

Interspecific Interactions and the r-K Continuum: Laboratory Comparisons of Geographic Strains of *Aedes Triseriatus*

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Interspecific interactions and the r-K continuum: laboratory comparisons of geographic strains of *Aedes triseriatus*

Todd P. Livdahl

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In an attempt to understand the significance of interspecific interactions to the evolution of parameters of population growth, aspects of larval success for two geographic strains of the treehole mosquito, *Aedes triseriatus*, are examined.

A strain from Illinois, beyond the known range of the predatory mosquito larva *Toxorhynchites rutilus*, exhibits success in single-species laboratory cultures which is consistently superior to that of a strain collected in North Carolina within the predator's range, at a spectrum of food levels. This result, based on observations of wing length, survivorship, development time and a composite index of success, permits the conclusion that the Illinois strain has the higher capacity for growth in conditions of high and low resource availability. However, the functional response relationships between *Toxorhynchites* feeding behavior and density of *A. triseriatus* larvae suggest that the North Carolina strain is more difficult for the predator to eat than the Illinois strain. A potential competitor, *Orthopodomyia signifera*, was least successful in the presence of the North Carolina strain of *Aedes triseriatus* according to the criteria of female wing length and a composite index.

These findings suggest that growth rates and single species competitive ability may be reduced in response to the evolution of effective interactions with other species.

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Для понимания значения межвидовых взаимоотношений для эволюции параметров популяционного роста исследовали разные аспекты развития личиночной фазы двух географических рас комара *Aedes triseriatus*, развивающегося в дуплах деревьев. Раса из Иллинойса, обитающая за пределами ареала хищных личинок комаров *Toxorhynchites rutilus* успешно развивалась в одновидовых культурах в лаборатории и значительно превосходила расу, собранную в Сев. Каролине в пределах ареала хищника на разных уровнях обеспеченности пищей. Этот вывод, основанный на показателях длины крыла, выживаемости, скорости развития и комплексном индексе процветания позволяет заключить, что раса из Иллинойса имела большую возможность роста в условиях высокой и низкой доступности ресурса. Однако, онтогенетические функциональные реакции пищевого поведения *Toxorhynchites* и плотности личинок *A. triseriatus* показывают, что раса из Иллинойса более трудна для добычи хищника, чем раса из Сев. Каролины. Потенциальный конкурент *Orthopodomyia signifera* менее успешно развивается в присутствии расы *Aedes triseriatus* из Сев. Каролины в соответствии с критериями длины крыла самок и комплексного индекса. Эти материалы показывают, что скорости роста и конкурентоспособность отдельных видов могут снижаться в ответ на развитие эффективных взаимодействий с другими видами.

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1. Introduction

The notion of the “r-K continuum”, set forth by MacArthur and Wilson (1967) and elaborated by Pianka (1970, 1972), Charlesworth (1971), Roughgarden (1971) and others, relies in part on the proposition that characteristics related to competitive ability in saturated environments evolve at the cost of features that contribute to rapid population growth in uncrowded environments. The intuitive appeal of this presumed reciprocity of selection has etched the terms “r- and K-selection” into the working vocabulary of many evolutionary ecologists despite several criticisms of the concept (Hairston et al. 1970, Wilbur et al. 1974, Stearns 1976, 1977, Whittaker and Goodman 1979).

If we focus our attention on the expected changes in population growth potential (r) and carrying capacity (K) as the important results of life-history modification, an immediate problem arises. Will K-selection actually result in an increased carrying capacity? Broad interpretations of K-selection predict the acquisition of features such as delayed maturity, extended periods of reproduction and parental care. It is not difficult to envision a reduction in r when such features are favored, but expected changes in K are not addressed directly by such predictions. Increased efficiency can boost K if body size does not increase in the process, but a larger size may actually reduce the equilibrium density of a population despite an increase in efficiency. Forms of contest competition within a population may be favored, resulting in a reduced carrying capacity (Green 1980). The acquisition of interspecific interference tactics could inflict costs to either r or K , or both parameters (Gill 1974), and similar results could arise from antipredator evolution.

Interpretations of K-selection that are broad enough to encompass all of these possibilities offer high powers of explanation, but the predictions of such theories lose their falsifiability. Southwood (1977) includes exploitative and interference competition with other species and prolonged duration of habitat quality in a definition of a K-selecting regime. Horn (1979), Stubbs (1977) and Pianka (1972) adopt similar views. No clear predictions about changes in the magnitude of K as a result of K-selection emerge from these explanatory efforts.

This liberalized use of the terms r- and K-selection has been questioned by Parry (1981), who points out four distinct meanings that have been given to the concept. On his suggestion, I take the narrowest view of r- and K-selection, from which a simple prediction of population growth parameters arises as a result of the contrasting evolutionary importance of resource availability: K should increase in response to competition, and r should increase in uncrowded conditions.

Stearns (1976, 1977) may be correct in his conclusion that existing models of life-history evolution lack the refinement necessary to produce falsifiable hypotheses. His statement (Stearns 1980) that perceptible tactics

are obscured when populations within a species are compared should be reconsidered in the light of the evidence presented here.

I planned these studies to investigate possible effects of interspecific competition and predation on relative magnitudes of r and K examining the response to food availability of geographic strains derived from communities of different compositions. Significant differences in the performance of the strains permit judgments about their relative values of r and K , and prompt the hypothesis that the observed differences could have arisen from contrasts in their native community compositions. Criteria for the establishment of this possibility are that the geographic strains must display differences in response to interacting species, or that the other species must be differentially affected by one of the geographic strains.

The principal species in this study is the mosquito *Aedes triseriatus*, which has a range that covers the eastern United States, extending north into Minnesota and Wisconsin and northeast to Maine (Carpenter and LaCasse 1955). The filter-feeding larvae of this species occupy water-filled treeholes, and are associated with two other filter-feeding mosquitoes, *Anopheles barberi* and *Orthopodomyia signifera* (occurring south of the Great Lakes), as well as the predaceous mosquito larva, *Toxorhynchites rutilus septentrionalis* (occurring south of the Ohio River Valley). All species are treehole specialists, although the female adults will oviposit in containers that resemble treeholes. Southeastern populations of *Aedes triseriatus* coexist with the predator, *T. rutilus*, and with the potential competitors. *Aedes triseriatus* from northern Illinois have not recently experienced this form of larval predation.

This paper concentrates on characteristics of *Aedes triseriatus* strains from northern Illinois and North Carolina. A strain from northern Wisconsin was also examined, but it was found to respond to various temperatures in a manner different from the Illinois and North Carolina strains (Livdahl 1978). The temperature bias involving the Wisconsin strain may produce artifactual laboratory differences. Therefore the Wisconsin strain is omitted from the comparisons presented here.

2. General methods

2.1. Collection

Brown plastic cups were suspended on the trunks of trees in forests near St. Charles and Batavia, Ill. and Chapel Hill, N.C. An oak slat was inserted to provide a suitable oviposition site for female *Aedes triseriatus*. In an effort to minimize the probability of obtaining a nonrandom sample of each strain, two distinct forests within each area were used. Thirty cups were distributed along transects within each site. Each cup was placed at least 50 m from its nearest neighboring cup.

The cups were suspended at heights between 1.5 and 2 m on the north sides of trees.

The cups were distributed in March, 1976. By late June both strains had deposited eggs. The slats with eggs were placed in sealed plastic bags to prevent desiccation and were transported to the laboratory for storage in humid conditions. The eggs remained unhatched until the appropriate experimental conditions could be established.

2.2. Larval treatment

For each experiment, eggs were hatched by submersion into a brewer's yeast suspension. Larvae that hatched within 24 h were dispensed into 2000 ml plastic cups containing 175 ml deionized water.

Dry dog food (Purina Dog Chow®) was the food resource in each experiment. It was ground and passed through a #60 screen, then stored in a vacuum desiccator in 100 g quantities to minimize clumping and to permit accurate weighing. Food was applied to each culture by sprinkling known quantities onto the water's surface.

Water and food were changed every two days to prevent fouling by bacteria and fungi. Animals were removed from the cups, the cups were rinsed in deionized water, and the larvae were returned to the cups. Fresh water and food were then added. Each cup was covered with a petri dish lid to minimize evaporation. Larval cultures were housed in controlled environment chambers at $26 \pm 1^\circ\text{C}$. Illumination was provided according to a 16L:8D photoperiod by 20 watt fluorescent lights housed in the door of the incubator. Positions of the cups within the incubator were randomized.

2.3. Pupal treatment

Pupae were removed from the larval cultures into water-filled plastic scintillation vials to facilitate the handling of emergent adults and the determination of time to emergence. An inverted jar was placed over each vial to prevent adult escape. The vials were checked daily for adult emergence.

2.4. Adult treatment

On the day of emergence, adults were removed, killed with ether and stored for later dissection and wing measurement. To determine the fecundity of females, adults were housed in $30 \times 30 \times 30$ cm screen cages for mating and blood meals. A wet layer of polyethylene foam covered the top of each cage to increase humidity, and a clear plastic hood enveloped each cage to reduce moisture loss. A sponge soaked in 10% sucrose solution provided the necessary carbohydrate, and I provided the blood meals. All females for which fecundity was to be determined were allowed to complete their bloodmeals, filling themselves to capacity.

It became apparent that males were failing to fertilize the females under these conditions. To obtain fecundity values that were not biased by infertility, an induced insemination technique was adapted from Gerberg (1970).

Inseminated females were transferred to 30 ml ventilated snap cap vials, lined with wet paper towel strips. The females usually oviposited within three days after the blood meal, and they usually died during or shortly after their efforts as a result of their confinement. Upon death, the females were removed and their abdomens dissected to determine the number of eggs remaining within. This number was added to the number of oviposited eggs to yield a total fecundity value. The left wing of the mother was mounted on a microscope slide for later measurement under a stereomicroscope at $25\times$ magnification using an ocular reticle.

2.5. Assessment of performance

The performance of experimental cohorts can be assessed in numerous ways. Correlates of the per capita rate of increase, such as development rates, adult size and survivorship can be compared, permitting judgments about expected relative cohort success. However, there is a possibility of ambiguous conclusions with this approach. One strain might develop more rapidly and produce smaller or fewer adults than another strain, resulting in a cloudy judgment about relative success.

Ideally, the observation of choice for quantifying cohort performance would be the per capita rate of change, calculated from schedules of mortality and fecundity. However, the data requirements for this calculation cannot be met for complex, replicated experimental designs using animals that demand considerable space and attention for successful reproduction. The following analyses will use a substitute for the per capita rate of change which combines larval development time, female biomass production and survival to adulthood. The composite index molds these three life-history features in a manner very similar to the way in which generation time, fecundity and survivorship combine to determine the per capita rate of change. The following performance value is computed for each cohort:

$$r' = \frac{\ln[(1/N_0)\sum_x A_x f(w_x)]}{D + [\sum_x x A_x f(w_x)] / \sum_x A_x f(w_x)} \quad (1)$$

in which N_0 is the original number of female larvae (assumed to be half the original total); w_x is the average wing length of females emerging on day x ; A_x is the number of females emerging on day x ; and $f(w_x)$ describes the relationship between fecundity and wing length, obtained from an independent least squares fit. The constant D represents the average delay time between female emergence and oviposition. I will arbitrarily use $D = 7$ days in the following analyses to allow

time for mating, acquisition of blood meals and egg maturation.

Analyses will also be presented for the following separate correlates of per capita rate of change for each cohort: mean female size (wing length); mean time of female emergence; and the proportion of larvae surviving to adult emergence.

3. Comparisons of r and K

Performance of the two strains of *Aedes triseriatus* is compared at four levels of food availability with a two way analysis of variance design. The following criteria are established for conclusions about relative values of r and K .

The two factors in the experiment are Strain and Food. A significant Food effect is required for any conclusion about relative K values. A significant effect due to Strain, with no Strain \times Food interaction, would indicate the relationship shown in Fig. 1a. This result would permit the conclusion that one strain exhibits superior performance at all levels of resource availability, indicating that both r and K are higher for one strain. A significant interaction would arise from the relationships shown in Figs 1b, c and d. The relationships shown in Figures 1b and c would produce Strain effects as well as significant interaction terms, resulting from differences in r (Fig. 1b) or K (Fig. 1c). The relationship described by Fig. 1d would produce a significant interaction term but no Strain effect, suggesting that one strain has the higher r while the other strain has the higher K .

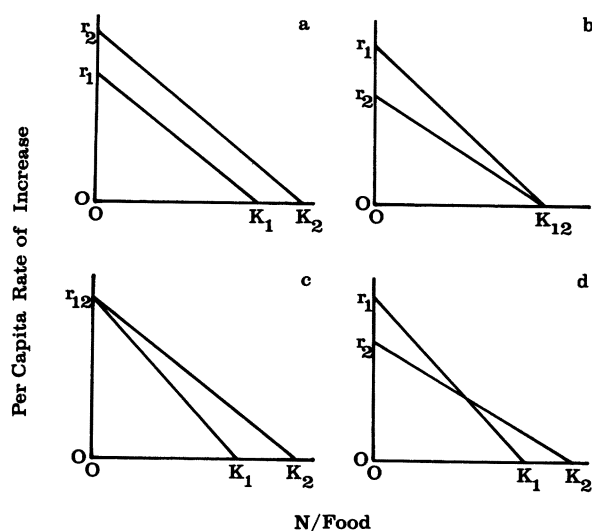


Fig. 1. Four possible hypothetical findings in a comparison of the performance of two strains at different levels of food or density.

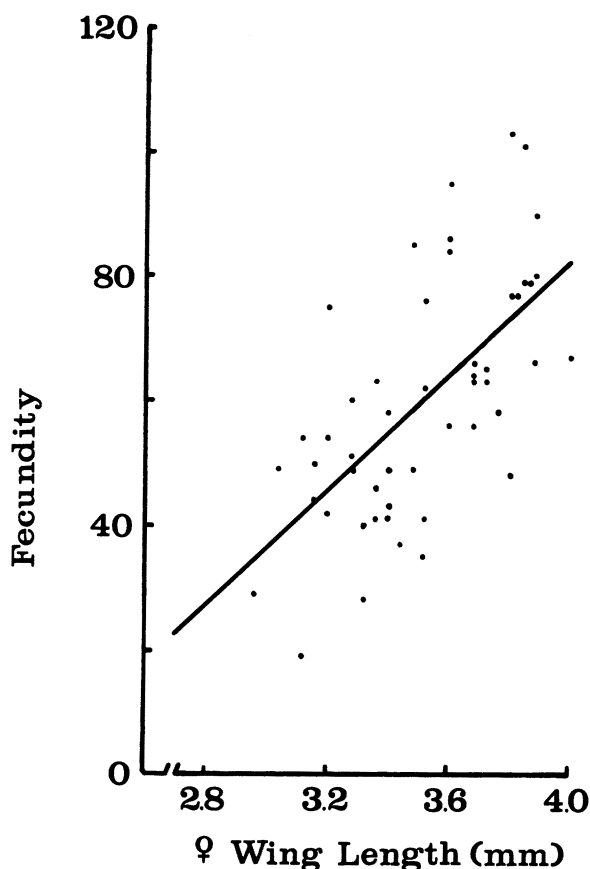


Fig. 2. The relationship between fecundity and female size in laboratory reared *Aedes triseriatus*.

3.1. Procedures

Larvae from each strain of *Aedes triseriatus* were hatched and dispensed into plastic cups at an initial density of 30 larvae per cup. Food was provided every two days in quantities of 4, 8, 16 or 24 mg per feeding, yielding average food levels of 2, 4, 8 or 12 mg per day. Three replicate cultures for each combination of Strain and Food level were used.

3.2. Results and interpretation

3.2.1. Fecundity in relation to female size

The relationship between fecundity and female size, $f(w_x)$, must be described before cohort performance can be assessed by Eqn. (1). A significant, positive relationship is shown in Fig. 2 ($r = 0.62$, $p < 0.001$). There are no significant differences among geographic strains of *Aedes triseriatus*. Therefore, the equation $Y = 46.13X - 102.19$ will be used to predict fecundity of females for each strain. First, the equation must be modified to project the number of female eggs produced by dividing each coefficient in half:

Tab. 1. Analysis of variance for mean female wing length per culture for two geographic strains of *Aedes triseriatus* reared at four food levels.

Source	df	SS	MS	F	P
Strain	1	0.028	0.028	7.52	<0.025
Food	3	0.178	0.059	16.04	<0.001
Strain × Food	3	0.129	0.043	11.54	<0.001
Error	16	0.060	0.004		
Total	23	0.395			

$f(w_x) = 23.17w_x - 51.10.$ (2)

3.2.2. Female size

The demonstration of a positive relationship between female size (wing length) and fecundity permits the analysis of wing length as a separate correlate of the per capita rate of growth. Because the sizes of individual females are likely to be interdependent observations in a competitive setting, this analysis uses the mean female wing length for each culture as the dependent variable.

Analysis of variance for mean female wingth (Tab. 1) detects a significant Strain effect and a significant Strain × Food interaction. The Illinois strain achieves larger size at the highest and lowest food levels (Fig. 3). Although the result does not coincide exactly with any of the cases in Fig. 1, it indicates that the Illinois strain has the higher values of *r* and *K*. The North Carolina strain exhibits less ability to capitalize on high food conditions, and more sensitivity to food scarcity.

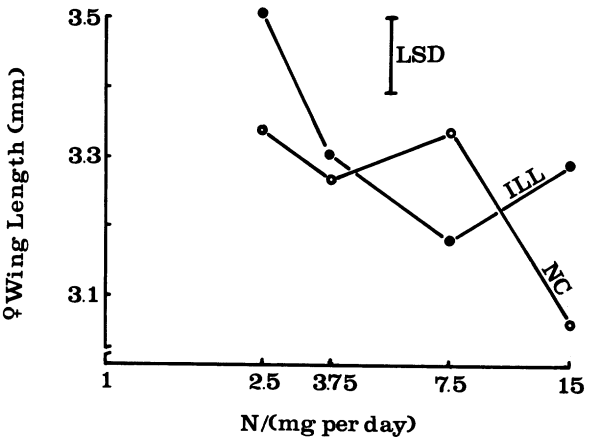


Fig. 3. Responses of mean female wing length per culture to variation in food for two geographic strains of *Aedes triseriatus*. Food is shown inversely on a logarithmic scale. LSD denotes Tukey's least significant difference for the comparison of means of experimental cells.

Tab. 2. Analysis of variance for mean female time to emergence per culture for two geographic strains of *Aedes triseriatus* reared at four food levels.

Source	df	SS	MS	F	P
Strain	1	132.73	132.73	30.90	<0.001
Food	3	1910.69	636.90	148.12	<0.001
Strain × Food	3	114.56	38.19	8.89	<0.005
Error	16	68.74	4.30		
Total	23	2826.72			

3.2.3. Female development time

Both strains exhibit a flexible development in response to food availability that produces the significant effect due to Food (Tab. 2). The significant interaction term arises from the opposite forms of nonlinearity exhibited by the two strains (Fig. 4). The Illinois strain exhibits more rapid development overall, resulting in the significant Strain effect. This result corresponds crudely with the relationship depicted in Fig. 1a, and again permits the conclusion that the Illinois strain has the higher values of *r* and *K*.

3.2.4. Survivorship

The response of larval survivorship to food level appears in Fig. 5. In this case, there is no significant Strain × Food interaction (Tab. 3), and the higher overall survival of the Illinois strain suggests that the relationship of the two strains is that depicted in Fig. 1a. Again, the conclusion is that the Illinois strain has the higher *r* and the higher *K*.

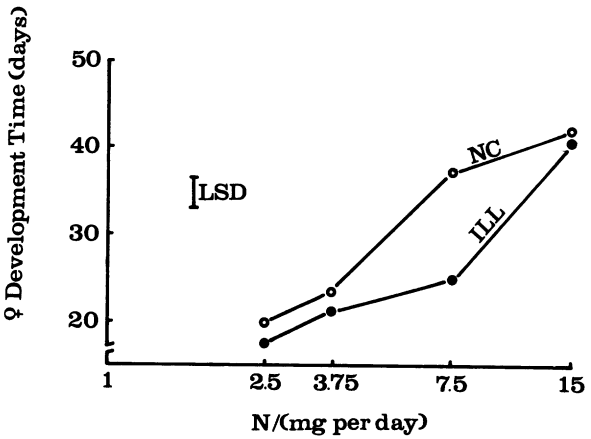


Fig. 4. Responses of the time to female emergence (mean value for each culture) to food for two geographic strains of *Aedes triseriatus*.

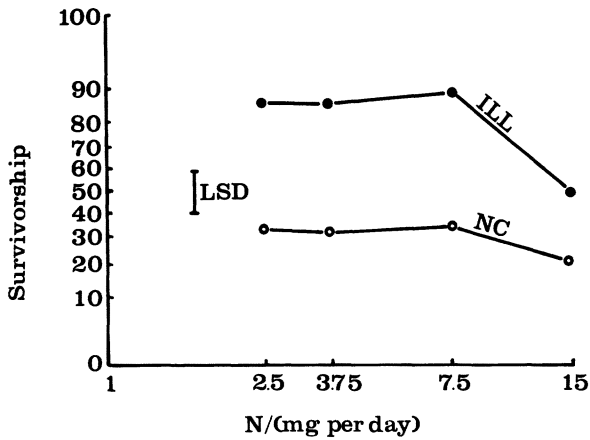


Fig. 5. Responses of survivorship to adulthood (both sexes) to variation in food. The axis of the ordinate converts percentage data into the more appropriate angular transformation ($y' = \sin^{-1} y^{1/2}$). LSD is in angular units.

3.2.5. Composite index of performance

A more informative comparison of relative r and K values can be achieved by computing r' for each culture according to Eqn. (1). Using Eqn. (2) as $f(w_x)$, the relationships depicted in Fig. 6 are obtained. The significant Strain effect (Tab. 4) arises from the consistently higher performance of the Illinois strain. The nonsignificant interaction term indicates a similar response by each strain to food availability.

An advantage of this composite index is that it permits crude projections of both r and K by solving for the intercepts of the least squares lines. K is obtained as the value of food availability when $r' = 0$, and r is crudely determined by the y -intercept. Locations of the least squares lines can now be compared by analysis of covariance.

A comparison of the slopes of least squares lines indicates that the two strains have nearly identical responses to food availability ($b_{ILL} = -0.032$; $b_{NC} = -0.035$; $t_{20} = 0.273$, n.s.). The significant Strain effect of Tab. 4 is corroborated by significantly different vertical locations

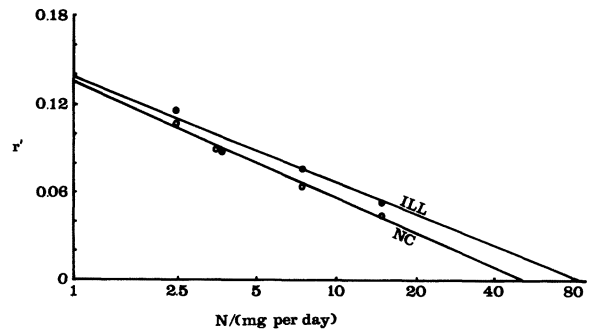


Fig. 6. Responses of a composite index of performance (r') to variation in food for two geographic strains of *Aedes triseriatus*. Mean values for each experimental cell are shown with lines of least squares for each strain.

of the two least squares lines ($t_{21} = 2.193$, $p < 0.05$).

These observed differences in the parameters of population growth could have arisen from numerous possible causes. Climatic differences present a likely possibility. Temperature is perhaps the most obvious source of variation between the two native climates, but a similar response to temperature variation was observed for these strains at 20 and 26°C.

I know of no a priori reason why the native environments of each strain would differ in the unpredictability or "stability" of physical variables. Each climate induces sufficient periods of dry weather to desiccate larval habitats, and both strains experience substantial periods during the winter when the treeholes are completely frozen. Both strains seem to have adapted to the most apparent sources of climatic stress, freezing and drought, in a similar manner with diapausing and desiccation-resistant eggs.

The evolution of interspecific competitive ability and antipredator adaption in the North Carolina strain provide additional possible explanations for the lower r and K of that strain, if these adaptations have demanded an obligatory allocation of larval resources. These explanations are treated as hypotheses in the next section. achieved interspecific competitive superiority.

Tab. 3. Analysis of variance for survivorship to adulthood for two geographic strains of *Aedes triseriatus* reared at four levels of food. The angular transformation was applied to remove the dependence of the variance on the mean in percentage data.

Source	df	SS	MS	F	P
Strain	1	5198.7	5198.7	127.65	<0.001
Food	3	1060.2	353.4	8.67	<0.005
Strain × Food	3	319.2	106.4	2.62	>0.05
Error	16	651.6	40.7		
Total	23	7229.7			

Tab. 4. Analysis of variance for a composite index of performance, r' , for two geographic strains of *Aedes triseriatus* reared at four food levels.

Source	df	SS	MS	F	P
Strain	1	3.35×10^{-4}	3.35×10^{-4}	5.30	<0.05
Food	3	1.25×10^{-2}	4.17×10^{-3}	65.87	<0.001
Strain × Food	3	1.93×10^{-4}	6.44×10^{-5}	1.02	>0.05
Error	16	1.01×10^{-3}	6.33×10^{-5}		
Total	23	1.40×10^{-2}			

4. Interspecific interactions

Geographic differences in life-history characteristics cannot be attributed confidently to differences in community structure until it is shown that interspecific interactions have been important enough to elicit changes in the degree to which the populations affect, or are affected by other species in the community. The invocation of the prey-predator interaction of *Aedes triseriatus* with *Toxorhynchites* as a possible cause of differences observed between the Illinois and North Carolina strains requires a demonstration that the sympatric strain (North Carolina) is less adversely affected by the predator than is the allopatric strain. Similarly, if interactions with competing species have played a role in the creation of the differences detected above, the North Carolina strain must exhibit some form of competitive superiority in the presence of competitors. This superiority can be detected either by finding that a competing species has a less adverse effect on the North Carolina strain, or that the competing species achieves less success with the North Carolina strain than in the presence of the Illinois strain.

4.1. Antipredator evolution in the North Carolina strain

The functional response of the predatory *T. rutilus* to the density of North Carolina and Illinois prey is presented elsewhere (Livdahl 1979) and will only be summarized here.

Newly hatched first instar *T. rutilus* larvae were exposed for 24 h to six densities (3, 6, 12, 18, 24, 48 larvae per 150 ml water) of the two strains of *Aedes triseriatus*. Functional response parameters of Holling's (1959) disc equation were estimated for each strain of prey.

The two strains did not experience different attack rates. However, the predator's handling time of the North Carolina strain was significantly higher than that of the Illinois strain ($t_{81} = 3.58$, $p < 0.001$), indicating that an investment in predator avoidance or defense remains a viable explanation for the relatively low r and K of the North Carolina strain.

4.2. Comparative competition with *Orthopodomyia signifera*

The intent of this study was to observe responses of characteristics that relate to population growth in a competitive situation. A number of results were expected, regardless of the evolutionary importance of interspecific competition. Increased development time, reduced female size and lower survivorship were expected to result from the addition of *Orthopodomyia* for each strain in varying degrees. An evolutionary premium on interspecific competitive ability in North Carolina should have selected for attributes that allow the magnitude of change of these characteristics to be reduced. Additionally, slower development, smaller

adult size and lower survivorship of *Orthopodomyia* could be expected if the North Carolina strain has achieved interspecific competitive superiority.

4.2.1. Procedures

This study was hampered by the relative paucity of *Orthopodomyia* in the field. This species has never been successfully bred in the laboratory, so the successful performance of the experiment depended on the accumulation of sufficient numbers of individuals from the field. The use of field collected individuals introduces additional sources of variation due to the unknown history of the larvae. The shortage of larvae required the use of three different instars of *Orthopodomyia* in the experiment. Consequently, there was high variation in the amount of time each individual was exposed to *Aedes triseriatus* prior to adult emergence, which should result in rather weak average experimental effects. These effects might not be detectable without much more replication. The low power of the tests present an unintended bias against the discovery of competitive differences among the *Aedes triseriatus* strains.

The scarcity of *Orthopodomyia* also hampered the determination of its impact on the strains of *Aedes triseriatus*. It was not known, prior to the initiation of the experiment, whether the number of *Orthopodomyia* used would be sufficient to produce a true competitive effect.

Orthopodomyia signifera larvae were intensively sought in the forests surrounding Chapel Hill, N.C. during the spring and summer of 1977. When individuals were obtained, they were placed in a refrigerator in an effort to arrest their development and to keep them alive until enough individuals could be accumulated for the initiation of the experiment.

Eggs of each strain of *Aedes triseriatus* were hatched by submersion in brewer's yeast suspensions and dispensed into cups as described earlier. Six cultures of 30 larvae per strain were initiated. *Orthopodomyia* individuals were introduced into three cultures per strain to comprise a "competition" treatment, consisting of the addition of two second instar, five third instar and five fourth instar larvae of *Orthopodomyia*.

Food was added in 16 mg quantities every two days, and the larvae, pupae and adults were handled by the procedures described above.

4.2.2. Results and interpretation

This experiment did not succeed in producing significant negative effects of *Orthopodomyia* on any of the *Aedes triseriatus* strains. A preferable experiment would have imposed *Orthopodomyia* on *Aedes triseriatus* at several food levels. The food level chosen was probably too high.

The scarcity of *Orthopodomyia* in the field prevented the use of cultures that contained only *Orthopodomyia*. Consequently, the absolute magnitude of the impact of *Aedes triseriatus* on this species cannot be determined.

Tab. 5. Summarized aspects of the relative performance of *Orthopodomyia signifera* when reared with each of three strains of *Aedes triseriatus*. Survivorship data are based on the angular transformation.

Variable	Strain	Mean ± S.E.	Differences
Survivorship	Wisconsin	51.50±3.25	Not significant
	Illinois	49.85±2.82	
	North Carolina	49.85±1.59	
Female development time (d)	Wisconsin	28.33±5.93	Not significant
	Illinois	31.56±1.10	
	North Carolina	35.33±1.45	
Female wing length (mm)	Wisconsin	3.17±0.03	N.C. < Ill., Wis.
	Illinois	3.19±0.03	
	North Carolina	2.97±0.07	
r'	Wisconsin	0.068±0.009	N.C. < Ill., Wis.
	Illinois	0.073±0.005	
	North Carolina	0.036±0.008	

However, comparisons of features of *Orthopodomyia* that relate to its performance can be used to determine the relative effects of each strain of *Aedes triseriatus* on *Orthopodomyia*, using a set of single classification analyses of variance, in which the treatment consists of the three strains of *Aedes triseriatus*. The strain from northern Wisconsin is included in these analyses to increase the power of the tests, although this strain was not crucial to the significance of the observed differences. As in the first section, mean adult sizes and mean development times for each culture are used as observations because individual values are probably not independent.

Survivorship. Survivorship does not differ significantly for *Orthopodomyia* when reared in the presence of these strains of *Aedes triseriatus* ($F_{2,6} = 0.89$, n.s.). Means are presented in Tab. 5.

Female development time. Similarly, no significant differences are evident in an analysis of female time to emergence (Tab. 5; $F_{2,6} = 0.96$, n.s.). The use of several fourth instar *Orthopodomyia* in each culture to initiate the experiment may have biased against the detection of differences, because a large fraction of them would be relatively unaffected by competition with any of the *Aedes triseriatus*. The only solution to this problem would involve separate analyses for each initial instar. Unfortunately, there was no accurate method of determining the initial instar of a particular emergent adult.

Female size. A similar difficulty should be expected when testing for differences in female wing length when it is reared in the presence of the three different *Aedes triseriatus* strains, but in this case there was enough variation among strains to overcome the probable bias mentioned above. The significant difference due to the strain of *Aedes triseriatus* arises from the lower values

attained by *Orthopodomyia* in the presence of the North Carolina strain (Tab. 5; $F_{2,6} = 7.46$, $p < 0.025$). No difference in wing length is detected between *Orthopodomyia* competing with the Illinois and Wisconsin strains (see Tab. 6).

Composite index of performance. *Orthopodomyia* has not been reported to oviposit in the laboratory. Consequently, a fecundity-size relationship is unavailable for this species. It seems reasonable to expect a relationship similar to that obtained for *Aedes triseriatus*. Eqn. (2) was used to compute r' for each culture of *Orthopodomyia*.

The result parallels the result for wing length. By the criterion of r' , the North Carolina strain restricts the success of *Orthopodomyia* more than either of the other strains (Tab. 5; $F_{2,6} = 7.31$, $p < 0.025$). Again, the Illinois strain and the Wisconsin strain permit similar success for *Orthopodomyia* (see Tab. 7).

This evidence that the North Carolina strain of *Aedes triseriatus* has a more detrimental effect on the performance of *Orthopodomyia* than do the other two strains supports the prediction of Gill's concept of alpha-selection, defined as a selective process that acts to increase competitive ability by favoring individuals with genotypes that permit the impairment of the reproduc-

Tab. 6. Results of pairwise comparisons for the female wing length of *Orthopodomyia signifera* reared in the presence of different strains of *Aedes triseriatus*, using The Newman-Keuls studentized range. Numbers outside the parentheses are the studentized ranges. Parenthesized numbers are the levels of significance for the comparisons.

	North Carolina	Illinois
Wisconsin	4.44 (<0.05)	0.44 (>0.05)
Illinois	4.88 (<0.05)	

Tab. 7. Results of pairwise comparisons for the composite index of performance, r' , of *Orthopodomyia signifera* reared in the presence of different strains of *Aedes triseriatus*, using the Newman-Keuls studentized range. Numbers outside the parentheses are the studentized ranges. Parenthesized numbers are the levels of significance for the comparisons.

	North Carolina	Illinois
Wisconsin	4.34 (<0.05)	0.61 (>0.05)
Illinois	4.97 (<0.05)	

tive rates of competing species. There are actually two ways in which selection can act on competition coefficients. Selection may favor an increase in the negative effect of individuals on the other species, or it may favor a reduced effect of the other species on the species in question. This experiment may document the former, but not the latter phenomenon.

5. Discussion

This study relies entirely on the comparative approach, which is subject to certain pitfalls. A major problem concerns an ignorance of the starting conditions for the evolutionary process. The construction of scenarios for the starting conditions of natural experiments is always speculative, and in this case we must assume that populations were initiated in Illinois at a later time than southeastern populations because the northern extensions of the range of *Aedes triseriatus* probably depended on glacial recessions and the later establishment of forests. The community structure within treeholes at the time of colonization by *Aedes triseriatus* is not known. For example, we can only assume that *Toxorhynchites* did not once have a more extensive range to the north. Moreover, knowledge of the present ranges of interacting species is necessarily incomplete. It is much easier to prove that a species is present within a particular geographic region than it is to demonstrate the absence of that species.

Finally, the demonstration that an interspecific interaction has been important does not imply that the interaction has been the definite cause of observed differences in life history phenomena. Such a demonstration merely establishes grounds for the possibility of such causation. The solution to these difficulties lies in the performance of long term experiments in which it is possible to observe evolutionary change in response to different controlled environments.

Several direct experiments of this sort have now been accomplished. Barclay and Gregory (1981) imposed density-dependent and density-independent selection on laboratory populations of *Drosophila melanogaster*, which focus on separate features of survival and reproduction. They observed improved larval survival under

“K-selection”, but discerned either no response or unpredicted responses for egg production, time to adult emergence and body size. The population growth potential, r , was only observed indirectly through these components, and changes in K were not examined. Taylor and Condra (1980) observed earlier adult emergence and reduced adult survivorship of *Drosophila pseudoobscura* in response to r -selection, although no differences in r were observed between r -selected and K -selected strains. Neither of these studies examined the responses of r -selected and K -selected strains to density or food levels, which might have shown differences in K as a result of selection. Neither of these studies is inconsistent with the most common interpretation of the “ r - K continuum”, although the authors do not view their results as strong support for the concept.

Direct observations of r and K were possible in Luckinbill’s (1978) experiments with *Escherischia coli*, which produced a contradiction to the idea of “tradeoffs” between attributes of r and K . Strains produced by r -selection also acquired increased carrying capacities, and strains evolving in steady environments achieved higher values of r . The results suggest that neither r or K had been optimized in the original strain, and that interference tactics can disrupt the r - K continuum.

In a related set of experiments with *Paramecium aurelia*, Luckinbill (1979) observed increases in K after r -selection. These experiments were initiated with a mixture of reproductively isolated strains, which are functionally different species, and the outcome can result from the superiority of strains that have high values for both r and K . However, the relative competitive abilities of six ciliate species were found to correlate negatively with r and K . Again, the r - K continuum is disrupted. If a tradeoff exists, it is not between these parameters of single population growth.

Tradeoffs are a necessary result of optimization, but they are not always required by natural selection. In fact, selection cannot continue after an optimal state is reached. Luckinbill’s results can be interpreted as an illustration of the suboptimal state of population growth parameters, in which there is room for improvement in both r and K . The results can also be viewed as evidence for a tradeoff between a separate measure of competitive ability (α) and both r and K .

The comparisons presented here are also contrary to the supposed dichotomy between r -selection and K -selection, and they may be viewed from the same two perspectives. The Illinois strain may have acquired attributes of higher r and K , while the North Carolina strain adapted to predation and achieved a means of interference competition. This explanation, which may apply if the common ancestor population had not yet reached an optimal state, requires no tradeoff among allocations toward different parameters of population growth. An alternative explanation is that the North

Carolina strain acquired interference competition tactics and adaptations to predation at the cost of both *r* and *K* attributes. These alternative explanations illustrate the primary weakness of comparative approaches to the study of life history evolution. The latter interpretation, which is consistent with Luckinbill's (1979) findings as well, would support the prediction of Gill (1974), that selection favoring interference tactics can result in diminished *r* and *K*. Neither interpretation is consistent with the unidimensional dichotomous view of *r*- and *K*-selection.

It might be argued that the *r*-*K*-dichotomy has been viewed too literally, that firm predictions about *r* and *K* are not made in the most common interpretation, and that the dichotomy is simply an attempt to explain the diversity of reproductive, developmental and survivorship patterns. Tradeoffs can exist among components of fitness with no necessary changes in *r* and *K*. For instance, broad interpretations of *r*- and *K*-selection predict that high juvenile survivorship may be achieved, but that a reduction in some other quality, such as fecundity or development rate is required. No net change in *r* or *K* is predicted, and the term *K*-selection serves only as a convenient label for relationships among internal life history details, not population growth parameters. Even this most liberal interpretation of the concept is unacceptable in this case, because the Illinois strain exhibits higher survivorship, more rapid development and larger adult size during food scarcity than does the North Carolina strain. No tradeoffs are apparent for these internal life history features. Tradeoffs appear only when interspecific interactions are viewed as separate axes in a selective space.

I conclude from these results that our present models of life history evolution should be modified to overcome either of two possible flaws: (1) the models rely too heavily on optimization, which is not necessarily achieved; or (2) not enough attention has been paid to environmental factors that may not be related directly to resources, such as interference competition and predation.

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