Evolution, 40(3), 1986, pp. 471–478

VARIABLE ITEROPARITY AS A LIFE-HISTORY TACTIC IN THE PITCHER-PLANT MOSQUITO *WYEOMYIA SMITHII*

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Abstract.—Larval density, but not geographic origin (Florida to Ontario), affected female fecundity among 12 populations of *W. smithii,* regardless of whether or not they had opportunity to take blood meals. Neither the degree of iteroparity nor male longevity varied with density or geographic region of origin, but longevity was greater among southern, potentially blood-feeding females, than among northern, nonbiting females. Among the southern females, iteroparity, but not fecundity, increased with opportunity to take blood meals. Specifically, there was no increase in fecundity among females whose larvae were nutritionally deprived relative to females whose larvae were well fed. I interpret the retention of hematophagy and facultatively augmented iteroparity in *W. smithii* as a means for females developing under predictably impoverished but irregularly opportunistic conditions to reallocate and temporally diversify their reproductive effort.

Received April 4, 1985. Accepted December 10, 1985

The dichotomy between those organisms reproducing only once (semelparity) or at repeated intervals (iteroparity) is deeply embedded in life-history theory (Cole, 1954; Stearns, 1976; Giesel, 1976; Wilbur, 1980). Like fitness, iteroparity and semelparity are concepts that everyone seems to understand, but the terms are rarely defined quantitatively. Fritz et al. (1982) argue that the temporal pattern of egg maturation and deposition relative to generation time rather than calendar time is the appropriate basis for discriminating semelparity from iteroparity. Still, the problem comes from defining how explosively an organism has to produce its only batch of propagules to be considered truly semelparous. Kirkendall and Stenseth (1985) provide a test for semelparity, and, while this test places confidence limits on the definitions of semelparity and iteroparity, the definition remains a dichotomy. As recognized by Moeur and Istock (1980), intermediate states exist, and the concept of iteroparity is flexible and varies according to the relative allocation of reproduction throughout the life of an individual or population. An individual or population that lays most of its eggs initially and then fewer with declining age would appear less iteroparous than one laying the same total number of eggs in several uniform batches over the same period. In this paper, I treat iteroparity as a continuous variable apart from the dichotomy between iteroparity and semelparity, consider variation in the degree of iteroparity among geographic populations of a mosquito, and discuss the manner by which longevity, fecundity, and iteroparity combine to form a life-history tactic in this mosquito.

Geographical Ecology of Wyeomyia smithii *(Coq.)*

To examine the role of variable iteroparity in life-history evolution, I consider the mosquito, *Wyeomyia smithii* which completes its juvenile development within the leaves of the carnivorous purple pitcher plant, *Sarracenia purpurea* L. Resources for *W. smithii* consist of the decomposing prey captured by its host leaf. Availability of this resource limits the biomass of mosquitoes sustainable within the leaf and determines whether and how many of the larvae will pupate and leave the leaf (Bradshaw and Holzapfel, 1983, 1986). Prey-capture by the host leaf is not continuous throughout the lifetime of the leaf (six months to a year or more); rather, leaves capture the most prey at 2–4 weeks of age and prey capture declines exponentially thereafter (Bradshaw, 1983; Bradshaw and Holzapfel, 1983). Resources for *W. smithii* in the leaves of *S. pururea* are thus transitory and dependent upon the timing of leaf opening. Leaves are maximally attractive to ovipositing females immediately upon opening, and attractability then declines exponentially with age of the leaf. Oviposition behavior is thus keyed to the plant's growth in a way which

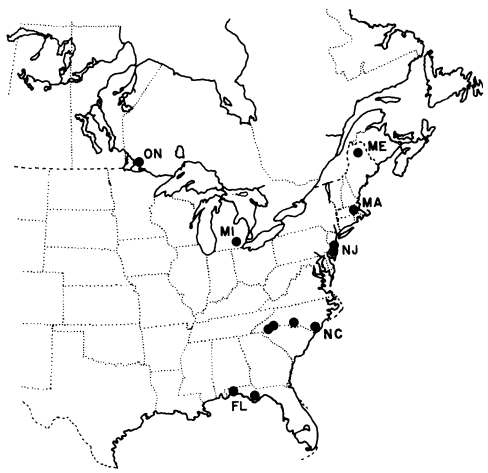

FIG. 1. Localities of origin of populations used in this study.

could allow the resulting larvae to develop at maximal resource influx.

At the southern end of its range, density of *W. smithii* (mosquitoes per unit prey captured by the host leaf) limits development and pupation success all year, including the winter while larvae are in diapause. Density-dependent constraints then abate with either increasing latitude or altitude (Bradshaw and Holzapfel, 1986). Along this latitudinal gradient, all populations are autogenous (do not require a blood meal for the first ovarian cycle). Populations from along the Gulf Coast or at low elevations in the Carolinas include females that will take a blood meal to mature the second and subsequent egg batches but are obligatorily autogenous for the first ovarian cycle. All populations from higher latitudes and altitudes produce repeated, small batches, but have never been known to bite (Bradshaw and Lounibos, 1977; Bradshaw and Holzapfel, 1983; Bradshaw, 1980; O'Meara and Lounibos, 1981; O'Meara et al., 1981).

An Index of Iteroparity, Ip

To quantify iteroparity, I have modified Kirkendall and Stenseth's (1985) $\theta_1 = \omega/\alpha$ where α and ω are the ages of first and last reproduction, respectively. θ_1 depends upon only two offspring, the first and the last, and ignores the number and timing of those in between. While the first offspring represents the maximal rate of propagule production achievable by a given individual or population under the circumstances, there is no similar significance ascribable to the last offspring produced. Instead of the last propagule, I use a weighted timing of propagule production so that when the bulk of reproduction follows α directly, the index of iteroparity (Ip) approaches 1 and when the bulk of reproduction is delayed, the index increases from 1:

$$\text{Ip} = (\Sigma\, xp_x)/\alpha \qquad (1)$$

where p_x is the proportion of total propagules produced by the individual or population at age x.

MATERIALS AND METHODS

I examined adult longevity, fecundity, and iteroparity at four densities among 12 populations representing six geographic zones of two localities each (Fig. 1): 30–31°N; 35°N, low elevation (10–150 m); 35°N, high elevation (900 m); 40°N; 42.5°N; and 46–49°N. I chose these zones so that I could compare the variation of life-history traits using two-way ANOVAs in which one factor was density and the other factor was geographic region of origin with two replicates from separate localities in each cell to assure independence of observations.

Stock Maintenance.—I collected all the populations used in this paper from the 1978–1979 overwintering generation. They have been maintained in the laboratory for 10 generations or fewer. I maintained stock colonies in larval diapause in a controlled temperature room at 21 ± 0.5°C on short days (L:D = 8:16) photoperiod with 30–50 larvae per 150 × 25 mm petri dish in distilled water. The stock colonies were fed (freeze-dried brine shrimp and guinea pig chow) and cleaned once per week. When I ran stocks through a generation to build up a population or to initiate an experiment, I always maintained the adult cage and collected eggs until all adults had died. I then thinned stocks or removed experimental animals so that a constant proportion was derived from each date of oviposition. In this way, I sought to maintain as much of the original variability within populations as possible.

Experimental Regimen.—My basic goal was to provide quasi-natural but highly con-

trolled conditions in the laboratory. Unless otherwise stated, I conducted all experiments in 15 ml distilled water added to leaves of intact pitcher plants in a 3 × 3 m controlled-temperature room. To approximate temperature conditions in nature (Bradshaw, 1980), I used a Love 105 program cam controller to impose a daily sine-wave thermoperiod from 12–28°C (mean = 21°C). I monitored temperatures within the room with recording thermistor probe thermometers and placed plants and adult cages around the periphery so as to avoid the effect of hot or cold spots within the room. To approximate the natural prey-capture of pitcher plants in nature (Bradshaw, 1983; Bradshaw and Holzapfel, 1984; Fish and Hall, 1978), I fed the *W. smithii* in each leaf 25 freeze-dried adults of *Drosophila melanogaster* on the day the larvae hatched and the experiment started. I then provided 100 more flies after one week, 50 more after two weeks, and 25 more after three weeks. Fungal mycelia would usually extend among flies on the water surface of leaves, especially at low mosquito densities. Consequently, after the addition of 100 flies, I examined the leaves three times per week and gently stirred the flies with a smooth glass paddle if visible mycelia were present.

I placed individual plants in polystyrene terraria (11 × 7 × 10.5 cm) 11 cm below two 48-W cool-white fluorescent lamps programmed for LD 17:7 photoperiod which led the thermoperiod by 3 hr. Three sets of plant lights plus two overhead 48-W cool-white fluorescent lamps provided bright "daytime." I approximated a transitory twilight with 0.5 hr of overhead lighting only, preceding and following the main photophase. This regimen provided unambiguously long days for all populations over the range studied (Bradshaw and Lounibos, 1977).

I placed pupae in 100 ml distilled water in plastic dessert dishes in adult cages located in the same room as the plants. Acrylic adult cages measured 30 × 20 × 20 cm and included: 1) a 10-cm access hole lined with surgical stockinette and covered by a hinged, latched acrylic door; 2) a recessed top, covered with an acrylic lid; 3) a 5-cm screened hole on the top for raisins; 4) a 0.3-cm hole in the center of the top for suspending mice within the cage; and 5) a 0.4-cm slot at the base of one side to insert and remove the liner. I lined the cage with two layers of 20 × 20 cm Whatman 3 MM chromatography paper. In addition, I covered the access slot with a 3 × 20 cm strip of chromatography paper bent at right angles. To maintain humidity inside the cages, I squirted distilled water on the paper liner and strip every 24–36 hr. During an experiment, I removed and replaced the paper strip and top liner three times per week. From the day of first adult eclosion until the last adult death, I provided one 15–60 ml (volume) freshly cut leaf of *S. purpurea* resting in a 70-ml squat glass jar filled with distilled water.

Experimental Procedures.—To start an experiment, I removed eggs daily from the leaf and jar, walls, pupal dish, and paper, washed them into distilled water in 150 mm petri dishes and maintained them in the thermoperiod room until hatching. On the day of hatch, I placed experimental cohorts into plant leaves and fed them according to the regimen given above. To produce similar-sized adult populations at each density, I used ten leaves at 10 larvae per leaf, five leaves at 20 larvae per leaf, four leaves at 40 larvae per leaf, and three or four leaves at 60 larvae per leaf. Starting 22–25 days after oviposition, I checked for and removed pupae three times per week with a teflon-tipped sabolt pipette. On the same days, I 1) scored adult ecdysis by counting the number of exuviae of each sex in the pupal dish; 2) removed and counted all eggs in the leaf and jar or on the walls and paper liner; and 3) removed, sexed, and counted all dead adults. I continued to census leaves for 90 days after oviposition; thereafter, I continued to monitor adult cages three times per week until all adults had died. These procedures permitted quantification of Ip from Equation (1) and longevity and fecundity defined as:

longevity = days from median eclosion to median death
fecundity = ln[(total number of eggs oviposited)/(total number of ecdysed females)]

To examine the effects of blood feeding, I conducted a separate series of experiments

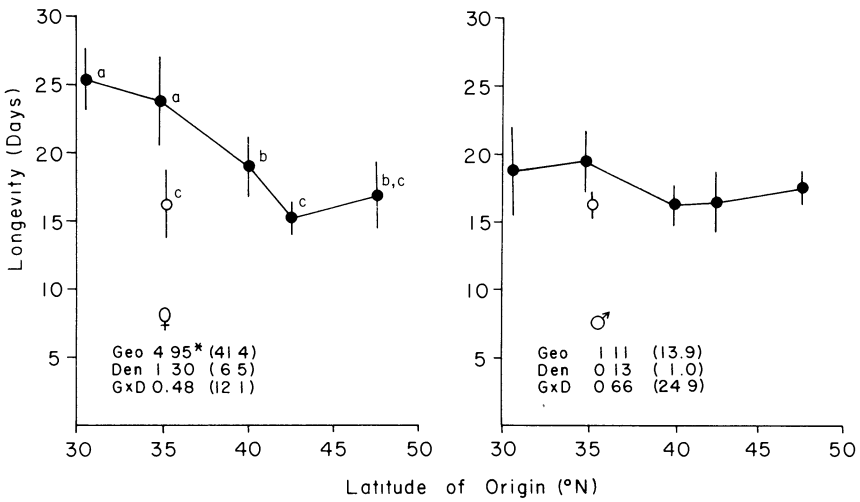

FIG. 2. Effects of geographic region and density on longevity of adult females and males. Solid circles represent the five low-elevation regions; open circles represent the higher-elevation region in North Carolina; lines connect means (±2 SE) along the latitudinal transect. The table in the lower left corner of each graph shows *F*-values for two-way ANOVA of longevity on geographic region (Geo) with *d.f.* (degrees of freedom) = [5, 24], density (Den) with *d.f.* = [3, 24], and their interaction (G × D) and *d.f.* = [15, 24]. Numbers in parentheses indicate percentage reduction in sums of squares. Means that share the same letter are not significantly different by Duncan's Multiple Range Test. All values of *F* are non-significant ($P > 0.05$) unless followed by *.

using only the four southernmost populations and provided them with a blood source three times per week from the day of first female ecdysis until the last death.

Preliminary tests consisting of holding an anesthethized mouse (*Mus musculis*) in my hand indicated that *W. smithii* are equally attracted to murine and human sources. I therefore offered blood-fed mosquitoes one anesthetized mouse for 20 min three times per week between the 12th and 15th hours of an 18-hr day to approximate the time of day (mid to late afternoon) I had been bitten by *W. smithii* in the field in north Florida. As an anesthetic, I used Innovar Vet which, as an opioid analgesic, maintained peripheral circulation and higher skin temperature than pentobarbital (Nembutal). I suspended anesthesized mice by their tails from the top of the cage in the zone of most active adult flight.

Density and Geography.—To examine the effects of density and geographic zone on adult longevity, fecundity, and iteroparity, I initiated cohorts of *W. smithii* at four densities for each of the 12 localities from which the original populations were sampled. I did not provide any opportunity for the resulting adults to take blood meals. I analyzed life-history traits by two-way ANOVAs using the two localities per geographic zone as replicates so that, in addition to main effects, I could test for density × geography interaction.

Blood Feeding.—To examine the response to opportunity for blood feeding, I initiated cohorts of *W. smithii* from the four southernmost localities (two from low elevation in North Carolina; two from north Florida) at four densities each and provided the resulting adults with opportunity to take blood meals throughout their adult life. I compared fecundity and iteroparity of these cohorts with cohorts from the same localities that had been denied an opportunity to blood-feed. Analysis consisted of two-way ANOVAs of 32 cohorts: 4 densities × 2 feeding treatments (blood, no blood) × 4 replicates (localities).

RESULTS

Density and Geography

Among males, the ANOVA did not reveal any significant effects on longevity attributable to density, geographic region, or their interaction (Fig. 2). Among females,

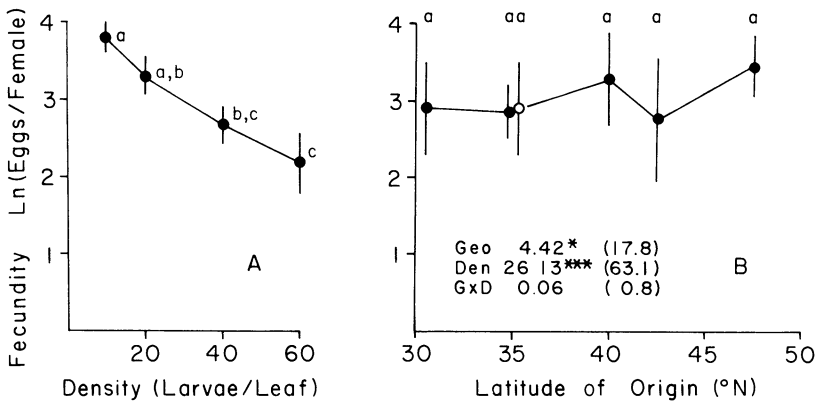

FIG. 3. Effects of A) density and B) geographic region on female fecundity. Solid circles represent the five low-elevation regions; open circles represent the high-elevation region in North Carolina. Lines connect means (± 2 SE) along the latitudinal transect. The table in the lower left corner of (B) shows *F*-values for two-way ANOVA of fecundity on geographic region (Geo), density (Den), and their interaction (G × D) with the same degrees of freedom as in Figure 2. Numbers in parentheses indicate percentage reduction in sum of squares. Means which share the same letter are not significantly different by Duncan's Multiple Range Test. Note that in (B) Duncan's Multiple Range Test failed to identify a significant difference between any two specific means even though an effect of geographic region is indicated by the ANOVA. All values of *F* are nonsignificant ($P > 0.05$) unless followed by * ($P < 0.05$) or *** ($P < 0.001$).

geographic region but not density or its interaction with geographic region affected longevity (Fig. 2). Adult females from the two southernmost regions lived longer than adults from more northern regions or higher elevations. Thus, geography-dependent adult longevity is a female-specific trait.

Autogenous fecundity in the absence of opportunity to take bloodmeals was significantly affected by geographic region and by density but not by their interaction (Fig. 3). Fecundity declined consistently with density (Fig. 3A), but Duncan's multiple range test failed to identify significant differences between any two geographic regions and mean fecundity did not exhibit any regular pattern with respect to latitude or altitude (Fig. 3B). Iteroparity averaged 1.26 and was unaffected by geographic region, density or their interaction (Table 1).

Blood-Feeding

When the four southern populations had opportunity to take blood meals, their fecundity was still affected by density but was not increased by opportunity to blood-feed (Fig. 4A). Iteroparity remained unaffected by density but increased significantly when females had opportunity to take blood meals (Fig. 4B). Female longevity was not affected by opportunity to take blood meals (Fig. 4C).

DISCUSSION

Longevity, fecundity, and iteroparity comprise a life-history tactic in *W. smithii.* Southern, biting females live longer than northern, nonbiting females, even in the absence of any opportunity to take blood meals. Southern females thus have greater potential temporal opportunity for reproductive effort than do northern females. When provided with a blood source, southern females capitalize upon this opportunity to increase facultatively the degree of iteroparity.

Evolution of *W. smithii,* based on geo-

TABLE 1. Effects of density and geographic region on autogenous iteroparity (Ip). RSS = percentage reduction in total sum of squares.

Source of variation	Sum of squares	*d.f.*	Mean square	*F*	RSS
Cells	0.3981	15	0.0259	1.71	51.6
Localities	0.0794	5	0.0159	1.05	10.5
Densities	0.1129	3	0.0376	2.48	15.0
Loc × Den	0.1968	15	0.0131	0.86	26.1
Residual	0.3645	24	0.0152		
Total	0.7535	47			

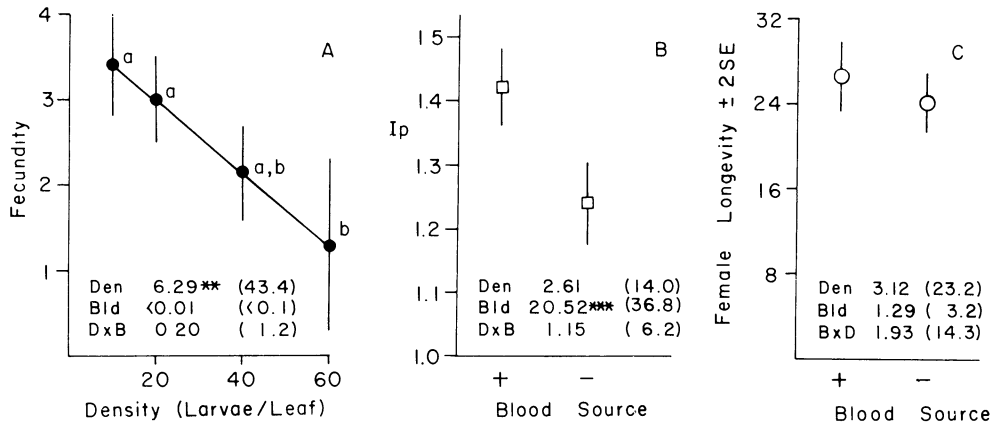

FIG. 4. Effects among southern females of density and opportunity to blood feed on A) fecundity = ln(eggs/female), B) iteroparity (Ip), and C) adult female longevity. Conventions and symbols as in Figure 2–3 except that in the ANOVA tables: density (Den) has *d.f.* = 3,24; opportunity to take a blood meal (Bld) has *d.f.* = 1,24; their interaction (D × B) has *d.f.* = 3,24; and, ** ($P < 0.01$).

graphic, morphological, and physiological characters (Bradshaw and Lounibos, 1977) has proceeded from south to north. The presence of blood-feeding females in southern but not northern populations is consistent with this conclusion. Thus, southern populations retain blood-feeding while northern populations, though possessing morphologically appropriate mouth parts (Hudson, 1970), have lost the trait. Concomitantly, female (but not male) longevity has declined.

Over geographic distances, *W. smithii* experience a latitudinal and altitudinal decline in the number of mosquitoes per unit prey captured by a host leaf; concomitantly, density-dependent age structure of the overwintering and vernal populations declines with increasing latitude or altitude (Bradshaw and Holzapfel, 1983, 1986).

In the south (30°N) over a year's time, pupation success averages 12%. Both the probability of a leaf's producing any pupae and pupation success in a leaf supporting pupation are inversely correlated with density (Bradshaw and Holzapfel, 1986). Mosquito larvae experience limiting density throughout the entire year. In the north (43°N), Istock et al. (1976) found that the biomass of larvae in pitcher-plant leaves was at or near saturation in the spring or fall but well below saturation levels during the summer. Thus, in the south there is a continual excess of adult fecundity above the carrying capacity of the environment for their offspring, while in the north, there are periods when collective adult survivorship and fecundity are not sufficient to saturate available resources. *W. smithii* females select and oviposit into the most recently opened leaves, regardless of the number of eggs already present (Bradshaw, 1983). It is only after the bulk of mosquito oviposition that the leaf catches its prey (Bradshaw, 1983; Bradshaw and Holzapfel, 1983; Fish and Hall, 1978). These prey constitute the resource base of the community and, consequently, determine the density per unit resource of mosquitoes in that leaf. Thus, despite seasonal components to density dependence in both the south (Bradshaw and Holzapfel, 1983) and the north (Istock et al., 1976), there is probably a large stochastic element in the degree of density-dependence among leaves. While very little is known about actual adult demography in nature, the above observations indicate that the impact of natural selection on larvae relative to adults declines with either latitude or altitude.

The decline in adult longevity and loss of facultative iteroparity in the derived northern populations is consistent with Istock's (1967) predictions that when the impact of selection is greater on the adult than the larval stage, "selection would favor reduction or loss of the adult phase." The retention and emphasis of facultative iteroparity

among southern populations is also consistent with strategies proposed for the exploitation of transient larval opportunities (Healy, 1974; Bell and Lawton, 1975; Wilbur, 1980; Albert, 1983) or the bet-hedging strategy of Stearns (1976). Yet, consistency with prevailing theory or with previous findings does not reveal the function that facultative iteroparity serves among the southern population of *W. smithii.*

Given the geographic pattern of density-dependent selection and local dynamics of prey capture by host leaves, blood-feeding could serve two functions within southern populations. Among several facultatively autogenous mosquitoes, adult blood-seeking behavior is inversely proportional to larval nutrition (Kardos, 1959; O'Meara and Krasnick, 1970; Lea, 1964). Facultative iteroparity in *W. smithii* might provide a means for larvae developing in nutritionally impoverished leaves to allocate all of their resources to development and rely upon blood-feeding for reproduction (Lounibos et al., 1982). Alternatively, females of this weak-flying species, because of facultative iteroparity, may be able to exploit new leaves as they first open (Bradshaw and Holzapfel, 1983; Bradshaw, 1980), thereby gaining the advantage of "being the first there" (Elton, 1958; Cole, 1983; Zwölfer, 1979; McLachlan and Cantrell, 1980; Livdahl, 1982). Two arguments now favor the latter interpretation. First, southern females "defer blood-feeding until after the initial autogenous clutch has been deposited" (O'Meara et al., 1981). *W. smithii* is therefore even less flexible than other facultatively autogenous species (including its congener, *W. vanduzeei* Dyar and Knab) which lay a reduced, autogenous batch after a frustrated search for a blood meal (Corbet, 1967; O'Meara, 1979). Second, opportunity to take a blood meal results in increased iteroparity but not increased female fecundity. At the same time, neither density nor its interaction with blood feeding affected iteroparity. Even if blood-feeding had increased fecundity, the lack of a significant interaction between blood-feeding and density (Fig. 4A) means that the effect of blood-feeding on fecundity is not density-dependent. The functional role of facultative iteroparity thus provides a means for females developing under predictably impoverished but irregularly opportunistic conditions to reallocate and temporally diversify their reproductive effort.

Acknowledgments

I thank Christina Holzapfel for many hours of enjoyable discussion and for reviewing the manuscript. I also thank anonymous reviewers for their careful consideration of this paper. Theodore Marks and, especially, Janet Battista devoted many consistent hours to the gathering and transcribing of data. I am grateful to the NSF for grants DEB78-22799 and DEB81-14953 which supported this research.

Literature Cited

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

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.

Bradshaw, W. E. 1980. Blood-feeding and capacity for increase in the pitcher-plant mosquito, *Wyeomyia smithii.* Env. Entomol. 9:86–89.

———. 1983. Interaction between the mosquito, *Wyeomyia smithii,* the midge, *Metriocnemus knabi,* and their carnivorous host, *Sarracenia purpurea,* pp. 161–189. *In* J. H. Frank and L. P. Lounibos (eds.), Phytotelmata: Terrestrial Plants as Hosts of Aquatic Insect Communities. Plexus, Medford, NJ.

Bradshaw, W. E., and C. M. Holzapfel. 1983. Life cycle strategies in *Wyeomyia smithii*: Seasonal and geographic adaptations, pp. 169–187. *In* V. K. Brown and I. Hodek (eds.), Diapause and Life Cycle Strategies in Insects. Junk, The Hague, Neth.

———. 1986. Geography of density-dependent selection in pitcher-plant mosquitos. *In* F. Taylor and R. Karban (eds.), The Evolution of Insect Life Cycles. Springer-Verlag, N.Y. *In press.*

Bradshaw, W. E., and L. P. Lounibos. 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. Evolution 31:546–567.

Cole, B. J. 1983. Assembly of mangrove ant communities: Patterns of geographical distribution. J. Anim. Ecol. 52:339–347.

Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103–137.

Corbet, P. S. 1967. Facultative autogeny in arctic mosquitoes. Nature 215:662–663.

Elton, C. 1958. The Ecology of Invasion by Animals and Plants. Methuen, London, U.K.

Fish, D., and D. W. Hall. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher-plant, *Sarracenia purpurea.* Amer. Midl. Natur. 99:172–183.

Fritz, R. S., N. E. Stamp, and T. G. Halverson. 1982. Iteroparity and semelparity in insects. Amer. Natur. 120:264–268.

GIESEL, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. Ann. Rev. Ecol. Syst. 7:57–79.

HEALY, W. R. 1974. Population consequences of alternative life histories in *Notophthalamus v. viridescens.* Copeia 1974:221–229.

HUDSON, A. 1970. Notes on the piercing mouthparts of three species of mosquitoes (Diptera: Culicidae) viewed with the scanning electron microscope. Can. Entomol. 102:501–509.

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. 1976. Ecology and evolution of the pitcher-plant mosquito. 3. Resource tracking by a natural population. Evolution 30:548–557.

KARDOS, E. H. 1959. The effects of larval nutritional level on development of autogeny in colony *Culex tarsalis* Coq. Proc. Calif. Mosq. Contr. Assoc. 27: 71–72.

KIRKENDALL, L. R., AND N. C. STENSETH. 1985. On defining "breeding once." Amer. Natur. 125:189–204.

LEA, A. O. 1964. Studies on the dietary and endocrine regulation of autogenous reproduction in *Aedes taeniorhynchus* (Wied.). J. Med. Entomol. 1:40–44.

LIVDAHL, T. P. 1982. Competition within and between hatching cohorts of a treehole mosquito. Ecology 63:1751–1760.

LOUNIBOS, L. P., C. VAN DOVER, AND G. F. O'MEARA. 1982. Fecundity, autogeny, and the larval environment of the pitcher-plant mosquito, *Wyeomyia smithii.* Oecologia 55:160–164.

MCLACHLAN, A. J., AND M. A. CANTRELL. 1980. Survival strategies in tropical rain pools. Oecologia 47: 344–351.

MOEUR, J. E., AND C. A. ISTOCK. 1980. Ecology and evolution of the pitcher-plant mosquito IV. Larval influence over adult reproductive performance and longevity. J. Anim. Ecol. 49:775–792.

O'MEARA, G. F. 1979. Variable expression of autogeny in three mosquito species. Int. J. Invert. Repr. 1:253–261.

O'MEARA, G. F., AND G. J. KRASNICK. 1970. Dietary and genetic control of the expression of autogenous reproduction in *Aedes atropalpus* (Coq.) (Diptera: Culicidae). J. Med. Entomol. 7:328–334.

O'MEARA, G. F., AND L. P. LOUNIBOS. 1981. Reproductive maturation in the pitcher-plant mosquito, *Wyeomyia smithii.* Physiol. Entomol. 6:437–444.

O'MEARA, G. F., L. P. LOUNIBOS, AND R. A. BRUST. 1981. Repeated egg clutches without blood in the pitcher-plant mosquito. Ann. Entomol. Soc. Amer. 74:68–72.

ZWÖLFER, H. 1979. Strategies and counter-strategies in insect population systems competing for space and food in flower heads and plant galls. Fortschr. Zool. 25:331–354.

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