhibits dramatic variation over the same geographical range; these variations persist among populations that are reared together in the laboratory. (1) Southern populations are more competitive than northern populations (fig. 5); density dependence is thus not without strong regional consequences. (2) Southern populations are capable of taking a blood meal, whereas populations from farther north are not (Bradshaw 1980a). Blood-feeding ability is associated with increased female longevity and facultatively augmented iteroparity but not increased fecundity. Retention of hematophagy in southern females may then be interpreted as a means for mosquitoes developing under predictably impoverished but irregularly opportunistic conditions to reallocate and temporally diversify their reproductive effort (Bradshaw 1986). Reasons for the reduction in adult longevity and concomitant loss of hematophagy among northern populations are unknown but may relate to an overall reduction in life-cycle complexity (Bradshaw 1986). (3) *W. smithii* is photoperiodic for the initiation, maintenance, and termination of larval diapause (Smith and Brust 1971; Bradshaw and Lounibos 1972; Evans and Brust 1972). The critical photoperiod for diapause initiation and maintenance tracks altitude and latitude of origin more closely than any other known ecogeographic character (Bradshaw 1976; Bradshaw and Lounibos 1977), including photoperiodism in other insects (F. Taylor and Spalding 1986). The diapause stage in *W. smithii* switches from the fourth instar in the south to the third instar in the north, but northern populations retain the ability to enter a second, fourth-instar diapause as a "fail-safe" mechanism against uncertain vernal environments (Lounibos and Bradshaw 1975; Bradshaw and Lounibos 1977).

Several life-history traits in *W. smithii* have clearly shown strong regional adaptation to density-dependent selection (competitive ability), stage-specific mortality (blood feeding and iteroparity), and climate (photoperiodic response). By contrast, capacity for increase and its components show no such regional adaptation (fig. 1). The lack of more-dramatic regional differences in capacity for increase and its components (fig. 1) points to the impotence of climate or density dependence, per se, to select for divergence of these traits in particular rather than to the evolutionary stasis of fitness traits among *W. smithii* in general.

The gradient of density-dependent selection can also be viewed as a gradient in stage-specific mortality. Density-dependent selection in southern populations is, above all, a source of mortality, and the important consideration may be the stage at which this mortality occurs, not its dependence on density. In the south, a small fraction of larvae hatching in pitcher-plant leaves survives to adulthood; the integral sum of adult survival and fecundity is sufficient to saturate pitcher-plant leaves year-round (Bradshaw and Holzapfel 1983, 1986). In the north, there are periods when a large proportion of available resources goes unused (Istock et al.

1976a); hence, the integral sum of adult survival and fecundity cannot keep pace with the availability of larval resources. Adults of southern populations live longer and display a temporally more flexible schedule of reproductive allocation than do those in northern populations. Northern populations encounter harsher winters and hence more-severe consequences of misdirecting their seasonal development than do southern populations. Diapause in southern populations is restricted to a single instar, but in northern populations diapause is more flexible and may occur twice in successive instars. Thus, patterns of life-history evolution in *W. smithii* conform more generally to predictions based on the evolution of complex life cycles (Istock 1967), bet hedging (Stearns 1976), habitat stability (Salisbury 1942; Southwood et al. 1974), or the exploitation of transient larval opportunities (Healy 1974; Bell and Lawton 1975; Wilbur 1980; Albert 1983; Bradshaw 1986) than to those based on density dependence alone.

'r'- and 'K'-Selection

The fundamental tenet of *r*- and *K*-selection is that selection density, per se, is a potent environmental force molding demographics of organisms (MacArthur 1962; MacArthur and Wilson 1967). Secondarily, there is an implied trade-off between fitness at high and low densities (but see Boyce 1984). In *W. smithii*, no regional differences are expressed under uniform conditions in the laboratory in capacity for increase, replacement rate, or mean generation time despite strong geographical differences in the degree of density-dependent selection among regions of origin (Bradshaw and Holzapfel 1986) and sufficient additive genetic variance in at least developmental time (Istock et al. 1976b) to respond to selection.

There was no correlation between $\max r_c$ or *K* determined under uniform conditions in the laboratory and the density per unit of resource in nature (fig. 3). Nonsignificant trends are opposite those expected from *r*- and *K*-selection. First, there was a positive correlation of $\max r_c$ and a negative correlation of *K* in the laboratory with density in nature. Second, the two localities that lack significant density-dependent development even during the spring "bottleneck" observed at other northern localities (Istock et al. 1976a; Bradshaw and Holzapfel 1983, 1986) exhibit lower than median $\max r_c$ and higher than median *K*. Furthermore (fig. 1), at any given single density in the laboratory, there are no differences in capacity for increase among populations. In seasonally varying environments, models of *r*- and *K*-selection that have assumed trade-offs between *r* and *K* genotypes have shown that *r* alleles should be favored over *K* alleles (1) as seasonal harshness increases (northward) (Roughgarden 1971) or (2) as the growing season decreases (northward) (King and Anderson 1971). Thus, seasonal selection in *W. smithii* parallels that of density-dependent larval development; indeed, seasonality may have contributed directly to the observed gradient in density-dependent development (Istock et al. 1976a; Bradshaw 1983; Bradshaw and Holzapfel 1983, 1986). Still, southern populations experiencing the greatest density-dependent development all year in nature do not realize a greater rate of increase at higher densities in the laboratory than do northern or high-elevation populations not experiencing these limitations. Similarly, northern populations relieved of density-dependent constraints, encountering a shorter growing season and enduring harsher winters

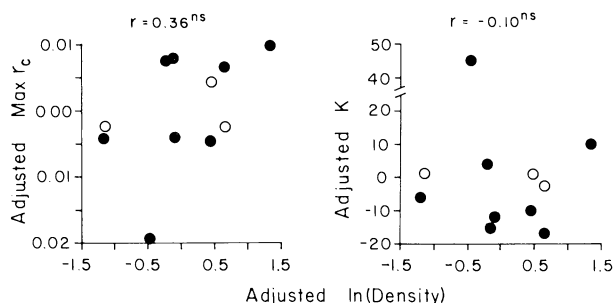


FIG. 6.—Relationship between max r_c or K determined under uniform conditions in the laboratory and the density per unit of resource in nature after max r_c , K , and density have been adjusted for regional (north/south) differences. Density was measured as the mean crowding of *W. smithii* per head capsule of prey in leaves of the overwintering generation (Bradshaw and Holzapfel 1986). Open circles, Southern populations; solid circles, northern populations.

in nature, do not realize greater fitness at low densities in the laboratory than do southern populations.

Density-dependent selection might have caused the divergence in population growth rates (if all other factors were constant), but in the particular populations studied, density may be a less effective force than other factors. Thus, putative selective forces that gave rise to the geographically divergent life-history traits described above may have swamped density-dependent development as a selective force. First, if this assertion were true, it would underscore the impotence of density-dependent developmental success in constraining the evolution of the population growth rate or its components. Second, if r - and K -selection played an important, albeit secondary, role within the “northern” and “southern” regions but the effects of r - and K -selection were occluded by selection for factors such as variable iteroparity, variable stage of diapause, and competitive ability, then max r_c and K should still correlate with density within the northern and southern regions. For iteroparity, stage of diapause, and competitive ability, the transition between phenotypes occurs between low-elevation North Carolina and either high-elevation North Carolina or New Jersey. Thus, the present study encompasses four “southern” and eight “northern” localities (table 1), for all of which except one southern locality (CR) estimates of mosquito density are known. To assess the correlation between max r_c or K and density corrected for region, we calculated mean density, mean max r_c , and mean K within each region and then calculated the regression of the deviation of max r_c or K from its respective regional mean on the deviation of density from its respective regional mean (fig. 6). Neither region-corrected max r_c nor region-corrected K correlated significantly with region-corrected density (fig. 6), and as with the uncorrected correlations (fig. 3), the signs of the nonsignificant correlations were opposite those predicted from r - and K -selection theory.

Finally (fig. 2), there is no trade-off among populations in capacity for increase at low and at high densities. These observations indicate that r - and K -selection

based on the simple effects of density alone is totally inadequate to explain the evolution of major demographic traits in *W. smithii*.

SUMMARY

Over its range, the pitcher-plant mosquito, *Wyeomyia smithii*, experiences a gradient in density-dependent development. In each of 12 populations from six geographical regions over a range of 19° latitude and 900 m in altitude, we determined capacity for increase and its components at four densities. We reared experimental populations in intact pitcher plants receiving near-natural conditions of light, temperature, and feeding.

Capacity for increase and its components, replacement rate and mean generation time, exhibited significant variation among densities and among localities within regions but not among regions. There was no trade-off among populations in capacity for increase at high and low densities. Consequently, variation in these fitness traits did not reflect major differences in climate or degree of density-dependent selection prevailing at the locality of origin. Hybrids between populations exhibited heterosis in capacity for increase and in both of its components. These results indicate that local populations of *W. smithii* can and have diverged with respect to capacity for increase and its components but that the simple effects of density alone are totally inadequate to explain the evolution of major demographic traits in this species. Since most organisms live in habitats that are more variable among localities than does *W. smithii*, we suspect that evolution at the level of the local population may be an important contributor to the evolutionary divergence of demographic traits in other species as well.

Despite a lack of differences in density tolerance among zones, southern populations exhibited greater competitive ability than did northern populations. Competitive ability can therefore evolve independently of density tolerance and can be assessed only by direct competition of the genotypes, populations, or species concerned.

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LITERATURE CITED

- Albert, A. M. 1983. Life cycle of Lithobiidae—with a discussion of the *r*- and *K*-selection theory. *Oecologia* (Berl.) 56:272–279.

- Ayala, F. J. 1965. Evolution of fitness in experimental populations of *Drosophila serrata*. *Science* (Wash., D.C.) 150:903–905.
- . 1968. Genotype, environment, and population numbers. *Science* (Wash., D.C.) 162:1453–1459.
- Barclay, H. J., and P. T. Gregory. 1981. An experimental test of models predicting life-history characteristics. *Am. Nat.* 117:944–961.
- Bauer, S. J., and M. B. Sokolowski. 1985. A genetic analysis of path length and pupation height in a natural population of *Drosophila melanogaster*. *Can. J. Genet. Cytol.* 27:334–340.
- Bell, G., and J. H. Lawton. 1975. The ecology of the eggs and larvae of the smooth newt (*Triturus vulgaris* (Linn.)). *J. Anim. Ecol.* 44:393–423.
- Bergmans, M. 1984. Life history adaptation to demographic regime in laboratory-cultured *Tisbe furcata* (Copepoda, Harpacticoida). *Evolution* 38:292–299.
- Boyce, M. S. 1984. Restitution of *r*- and *K*-selection as a model of density-dependent natural selection. *Annu. Rev. Ecol. Syst.* 15:427–447.
- Bradshaw, W. E. 1976. Geography of photoperiodic response in a diapausing mosquito. *Nature* (Lond.) 262:384–386.
- . 1980a. Blood-feeding and capacity for increase in the pitcher-plant mosquito, *Wyeomyia smithii*. *Environ. Entomol.* 9:86–89.
- . 1980b. Thermoperiodism and the thermal environment of the pitcher-plant mosquito, *Wyeomyia smithii*. *Oecologia* (Berl.) 46:13–17.
- . 1983. Interaction between the mosquito, *Wyeomyia smithii*, the midge, *Metrocnemus knabi*, and their carnivorous host, *Sarracenia purpurea*. Pages 161–189 in J. H. Frank and L. P. Lounibos, eds. *Phytotelmata: terrestrial plants as hosts of aquatic insect communities*. Plexus, Medford, N.J.
- . 1986. Variable iteroparity as a life-history tactic in the pitcher-plant mosquito, *Wyeomyia smithii*. *Evolution* 40:471–478.
- Bradshaw, W. E., and C. M. Holzapfel. 1983. Life cycle strategies in *Wyeomyia smithii*: seasonal and geographic adaptations. Pages 167–185 in V. K. Brown and I. Hodek, eds. *Diapause and life cycle strategies in insects*. Junk, The Hague.
- . 1986. Geography of density-dependent selection in pitcher-plant mosquitoes. Pages 48–65 in F. Taylor and R. Karban, eds. *The evolution of insect life cycles*. Springer-Verlag, New York.
- Bradshaw, W. E., and L. P. Lounibos. 1972. Photoperiodic control of development in the pitcher-plant mosquito, *Wyeomyia smithii*. *Can. J. Zool.* 50:713–719.
- . 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution* 31:546–567.
- Buzzati-Traverso, A. A. 1955. Evolutionary changes in components of fitness and other polygenic traits in *Drosophila melanogaster* populations. *Heredity* 9:153–186.
- Dingle, H., W. S. Blau, C. K. Brown, and J. P. Hegmann. 1982. Population crosses and genetic structure of milkweed bug life histories. Pages 209–229 in H. Dingle and J. P. Hegmann, eds. *Evolution and genetics of life histories*. Springer-Verlag, New York.
- Dobzhansky, T. H. 1950. *Evolution in the tropics*. *Am. Sci.* 38:209–221.
- Emlen, J. M. 1970. Age-specificity and ecological theory. *Ecology* 51:588–601.
- Endler, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton University Press, Princeton, N.J.
- Evans, K. W., and R. A. Brust. 1972. Induction and termination of diapause in *Wyeomyia smithii* (Diptera: Culicidae), and larval survival studies at low and subzero temperatures. *Can. Entomol.* 104:1937–1950.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*. 2d ed. Longman, London.
- Fish, D., and D. W. Hall. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea*. *Am. Midl. Nat.* 99:172–183.
- Fisher, R. A. 1958. *The genetical theory of natural selection*. 2d ed. Dover, New York.
- Giesel, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7:57–79.

- Giesel, J. T., and E. E. Zettler. 1980. Genetic correlations of life historical parameters and certain fitness indices in *Drosophila melanogaster*: r_m , r_s , diet breadth. *Oecologia* (Berl.) 47:299–302.
- Gill, D. E. 1972. Intrinsic rates of increase, saturation densities, and competitive ability. I. An experiment with *Paramecium*. *Am. Nat.* 106:461–471.
- . 1974. Intrinsic rate of increase, saturation density, and competitive ability. *Am. Nat.* 108:103–116.
- Gould, S. J. 1977. *Ontogeny and phylogeny*. Belknap Press of Harvard University Press, Cambridge, Mass.
- Groeters, F. R., and H. Dingle. 1987. Genetic and maternal influences on life history plasticity in response to photoperiod by milkweed bugs (*Oncopeltus fasciatus*). *Am. Nat.* 129:332–346.
- Hairston, N. G. 1983. Alpha selection in competing salamanders: experimental verification of an a priori hypothesis. *Am. Nat.* 122:105–113.
- Hairston, N. G., D. W. Tinkle, and H. M. Wilbur. 1970. Natural selection and the parameters of population growth. *J. Wildlife Manage.* 34:681–690.
- Healy, W. R. 1974. Population consequences of alternative life histories in *Notophthalmus v. viridescens*. *Copeia* 1974:221–229.
- Istock, C. A. 1967. The evolution of complex life-cycle phenomena: an ecological perspective. *Evolution* 21:592–605.
- Istock, C. A., K. J. Vavra, and H. Zimmer. 1976a. Ecology and evolution of the pitcher-plant mosquito. 3. Resource tracking by a natural population. *Evolution* 30:548–557.
- Istock, C. A., J. Zisfein, and K. J. Vavra. 1976b. Ecology and evolution of the pitcher-plant mosquito. 2. The substructure of fitness. *Evolution* 30:535–547.
- King, C. E., and W. W. Anderson. 1971. Age-specific selection. II. The interaction between r and K during population growth. *Am. Nat.* 105:137–156.
- Laughlin, R. 1965. Capacity for increase: a useful population statistic. *J. Anim. Ecol.* 34:77–91.
- Lloyd, M. 1967. 'Mean crowding.' *J. Anim. Ecol.* 36:1–30.
- Lounibos, L. P., and W. E. Bradshaw. 1975. A second diapause in *Wyeomyia smithii*: seasonal incidence and maintenance by photoperiod. *Can. J. Zool.* 53:215–221.
- Luckinbill, L. S. 1978. r - and K -selection in experimental populations of *Escherichia coli*. *Science* (Wash., D.C.) 202:1201–1203.
- . 1979. Selection and the r/K continuum in experimental populations of Protozoa. *Am. Nat.* 113:427–437.
- . 1984. An experimental analysis of a life history theory. *Ecology* 65:1170–1184.
- MacArthur, R. H. 1962. Some generalized theorems of natural selection. *Proc. Natl. Acad. Sci. USA* 48:1893–1897.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Markow, T. A. 1979. A survey of intra- and interspecific variation for pupation height in *Drosophila*. *Behav. Genet.* 9:209–217.
- Marks, R. W. 1982. Genetic variability for density sensitivity of three components of fitness in *Drosophila melanogaster*. *Genetics* 101:301–316.
- Mueller, L. D. 1985. The evolutionary ecology of *Drosophila*. *Evol. Biol.* 19:37–98.
- Mueller, L. D., and F. J. Ayala. 1981. Trade-off between r -selection and K -selection in *Drosophila* populations. *Proc. Natl. Acad. Sci. USA* 78:1303–1305.
- Mueller, L. D., and V. F. Sweet. 1986. Density-dependent natural selection in *Drosophila*: evolution of pupation height. *Evolution* 40:1354–1356.
- Murphy, G. I. 1968. Patterns in life history and the environment. *Am. Nat.* 102:391–403.
- Pianka, E. R. 1970. On r - and K -selection. *Am. Nat.* 104:592–597.
- Rose, M. R. 1984. Genetic covariation in *Drosophila* life history: untangling the data. *Am. Nat.* 123:565–569.
- Roughgarden, J. 1971. Density-dependent natural selection. *Ecology* 52:453–468.
- Salisbury, E. J. 1942. *The reproductive capacity of plants*. G. Bell, London.
- Schaffer, W. M. 1974a. Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303.

- . 1974*b*. Optimal reproductive effort in fluctuating environments. *Am. Nat.* 108:783–790.
- Smith, S. M., and R. A. Brust. 1971. Photoperiodic control of maintenance and termination of larval diapause in *Wyeomyia smithii* (Coq.) (Diptera: Culicidae) with notes on oogenesis in the adult female. *Can. J. Zool.* 49:1065–1073.
- Sokolowski, M. B., and R. I. C. Hansell. 1983. Elucidating the behavioral phenotype of *Drosophila melanogaster* larvae: correlations between larval foraging strategies and pupation height. *Behav. Genet.* 13:267–280.
- Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. *Am. Nat.* 108:791–804.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3–47.
- . 1977. The evolution of life-history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:145–171.
- Taylor, C. E., and C. Condra. 1980. *r*-selection and *K*-selection in *Drosophila pseudoobscura*. *Evolution* 34:1183–1193.
- Taylor, F., and J. B. Spalding. 1986. Geographical patterns in the photoperiodic induction of hibernal diapause. Pages 66–85 in F. Taylor and R. Karban, eds. *The evolution of insect life cycles*. Springer-Verlag, New York.
- Wilbur, H. M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.* 11:67–93.
- Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108:805–817.