

LIFE CYCLE STRATEGIES IN *WYEOMYIA SMITHII*: SEASONAL AND GEOGRAPHIC ADAPTATIONS

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INTRODUCTION

Low latitudes and altitudes have been credited with more biotic and fewer physical limiting factors (Dobzhansky 1950), greater stability (Cody 1966), longer growing seasons (King & Anderson 1971), and fewer seasonally related sources of density-independent mortality (Roughgarden 1971) than higher latitudes and altitudes. In the absence of other considerations, these conditions should lead to:

1. shorter generations in the north,
2. earlier age at first reproduction in the north,
3. larger clutches in the north,
4. semelparity in the north, iteroparity in the south,
5. higher capacity for increase in the north.

These predictions are derived from correlations between environmental conditions and the r-K continuum (Pianka 1970; Stearns 1976). Southern organisms living in stable environments with few physical limiting factors, many biotic limiting factors, few sources of density-independent mortality, and longer growing seasons should fill up and saturate their habitats, i.e., approach K, the carrying capacity. In contrast, northern environments are supposedly characterized by the complementary set of conditions which would place a premium on productivity rather than efficient use of resources (MacArthur & Wilson 1967); at these latitudes, selection would then maximize innate capacity for increase or r_{max} . Several studies among a variety of organisms tend to support one or more of these generalizations, either at single localities (Gadgil & Solbrig 1972; Abrahamson & Gadgil 1973) or along geographic gradients (Johnston 1954; Dunmire 1960; Lord 1960; Johnson & Cook 1968; Smith & McGinnis 1968; Tilley 1973; McNaughton 1975; Giesel 1976). However, there are now a considerable number of exceptions and at least one major conceptual alternative to the concept of the r-K continuum. This alternative, termed bet-hedging, predicts syndromes of life-history parameters which are essentially the direct opposites of r- and K-selection (Murphy 1968; Schaffer 1974a, b; Stearns 1976). Bet-hedging has been correlated with situations where the probability of survival is greater among adults than juveniles (Stearns 1976). Other factors, which become apparent

only when the bionomics of the individual species are considered, may also come into play and may or may not conveniently fit into either a bet-hedging or r-K conceptual framework (Tinkle & Ballinger 1972; Menge 1974; Wilbur *et al.* 1974; Giesel 1976; Stearns 1976).

Along geographic gradients, physical and/or biotic factors may interact so as to effect non-linear or reverse selective pressures. The Atlantic salmon (Schaffer & Elson 1975) has adapted to unpredictably harsh river conditions by producing offspring which return to their home river after a varying number of years at sea. As the frequency of harsh river conditions increases with latitude, so does the variance in return time. However, the number of years that juveniles spend in rivers also increases with latitude so that rivers become, in a sense, predictably harsh at far northern latitudes. Consequently, both time spent at sea and its variance are maximum at intermediate latitudes.

Problems in geographic correlates may also arise when localities are not carefully matched so that supposed geographic gradients actually reflect contrasting selective pressures or drastically different local habitats. Lackey (1978) found larger litters, earlier age at first reproduction, and shorter intervals of time between litters of mice in Mexico than in Michigan. He was, however, comparing a wet-dry season climate with a warm-cold season climate and, 'because the habitat of the northern population is primarily forest, whereas in Campeche (Mexico) these mice are found only in fields, the observed biological differences between those two populations may represent an outcome of different selection pressures attributable in some way to habitat'.

Many studies concerning life-history tactics along geographic gradients are based on field data alone. However, variation of life-history patterns in the field may (Johnson & Cook 1968) or may not (Hickman 1975) be confirmed by life-history patterns observed under controlled conditions. To investigate geographic variation in life-history patterns, we have chosen to work with the pitcher-plant mosquito, *Wyeomyia smithii*. Throughout its range from Florida to Labrador and west to Saskatchewan (24° of latitude, Fig. 1), *W. smithii* is a single species of mosquito living in the water-filled leaves of a single species of plant, the carnivorous purple pitcher plant, *Sarracenia purpurea* (Fig. 2) (Bradshaw & Lounibos 1977). Whereas the microhabitat of the plant may change along this gradient, it is difficult to imagine a less variable environment for the mosquito. The climatic gradient in eastern and central North America is primarily one of temperature (Visher 1954; National Oceanographic and Atmospheric Administration 1968). Critical photoperiod for the onset and maintenance of dormancy in *W. smithii* correlates closely with latitude and altitude of origin (coefficient of determination, $r^2 = 0.96$; Bradshaw 1976), suggesting that *W. smithii* track closely the changing climate along this gradient.

DENSITY-DEPENDENT SELECTION IN *W. SMITHII*

Immature *W. smithii* occupy a discrete habitat. The dimensions of the pitcher-plant leaves define the physical habitat available to the mosquitoes.

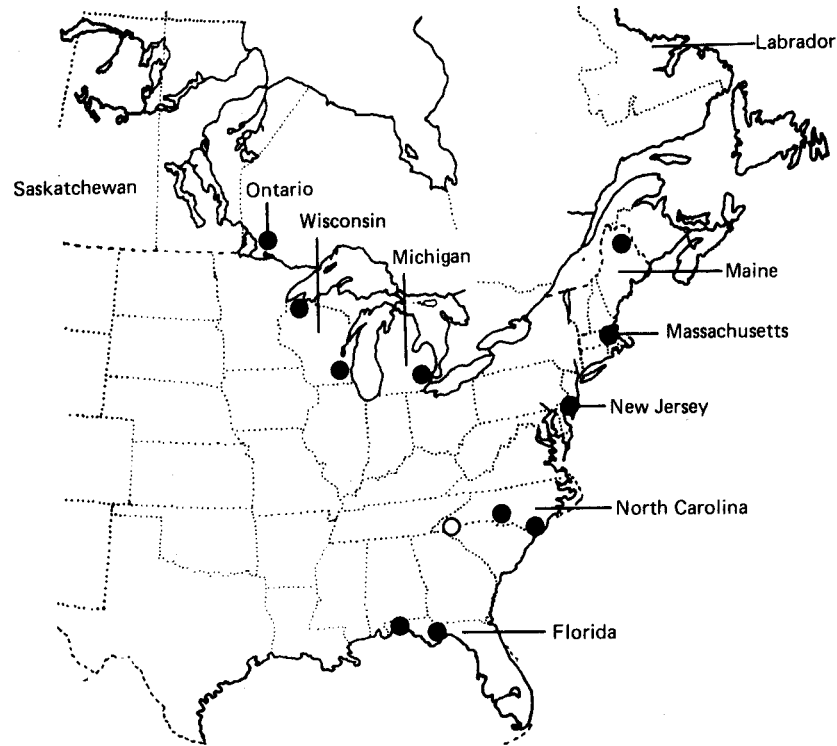


Fig. 1. Map of localities in North America from which *W. smithii* were collected for this study. The open circle in western North Carolina indicates 2 localities at higher elevation (900 m).

They may therefore be readily censused with or without replacement and their densities accurately estimated in the field. That such densities may be a factor limiting *W. smithii* populations may be inferred from the positive correlation between population size and leaf volume (Evans 1971; Paterson 1971). This correlation alone will not give a complete picture of density limitation since females may adjust the number of eggs oviposited in a leaf according to leaf size (Mogi & Mokry 1980). What are needed are either (1) actual observations of density-dependent limitations to growth, development, metamorphosis, and/or adult fecundity and survivorship or (2) an assessment of the degree to which *W. smithii* saturate their environment, i.e., approach their carrying capacity, in the field.

To estimate the latter parameter, Istock (Istock *et al.* 1976) undertook a series of convergence experiments in a northern bog (Fig. 3). To one set of pitcher-plant leaves, he added extra freshly hatched first instar *W. smithii*; another set of leaves he left as natural controls. The basic concept was to see whether there were more resources available in leaves than were being utilized by the natural population. A similar biomass of mosquitoes in the experimental and control leaves would indicate that there were little or no resources available to support supernumerary mosquitoes, i.e., that they were saturating their environment. A greater biomass in the experimental than the control leaves would, however, indicate that there were more



Fig. 2. The carnivorous purple pitcher plant, *Sarracenia purpurea*. The range of this species extends from the Gulf of Mexico (about 30°N) to about 60°N (McDaniel 1971; Evans 1971). The pitcher-shaped leaves may hold up to 100 ml of water, catch up to 1000 insects in a single season, and serve as host for as many as 300 mosquitoes (*Wyeomyia smithii*).

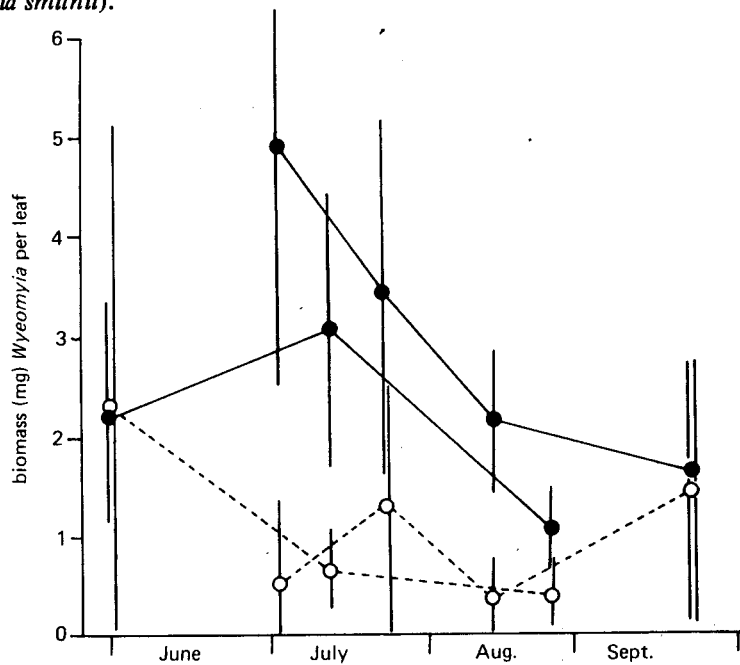


Fig. 3. A composite of several convergence experiments run in a northern bog during 1973 and 1974. ● = carrying capacity estimated by adding supernumerary first instars to the leaves; ○ = biomass observed in control leaves to which only water was added. Vertical lines show 95% confidence limits (from Istock *et al.* 1976).

resources available than being utilized and that the population was below its carrying capacity. Istock (Fig. 3) observed that during the spring and fall, the experimental and control leaves supported a similar biomass; during the summer, the biomass in the experimental leaves exceeded that in the controls. Apparently, vernal and autumnal populations were saturated while those during most of the warmer growing season were well below the carrying capacity.

Not all the leaves are average leaves and a prediction that follows from Istock's observations is that growth and development in the spring and fall should be correlated with density. During the spring of 1976, we sampled *W. smithii* in Massachusetts at the same latitude as Istock's bog in New York. At this latitude, *W. smithii* overwinter and diapause exclusively in the third instar (Bradshaw & Lounibos 1977); yet, the mean age (average instar number) of *W. smithii* in the leaves varied from the third instar to pupae. Furthermore, the average instar number in a leaf was negatively correlated with population size (mosquitoes per leaf, Fig. 4), thus corroborating our predictions based on Istock's results (Fig. 3).

To extend these studies to a geographical scale, we ran a series of convergence experiments in a Florida pine savannah at the extreme southern extent of *W. smithii*'s range, about 12° of latitude further south than Istock's bog. To one set of leaves, we added 100 first instars of *Wyeomyia*, obtained from leaves in the field on that same day. To another set of leaves, we added only the few ml of water necessary to transfer our experimental larvae. As shown in Fig. 5, there was no significant difference between the biomass of mosquitoes supported by experimental and control leaves. Thus, in marked contrast to the northern populations, the southern one we investigated remained saturated throughout the spring, summer, and fall.

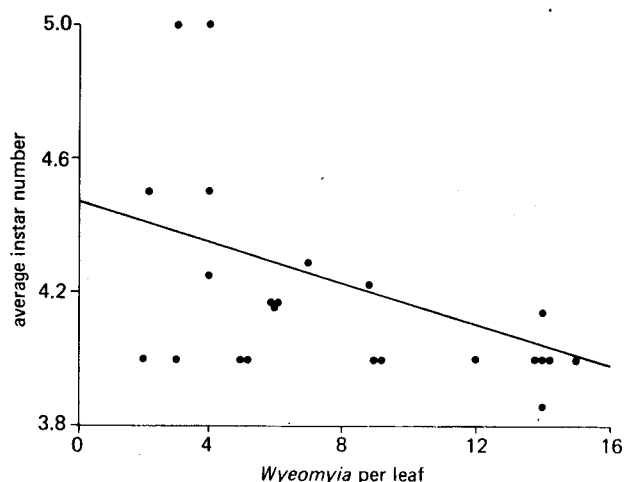


Fig. 4. Relationship between mean age (average instar number, with the pupal stage scored as 5) and population size (*Wyeomyia* per leaf) during the spring of 1976 in eastern Massachusetts. Average instar number = $\sum in_i / \sum n_i$, where n_i = number of larvae in the i th instar. $r = 0.59$, $P < 0.01$; $Y = 4.5 - 0.036X$.

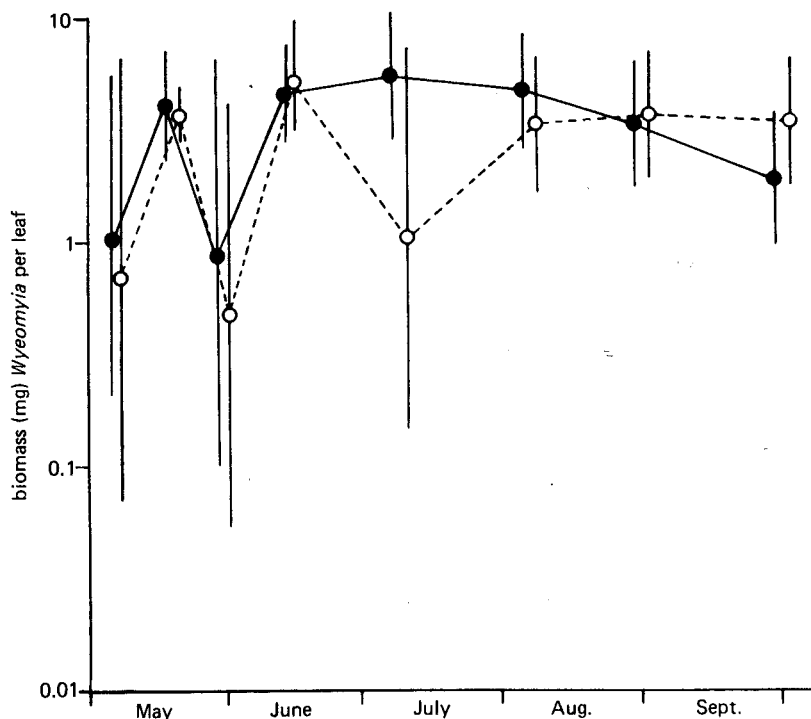


Fig. 5. Convergence experiments run in a southern pine savannah in 1978. \circ = biomass sustained in leaves to which only a few ml of water were added (control). \bullet = carrying capacity estimated by adding 100 additional first instars to each leaf.

On a more detailed examination, the biomass in both the experimental and control leaves oscillates considerably during the early part of the year but appears to stabilize later. This pattern resembles a damped oscillation and suggests finer tuning of populations to available resources during the year. We believe resource tracking is indeed improving during the year and to investigate this phenomenon, it is necessary to describe just what constitutes a resource to *W. smithii*.

The main input of organic material into the pitcher-plant community consists of insect prey captured by the host plant. Figure 6 shows prey capture by the pitcher-plant leaves and oviposition behavior of *W. smithii* into these leaves. *S. purpurea* leaves catch the most prey when they are 2–4 weeks old; neither younger nor older leaves are as alluring to prospective victims. The resources presented in pitcher-plant leaves are therefore not continuous and ongoing; rather, they occur in a pulse early in the life of a leaf. *Wyeomyia*, unlike prey, appear to be attracted primarily by the very youngest leaves. Attractibility of leaves then falls off exponentially with age. The net result is that *W. smithii* oviposit into leaves just prior to the time when resources will be the most abundant; resources would then increase as the mosquitoes develop.

The implication of these observations is that the limiting resource in the leaves of *S. purpurea* is the prey captured by that leaf. We therefore examined the biomass of *W. smithii* supported in a leaf and the number of prey

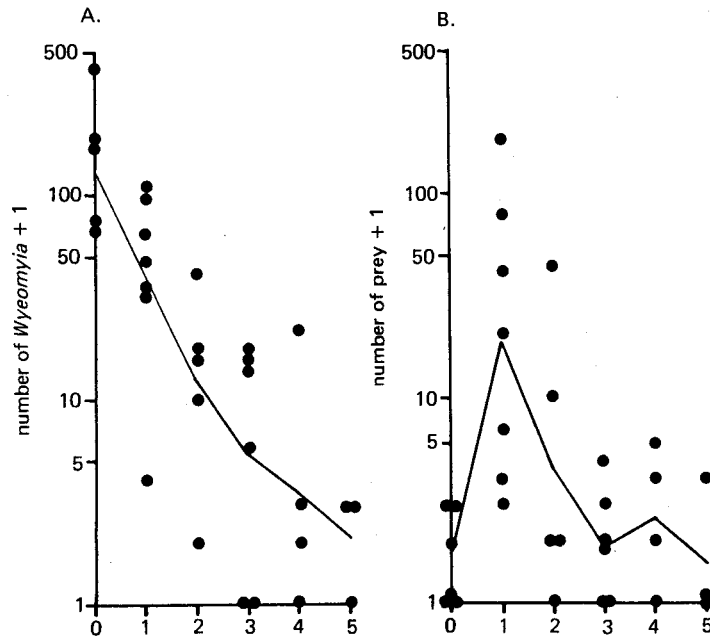


Fig. 6. Change with age in attractability of leaves of *S. purpurea* to A: *W. smithii* for oviposition; B: insect prey. Leaves in the field in north Florida were sucked out, flushed three times with distilled water, half filled with distilled water, and left for 3 weeks, after which time they were destructively sampled and the number of *Wyeomyia* and number of intact insect prey were censused. Since the basal sheaths of the leaves overlap one another, they may be ranked according to their ages by examination of the basal sheaths. Rank 0 = leaves opened during the experiment; rank 1 = youngest leaves on the plant at the start of the experiment. Lines connect geometric means.

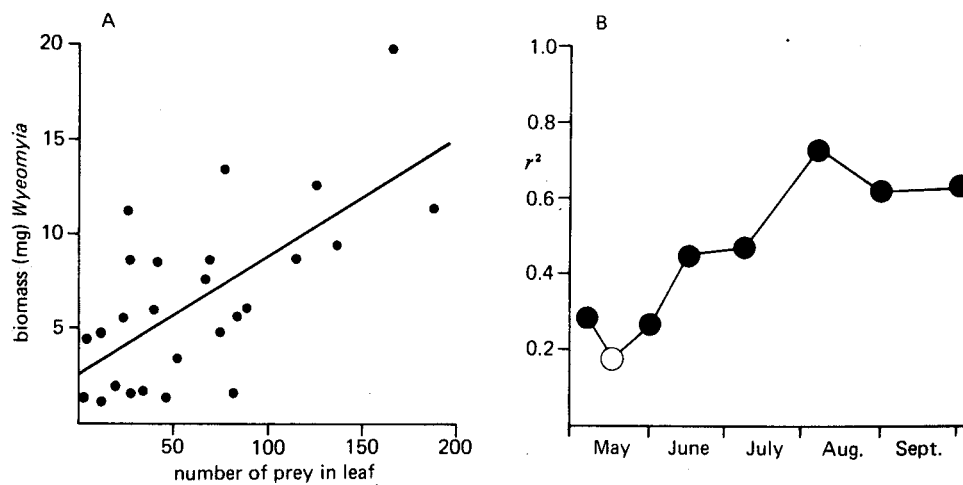


Fig. 7. Biomass of *W. smithii* sustained by prey captured by the host leaf of *S. purpurea*. A: correlation between biomass and number of prey in the leaf, $r = 0.45$, $P < 0.001$; B: the coefficient of determination (r^2) for this same relationship at various times of the year. ● = significant correlations ($P < 0.05$); ○ = non-significant ($P > 0.05$) correlation.

captured by the leaf. Figure 7A shows a direct correlation between the standing crop of mosquitoes and the number of insects captured by their host. The square of the correlation coefficient, also called the coefficient of determination, indicates the amount of variation in the dependent variable explained by taking the independent variable into account. In the present situation, the coefficient of determination (r^2) gives the amount of variation in mosquito biomass explained by the number of insect prey captured by the leaf. As biomass of mosquito becomes more exactly predictable from prey capture, then the more closely the mosquitoes are tracking the available resource and the closer this fraction will approach the value of 1.0. Figure 7B shows the coefficient of determination for the correlation between biomass of mosquito and prey capture as a function of time of year. As predicted from the apparent damped oscillation of biomass in the leaves during the year (Fig. 5), resource tracking is improving as the year progresses. The data in Fig. 7 thus provide direct support for the models of King & Anderson (1971) which suggested that prolonged growing seasons would provide greater opportunity for populations to saturate their environments.

Istock's experiments (Fig. 3) show that in a northern bog, *W. smithii* experience vernal and autumnal periods of density-dependent selection while during the major portion of the growing season, *W. smithii* develop relatively free from such constraints. Our results in a southern pine savannah show that the southern populations saturate their environment during the spring, summer, and fall. Neither set of data shows what is happening to the overwintering populations; nor, does either set of data indicate what is happening at intermediate latitudes.

Evidence for a continuum in density-dependent selection at intermediate latitudes comes from examination of overwintering populations. Along the Gulf of Mexico and at low elevations in the Carolinas, diapause normally occurs in the fourth instar (Bradshaw & Lounibos 1977); yet, much of the population at these localities overwinters as second or third instars (Fig. 8). Why should populations characterized by an older stage of diapause overwinter as younger instars? Figure 9 shows that the mean stage of development or average instar number is dependent upon the prey captured by their host leaves. Along the Gulf Coast (Fig. 9D), although diapause occurs in the fourth instar and one would expect all of the population to be in that instar, most of the population is actually younger. Average instar number is inversely correlated with density, measured as the number of mosquitoes per unit prey captured by the leaf. Much the same pattern is observed at low elevations in North Carolina (Fig. 9B) but not at high elevations in North Carolina (Fig. 9C) or at northern latitudes (Fig. 9A). While these data indicate density-dependent age structure among the overwintering population at southern and intermediate latitudes, they do not show the consequences of this age distribution. To examine these consequences, we censused a number of leaves in a Florida pine savannah in January and then followed development through the ensuing spring. Figure 10 shows that the probability of undergoing metamorphosis in the spring was directly dependent upon the mean age of larvae in a given leaf during the previous winter.

The data in Figs. 5 and 9 illustrate two points. First, among southern

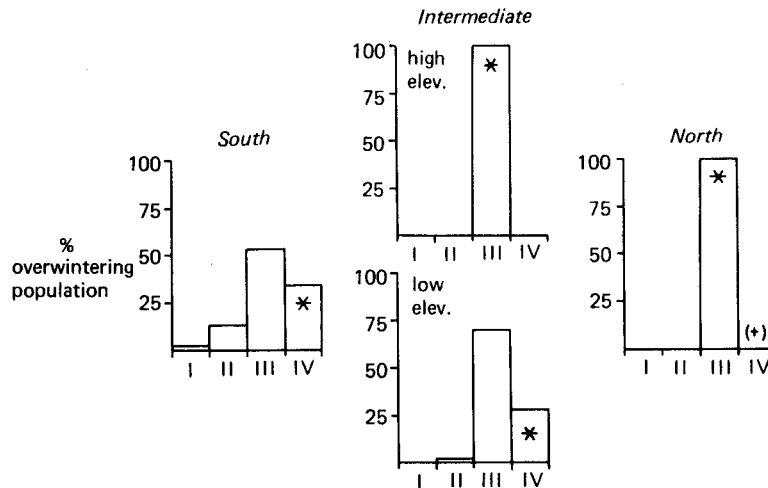


Fig. 8. Age distribution of overwintering *W. smithii* at various latitudes and altitudes. South: several localities on the Gulf Coast in Florida, Alabama, and Mississippi; Intermediate, top: high elevation in North Carolina at 900–1000 m; Intermediate, bottom: low elevation in North Carolina at 10–200 m; North: several localities in New Jersey, Michigan, Massachusetts, Maine, Ontario, Quebec, New Brunswick, and Nova Scotia. * = diapausing instar.

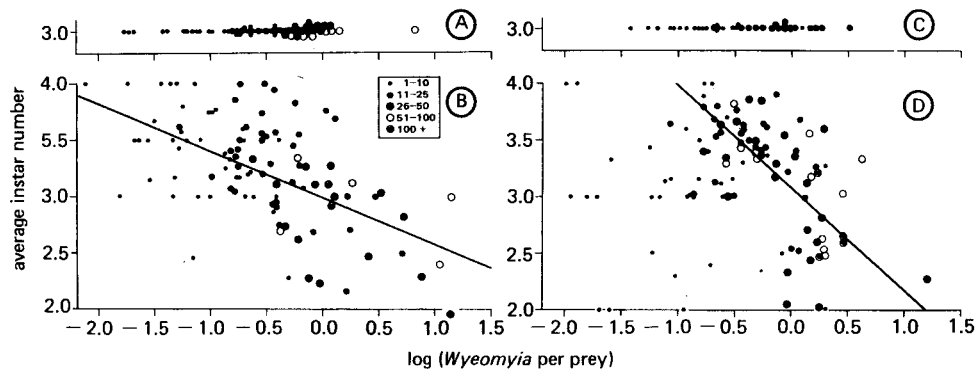


Fig. 9. Effect of larval density (*W. smithii* per prey captured by the leaf) on the age structure of the overwintering population. Regressions were summed over individuals. A: northern latitudes, 2 populations, $r = 0.00$; B: low elevation in North Carolina, 3 populations, $r = -0.54$, $P < 0.001$; C: high elevation in North Carolina, 2 populations, $r = 0.00$; D: low elevation along the Gulf Coast, 3 populations, $r = -0.60$, $P < 0.001$.

populations, there is no relief from density-dependent selection. At these latitudes, not even winter or diapause provides an escape from resource-dependent development. Second, density-dependent selection does exist, at least to some extent, at intermediate latitudes. We therefore conclude that in the range of *W. smithii*, there is a continuum, extending from severe density-dependent selection all year in the south to mild density-dependent selection occurring only during the spring and fall at latitudes as much as 12° further north.

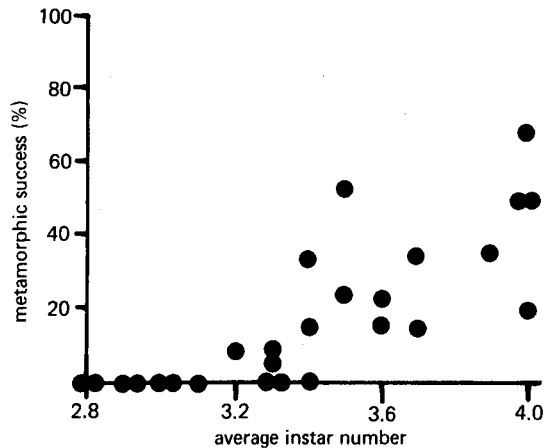


Fig. 10. Metamorphic success (percentage of the January 30 population which had pupated by May 1, 1978) as a function of average instar number of the overwintering population (censused January 30).

LIFE-HISTORICAL CONSEQUENCES

Theories of r- and K-selection hinge mainly upon the degree of density-dependent selection impinging upon the population; the concept of bet-hedging rests primarily upon which stages of the life cycle mortality falls. Where mortality is suffered primarily by adults, the predictions of bet-hedging are similar to those of r-selection; where mortality is inflicted mainly on the juveniles, the predictions of bet-hedging are similar to those of K-selection (Stearns 1976). In *W. smithii*, the populations along the Gulf Coast experience the greatest degree of density-dependent restraint to growth and development (Figs. 5 and 9D); they would therefore appear more K- than r-selected. However, densities which retard development may also limit metamorphic success (Fig. 10). Thus *W. smithii* illustrates a situation where the predictions of r- and K-selection are not mutually exclusive, namely, where a major source of variable juvenile mortality is density dependent. Life-history traits in *W. smithii* which depart from the syndrome of traits predicted from these theories are therefore likely to point out situations or general circumstances where either theory must be forced to fit the circumstances or simply does not apply.

To examine the life-historical consequences of the geographical gradient described above, we reared *W. smithii* from 13 localities from day of hatch until pupation in the leaves of *S. purpurea* to which we had added 200 *Drosophila melanogaster* on the same day as ten first instars of *W. smithii*. We placed the plants under a bank of fluorescent lights in a room programmed to provide a 17L:7D photoperiod and a smooth sine-wave thermoperiod which lagged the photoperiod by 4 hours and had daily maxima and minima of 32 and 18°C, respectively. The intention was to provide a quasi-natural environment with an unambiguous long-day photoperiod and strong thermoperiod to elicit maximal rate of development and capacity for increase (Bradshaw & Lounibos 1977; Bradshaw 1980b). We removed pupae from the leaves and maintained the adults in lucite cages at a humidity near saturation in the

same room. From the day of first adult ecdysis, we provided a fresh leaf of *S. purpurea* for oviposition. We collected and tallied eggs 3 times per week until all adults had died. Then,

$$\text{replacement rate} = \frac{\sum E_x}{E_p} = R_o$$

where E_p is the number of eggs in the parental cohort and E_x is the number of F_1 eggs oviposited at time x ,

$$\text{mean generation time} = \frac{\sum x E_x}{\sum E_x} = \tau$$

and

$$\text{capacity for increase} = \frac{\ln(R_o)}{\tau} = r_c.$$

As predicted from theory and natural conditions experienced by *W. smithii* along the geographic gradient in eastern North America, capacity for increase was proportional to latitude from 30 to about 43°N (Fig. 11A). However, contrary to the predictions of these theories, it declined again towards 49°N. The higher capacities for increase resulted from both a

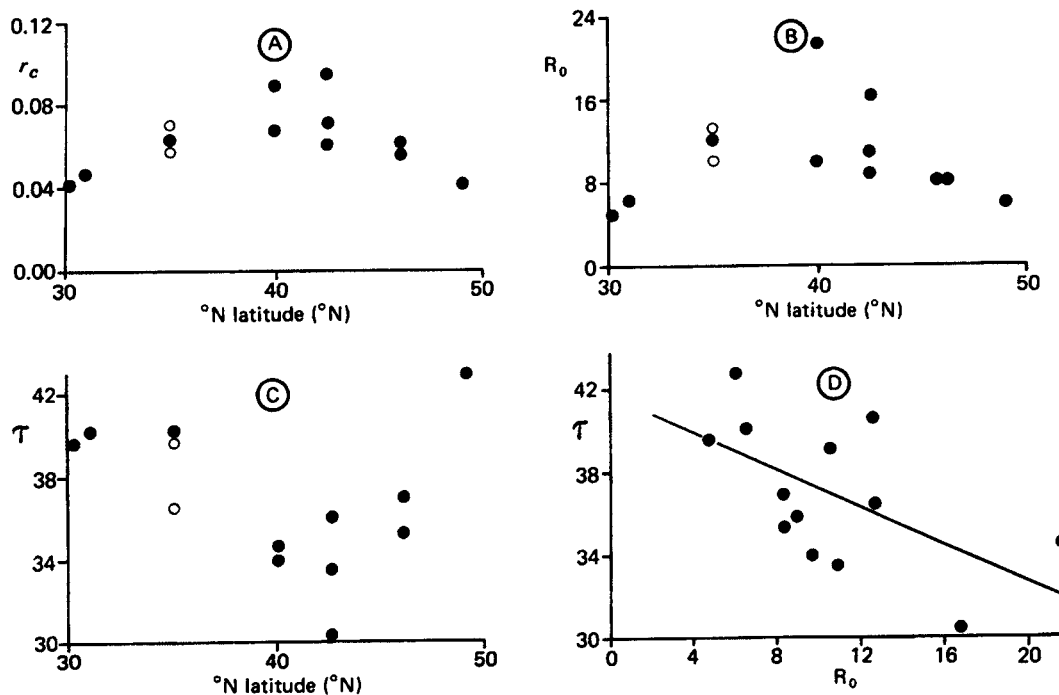


Fig. 11. Life history traits of *W. smithii* from the Gulf Coast (north Florida) to Canada. A-C: change in capacity for increase (r_c), replacement rate (R_o) and mean generation time (τ) with latitude. \circ = high elevation populations at 900 m in North Carolina \bullet = lower elevation populations; D: relationship between generation time (τ) and replacement rate (R_o).

shorter mean generation time (Fig. 11C) and higher replacement rate (Fig. 11B) than those observed among populations with a lower capacity for increase. Because of the sensitivity of r_c to variation in τ , Lewontin (1965) proposed that most of the variability in intrapopulation life-history traits would be related to R_o , natural selection tending to minimize τ in all populations. In part, Lewontin's prediction is borne out in *W. smithii* since, over the geographical range considered, the coefficient of variation is lower for τ (10%) than for R_o (43%). In addition, if evolution in *W. smithii* has proceeded from south to north (Bradshaw & Lounibos 1977), there has been a trend towards shorter generations from the Gulf Coast to about 43°N. But, Lewontin's argument does not by itself explain why southern populations do not also have shorter generations or why generation time again rises north of about latitude 43°. Rather, we must look elsewhere for the adaptive significance of longer generation time in the south and far north.

Traditionally, *W. smithii* are believed not to take a blood meal and *W. smithii* from all latitudes are capable of producing at least one clutch of eggs without having access to a blood meal (Smith 1902; Price 1958; Hudson 1970; Smith & Brust 1971; Bradshaw & Lounibos 1977). However, populations from along the Gulf Coast and from low elevations in North Carolina will bite and take blood (Bradshaw 1980a). Superficially, then, the low latitude populations would appear to be iteroparous and the northern populations semelparous, a situation consistent with both r- and K-selection and bet-hedging, as discussed above. But, if we define iteroparity in mosquitoes as multiple ovarian cycles, then the northern populations are iteroparous also since, uniquely among mosquitoes, they are capable of maturing several clutches of eggs without recourse to blood feeding (O'Meara *et al.* 1981). Among the southern, biting, populations, each ovarian cycle, the first without blood and the subsequent ones requiring it, are of about the same size. Among the northern, non-biting populations, the first ovarian cycle produces a clutch as large as or larger than any among the southern populations but each subsequent cycle produces many fewer. Thus, while both high and low capacity for increase populations are iteroparous, they differ with respect to the allocation of their reproductive effort.

We maintain that allocation of reproductive effort is the essence of the theoretical arguments and that semel- or iteroparity are convenient paradigms around which to build these theories. Nonetheless, one is left with the question of why delay a major portion of one's reproductive effort? Even though large by northern standards, second clutches of eggs produced among southern populations do not appreciably augment their capacity for increase since the time required to mature this clutch (increased generation time) largely offsets the increased fecundity (Bradshaw 1980a). Because only the youngest leaves will provide the best future resources (Fig. 6), ovipositing females are provided with a mosaic of habitats which vary in time as well as space. If, when a female emerges and mates, most of the leaves are either older or currently saturated with other *W. smithii*, commitment of one's major reproductive effort at that time and place would be ill-advised. By allocating a higher proportion of their reproductive effort to subsequent ovarian cycles, southern females may be better able to capitalize on the new

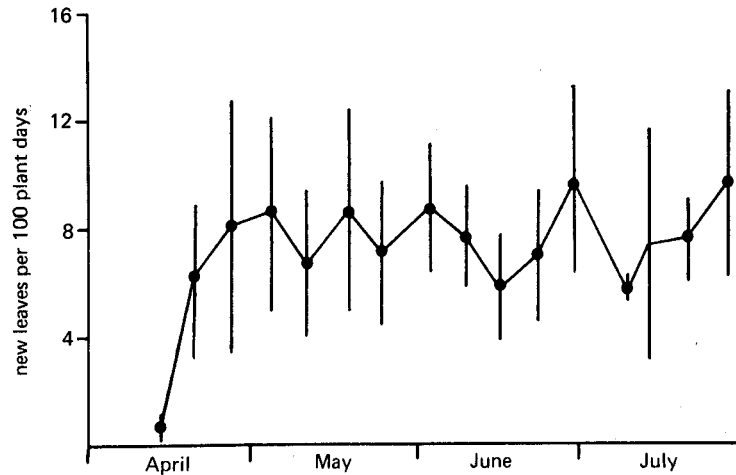


Fig. 12. Early and mid-summer production of new leaves on 109 pitcher-plants in north Florida. New leaves are those which opened since the previous weekly census. Vertical lines show exact 95% confidence limits.

leaves which are continuously opening during the summer (Fig. 12). As one proceeds northwards, density-dependent juvenile mortality or retardation of development abates and, at the same time, most of the young leaves available to an ovipositing female will be likely to support the development of her progeny. Natural selection has therefore presumably resulted in the allocation of greater (but not exclusive) reproductive effort to earlier adult age.

Over the same latitudes (30–43°N), where an increasing proportion of reproductive effort has been allocated to earlier ages, there has also been a decline in mean generation time (Fig. 11C). The principle of allocation (Levins 1968) would predict a trade-off between the two components of

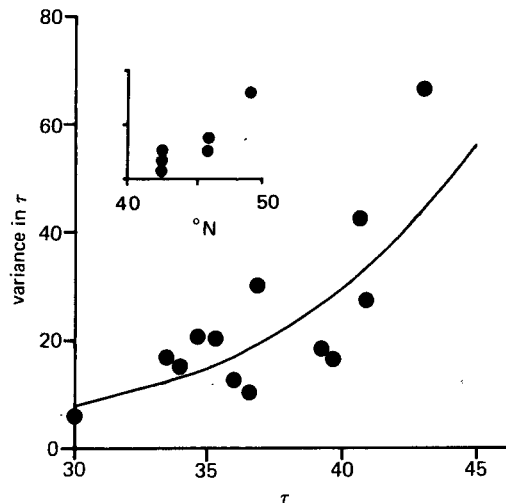


Fig. 13. Dependence of the variance in τ on τ itself ($r = 0.80$, $P < 0.01$) among the 13 populations illustrated in Fig. 11. Inset, increase in the variance of τ over the zone of latitudinal transition (42.5–49°N) from a bi- to univoltine life cycle.

fitness, R_0 and τ , so that among a number of populations these factors should be positively correlated. Instead, our data show a reciprocal relationship between R_0 and τ (Fig. 11D). This argument applies only where r-selection is a reasonable approximation of the factors impinging on a population. Higher latitudes would present such a situation and where r_c is an appropriate measure of fitness, selection should, as Lewontin (1965) suggested, favor a low τ . At other latitudes, other factors may be important and strong selection for a short generation time would be relaxed. Under the latter circumstance, a decrease in directional or stabilizing selection should result in greater variation in τ . Indeed, we observe that the variance in τ is proportional to τ itself (Fig. 13).

The relationship in Figs. 11 and 13 and our discussion above suggest that maximization of r_c is not the predominate or only measure of fitness; a variety of other measures may also be major or overriding considerations (Menge 1974, Wilbur *et al.* 1974; Stearns 1976). Although a combination of bet-hedging and r- and K-selection may conceptually account for the changes in fecundity, generation time, and capacity for increase in *Wyeomyia* from latitudes 30–40°N, neither readily accounts for the subsequent decline in capacity for increase observed at 46–49°N.

VOLTINISM AND LIFE-CYCLE STRATEGY

To what extent is the divergence of the more northern populations from previous theory simply an exception due to the peculiarities of *W. smithii* or to what extent might this divergence parallel the life-history traits of other organisms and hence constitute a pattern or syndrome of predictable traits? We believe the latter interpretation to be true and that the underlying general pattern here relates to change in voltinism, particularly the change from a bi- to univoltine life cycle.

Masaki (1973) proposed that, within the univoltine area, as the duration of the growing season increases southwards, so also should development time, permitting larger, and presumably more fecund, adults. 'In the bivoltine area, however, the growing season is shared by two generations. The time available for development of one generation should therefore be much shorter near the northern margin of the bivoltine area than at the southern margin of the univoltine area. The trend of variation... would accordingly be disrupted and reversed in the zone where the life cycle changes from univoltine to bivoltine.'

In north Florida, we estimate that *W. smithii* may be able to complete up to five generations per year. Moving northwards, the number of degree days during the growing season declines and, in order to complete five generations, *W. smithii* would have to develop faster or commence development at an earlier (and riskier) time of year. However, the cost to fitness of having four instead of five generations per year may not be as great as the cost of modulating other life-history traits, particularly at latitudes where selection for minimum generation time is less intense (see previous section). Proceeding still further northwards, the number of possible generations declines as does

the degree of density-dependent selection. In addition, the cost to fitness of going from a five to a four generation life cycle is not as great as going from a bi- to univoltine life cycle. One may then expect to see the greatest changes in generation time at latitudes where (1) generation time is likely to be an important component of fitness and/or (2) there is a change from bi- to univoltine life cycles.

As shown in the previous section, density-dependent mortality abates among more northern populations and it is somewhere in the north that the change from a bi- to univoltine life cycle must take place. Istock (Istock *et al.* 1976; Istock 1978) found two or, rarely, three generations in New York State (42.5°N) during 3 years of observation. Lounibos & Bradshaw (1975) concluded from two years of observations that *W. smithii* were mainly bivoltine at the same latitude. Judd (1959) showed two distinct generations during 1956 in southwestern Ontario (43°N). At 45.5°N in Michigan, Kingsolver (1979) found either one or two generations possible. Evans (1971) followed the seasonal development of *W. smithii* at 49°N in Ontario; he observed a univoltine cycle in each of three bogs and during two years in one of them. Although Brust (personal communication) says that some *W. smithii* may occasionally produce a second generation at this latitude, the above observations indicate that *W. smithii* change from a principally bi- to univoltine life cycle between latitudes around 43 and 49°N.

We do not consider it coincidental that over this same range of latitudes (43–49°N) both the mean and variance in generation time increase (Fig. 13). Were the thermal environment uniform within bogs or between years, then one might expect an abrupt change from a bi- to univoltine life cycle. However, Istock (Istock *et al.* 1976; Istock 1978) has proposed that between-year variation in temperature (growing season) may be responsible for maintaining a finite level of genetic variation in development time. Similarly, Kingsolver (1979) has described the thermal heterogeneity within a bog and proposed selection for varying thermal optima for development. Kingsolver (1979) also points out that variation in developmental rate at a constant temperature could reflect variation in development time, *per se*, variation in thermal optima, or a combination of both. The important point is that, if there is heritable variation in development time at 42.5°N (Istock's bog) then one could expect even more variation at 45.5°N (Kingsolver's bog) where a mixed bi- and univoltine strategy would be favored by the temporal and spatial mosaic of thermal habitats.

Finally, at latitudes where univoltinism is the exclusive life-cycle strategy, selection for minimal generation time will be relaxed since all members of the population, regardless of how fast they develop, will have the same generation time: one year. However, within the range of the univoltine life cycle, northern univoltines will experience increased selection for shorter developmental time or lower thermal optima if they are to complete even one generation in a single season. We therefore expect generation time and its variance to again decline at far northern latitudes near the limits of *W. smithii*'s range, approximately 54–55°N.

Masaki (1967, 1973, 1978) has examined life-history patterns in a variety of crickets where similar trends are observed. Among a univoltine species

(Masaki 1967) or univoltine populations of potentially multivoltine species (Masaki 1973, 1978), development time declines with latitude. Among the potentially multivoltine species, development time is maximal in the zone of transition between the uni- and bivoltine areas. In the case of *Pteronemobius fascipes* (Masaki 1973), the population is polymorphic for response to photoperiod which, in turn, determines developmental rate. Masaki's findings with a very different insect suggest that the arguments we proposed for *W. smithii* are not unique, or even original. The similarity in the response between these two orders of insects does indicate that a general, predictable pattern of life-history traits may underly the transition from bi- to univoltine life cycles.

CONCLUSIONS

In this paper, we have examined the life-history traits of the pitcher-plant mosquito, *W. smithii*. It is a species that lives within a uniquely uniform habitat over a wide geographical range and has, in terms of its photoperiodic response, shown an equally unique degree of geographical tracking. In the southern portion of their range, they undergo severe density-dependent selection which imposes variable juvenile mortality during the summer, fall, winter, and spring. The severity of this density-dependent selection abates with increasing altitude and latitude. Concomitantly, populations from these latitudes and altitudes exhibit progressively greater capacities for increase, shorter generation times, and higher fecundities as well as a re-allocation of reproductive effort to earlier adult ages. These trends in life-history traits continue to the point where *W. smithii* pass from a bi- to univoltine life cycle.

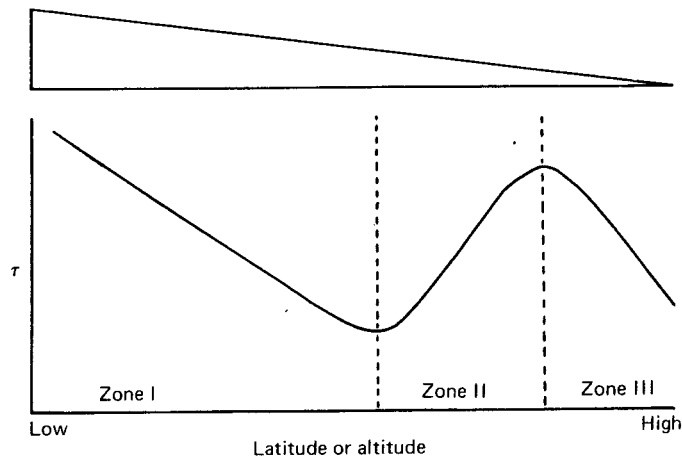


Fig. 14. Idealized diagram of change in r over a geographic gradient. The height of the wedge at the top of the figure illustrates the presumed degree of density-dependent selection. Zone I indicates the range of bi- or multivoltine life cycles, Zone III, the range of the univoltine life cycle, and Zone II, the transition zone between the bi- and univoltine life cycle. In Zone I, r is determined primarily by the degree of density-dependent mortality. In Zone II, r should reflect the frequency of uni- and bivoltine cycles in the population as well as variation in the annual and within-bog temperature. In Zone III, r will reflect primarily the length of the growing season.

In this transition zone, strategies are apparently mixed, as mean generation time and its variance both increase, resulting in lower capacities for increase. While we do not yet possess the data to confirm our hypothesis, we predict that, within the range of univoltine populations, generation time and its variance will again decline with latitude in the most northern portion of *W. smithii*'s range. The similarity between geographic patterns in generation time in *W. smithii* and development time in crickets suggest that a general, predictable pattern is involved (Fig. 14). At southern and intermediate latitudes where multivoltine life-cycles are possible, life-history syndromes are predictable from theory surrounding the degree of density-dependent selection (r- and K-selection) or the degree of variable juvenile/adult mortality (bet-hedging). However, in geographical zones where there is a transition from bi- to univoltine life cycles, seasonal selection becomes the overriding consideration.

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