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GEOGRAPHIC VARIATION AND THE EVOLUTION OF REPRODUCTIVE ALLOCATION IN THE PITCHER-PLANT MOSQUITO, *WYEOMYIA SMITHII*

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Abstract.—We measured the egg size of six geographic populations of the pitcher-plant mosquito, *Wyeomyia smithii,* from Florida (30°N) to Ontario (49°N). Populations from northern latitudes produced larger eggs than populations from southern latitudes. Egg size increased with increasing latitude more rapidly when larvae were reared under low rather than high density. One southern (30°N) and one northern (49°N) population of *W. smithii* that persisted through 10 generations of selection for increased persistence under conditions of chronic thermal- and nutrient-limiting stress (conditions similar to southern rather than northern habitats) produced smaller eggs more rapidly than unselected control lines. However, there were no differences in lifetime fecundity or fertility between control and selected lines. Thus, laboratory evolution in an environment representative of extreme southern latitudes caused evolutionary changes consistent with geographic patterns of egg size. These results implicate temperature as a selective factor influencing the geographic variation of egg size in *W. smithii,* and demonstrate a novel trade-off in reproductive allocation between egg size and egg maturation time.

Key words.—Egg size, life-history trade-offs, reproductive allocation, thermal selection, *Wyeomyia smithii.*

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Reproductive success is a fundamental component of Darwinian fitness. Reproductive success is itself comprised of several components, including propagule size, propagule number, propagule viability, and rate of propagule production. Because of functional and genetic constraints, it is not possible to maximize simultaneously all of these components of reproductive success. The optimal allocation of resources among these components then involves adaptive compromises or trade-offs among them (Williams 1966; Roff 1992; Stearns 1976, 1992). (*) The most frequently studied trade-offs are those between the number and size of propagules (Salisbury 1942; Cody 1966; Smith and Fretwell 1974; Wilbur 1977; Sinervo and Licht 1991; Hard and Bradshaw 1993; Schwarzkopf et al. 1999; Fox and Czesak 2000) and between the number and rate of propagule production (Ricklefs 1968; Harvey 1977; Montague et al. 1981; Dingle 1986; Wicklund et al. 1987; Charnov and Skinner 1988; Solbreck et al. 1990), with the underlying assumption that larger propagules result in higher individual offspring fitness than smaller propagules (Smith and Fretwell 1974; Sibly and Calow 1983; Hawley 1985; Parker and Begon 1986; Godfray 1987; McGinley et al. 1987; Fleming and Gross 1990; Bernardo 1996; Fox and Czesak 2000). Phenotypic trade-offs in reproductive allocation are widespread (Reznick 1985); but hypotheses attempting to explain the evolution of reproductive allocation must be considered at the genetic rather than the phenotypic level (Partridge and Harvey 1985; Reznick 1985, 1992; Bell and Koufopanou 1986; Willis et al. 1991).

The observation of repeatable geographic clines provides strong inference for natural selection acting on a trait (Levins 1968; Endler 1986). The consistent increases in egg size as a function of latitude or altitude both on different continents within the same species (*Drosophila melanogaster*: Azevedo et al. 1996) and across taxonomic groups ranging from frogs (Berven 1982) to insects (Clarke et al. 1991; Blackenhorn and Fairbairn 1995; Azevedo et al. 1996) suggests that climatic variation along latitudinal or altitudinal gradients provides a general selective force influencing the evolution of egg size. However, Gould and Lewontin (1979) and Huey and Berrigan (1996) provide cogent discussions of the perils of making this type of assumption without corroborating evidence.

Herein, we consider potential evolutionary trade-offs in reproductive allocation of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.). We first show that there is genetic variation in egg size among populations over a range of 19° of latitude in eastern North America. We then seek the corroborating evidence linking geographic variation in egg size to selection by asking if exposure to high temperature and low food, which represent an extreme southern environment for *W. smithii* in nature, results in an evolutionary shift of reproductive allocation toward the southern pattern. Together, these findings implicate temperature as a selective force maintaining a latitudinal gradient in egg size and indicate a novel trade-off between egg size and rate of egg maturation in *W. smithii.*

Materials and Methods

Wyeomyia smithii

Adult *W. smithii* lay their eggs exclusively within the water-filled leaves of the carnivorous purple pitcher plant, *Sarracenia purpurea* L. Within these leaves, developing larvae utilize decomposing prey as a food source. The geographical distribution of *W. smithii* follows that of *S. purpurea* from

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* Reproductive effort, or reproductive investment, is the amount of total resources committed to reproduction; reproductive allocation is how reproductive effort is divided up among the various components of reproduction; egg size refers strictly to the size of progeny produced as eggs (as opposed to progeny produced as seeds or by live birth).

the Gulf of Mexico north to Labrador and west to Saskatchewan. Southern larvae experience severe density-dependent constraints to development, and these constraints abate with increasing latitude as the per capita availability of resources increases (Bradshaw 1983; Bradshaw and Holzapfel 1986). Consequently, the food supply of *W. smithii* ranges from limiting at warmer southern latitudes to adequate at cooler northern latitudes.

Latitudinal Variation in Egg Size

For all experiments described below, approximately 2000 larvae were collected from pitcher plants at each geographical locality during early spring when 100% of the population was available for sampling as larvae (Bradshaw and Holzapfel 1996; Armbruster et al. 1999). Details of the collection and maintenance of lines used to examine latitudinal variation in egg size can be found in Hard et al. (1993). Briefly, six populations (corresponding to localities WI, CR, GS, FV, KC, and DL in earlier publications from this lab) were collected from 30°N to 49°N and maintained under near-optimal laboratory conditions for 17 generations. Each generation consisted of an effective population size ($1/N_e = 1/4N♂ + 1/4N♀$) of at least 91 adult mosquitoes.

Five cohorts of 20 or 40 larvae each per population in the F_{17} laboratory generation were grown in intact pitcher-plant leaves under near-optimal midsummer conditions of a long-day photoperiod (L:D = 18:6), a warm : cool = 29:13°C (mean = 21°C) smooth, sine-wave thermoperiod, and 80% relative humidity. Developing larvae were fed 200 freeze-dried *Drosophila melanogaster* (Miegen) over 21 days. Pupae were collected every Monday, Wednesday, and Friday; sexed; pooled across cohorts within populations; and transferred to 12-L acrylic adult cages (one adult cage per population) provisioned with a freshly cut leaf of *S. purpurea* to stimulate oviposition and pesticide-free raisins for adult nutrition. Eggs were removed from the adult cages every Monday, Wednesday, and Friday and floated on distilled water. The length (L) and width (W) of 100 haphazardly chosen eggs from each population at each density were measured to the nearest 0.01 mm using an ocular micrometer mounted on a dissecting microscope at a magnification of 45×. The size of each egg was then calculated as the volume (V) of a prolate spheroid (Berrigan 1991; Bradshaw et al. 1993):

$$V = \pi L W^2/6. \quad (1)$$

Egg sizes were approximately normally distributed, and thus no transformations were applied to these data. To examine the effects of latitude and larval density on egg size, we performed ANCOVA (Type III sums of squares in Proc GLM; SAS Institute 1985) to test for the effects of latitude as a covariate, larval density (20 or 40) as a fixed effect, and latitude-by-density interaction (each with df = 1, 8).

Evolution of Reproductive Allocation

Details of the experimental procedures used to examine the evolution of life-history traits under conditions of chronic thermal- and nutrient-limiting stress have been provided in an earlier paper (Armbruster et al. 1999). Briefly, larvae from two southern populations (30°N in Alabama and Florida; localities LI and WI, respectively) and two northern populations (46°N and 49°N in Maine and Ontario; localities KC and DL, respectively) were reared through four generations of laboratory maintenance and were then subjected to 10 generations of truncation selection for rapid development under conditions of chronic thermal- and nutrient-limiting stress. Early-pupating larvae tend to be phenotypically larger and therefore emerge as more fecund adults (Bradshaw and Holzapfel 1992) than later-developing larvae, and there is no genetic trade-off between development time and either survivorship or fecundity under near-optimal conditions (Bradshaw and Holzapfel 1996). Consequently, lines selected for fast development achieve higher fitness (r_c) than lines selected for slow development (Bradshaw and Holzapfel 1996). Therefore, we assume that selection for faster development in the present experiment is tantamount to selection for higher fitness.

The stressful conditions were designed to impose ecologically realistic (Bradshaw et al. 2000), broad physiological stress near the threshold of population persistence over the entire life cycle. Temperature consisted of a warm : cool = 35:18°C (mean = 27°C) smooth, sine-wave thermoperiod that averaged 6°C warmer than the near-optimal conditions. Humidity varied as a high : low = 80:60% smooth, sine-wave cycle where the daily low humidity occurred at peak temperature. Developing larvae were provided with a diet of five freeze-dried *D. melanogaster* per larva over 21 days, which was one-half of the near-optimal food ration. These stressful conditions caused an approximately 50% reduction in fitness (r_c) relative to near-optimal conditions and caused two of the four populations (one northern, one southern) to die off during the course of 10 generations of selection (Armbruster et al. 1999). Herein, we consider the two persisting populations from Alabama (AL) and Maine (ME).

Control lines were maintained as diapausing larvae on an unambiguous short day (L:D = 8:16) at constant 21 ± 0.5°C. Every 4 months, they were transferred to long days (L:D = 18:6) and reared to adulthood under near-optimal conditions of temperature (warm : cool = 29:13°C thermoperiod) and constant 80% relative humidity with abundant food provided ad libidum. The next generation was reared on the same short-day regimen to induce and maintain diapause. During the course of the selection experiment, the control lines completed four cycles (generations) of diapause and development. Fitness (r_c) in the control lines did not differ before and after these four generations. Therefore, the control lines provide an appropriate standard against which to judge the effects of selection in the selected lines (Armbruster et al. 1999).

After selection, both selected and control lines were run through three generations on long days (L:D = 18:6) at constant 21°C with near-optimal food rations to control for parental, grandparental, and great-grandparental effects (Crill et al. 1996). We then measured the size (eq. 1) of 125 haphazardly chosen eggs each from the selected and control lines of both the AL and ME populations (500 total eggs).

To determine egg maturation time, fecundity, and fertility in the control and selected lines, five cohorts of 40 larvae each from each population (20 total cohorts) were established in individual, intact pitcher-plant leaves under the same stressful conditions as were imposed during selection. In-

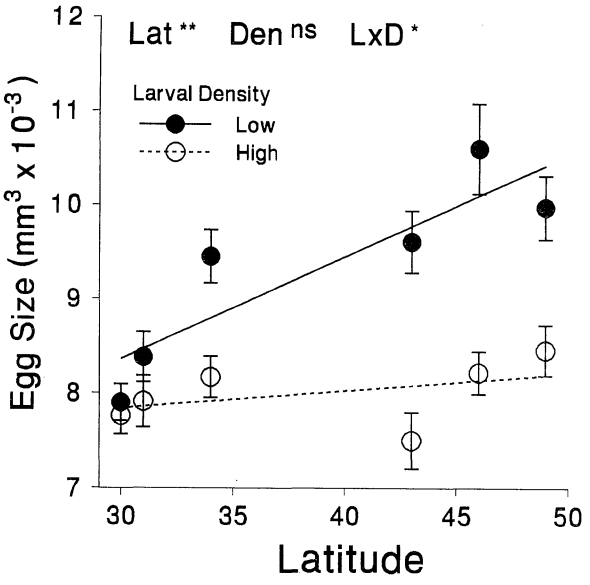

FIG. 1. Effect of latitude of population origin and rearing density (closed circle, 20 larvae/leaf; open circle, 40 larvae/leaf) on mean egg size (±2 SE) of *Wyeomyia smithii.* Results of ANCOVA: effects of latitude of origin ($P < 0.01$), larval density (ns), latitude-by-density interaction ($P < 0.05$).

dividual leaves were checked for pupal development and pupae were removed every Monday, Wednesday, and Friday to a dish of distilled water in 0.95-L, single-cohort adult cages. The adult cages were provided with pesticide-free raisins for adult nutrition and a freshly cut leaf of *S. purpurea* for oviposition. Adult mosquitoes were allowed to eclose, mate, and lay eggs. Eggs, pupal exuviae, and dead adults were collected and their numbers recorded every Monday, Wednesday, and Friday. The number of larvae hatching from each collection of eggs was recorded. Fecundity was measured as the total eggs produced per adult female eclosing into the cage, fertility as the percentage of the total eggs that hatched, and egg maturation time as the interval from mean adult female eclosion to oviposition of the mean egg. Egg maturation time therefore refers to the rate of oogenesis achieved by the adult female mosquito.

Egg sizes and maturation times were approximately normally distributed, and thus no transformations were applied to these data. Fecundities were subjected to a $\log_{10}$ transformation. Fertilities (proportions) were arcsine-square-root transformed. In both cases, the transformations improved the fit of the data to a normal distribution. We performed two-way ANOVAs using S-Plus version 4.5 (Mathsoft 1997). To examine the effects of selection on egg size, we tested for effects of selection (SEL, CON), population (AL, ME), and selection-by-population interaction (all with df = 1, 496). To examine the effects of selection on egg maturation time, fecundity, and fertility, we tested for effects of selection (SEL, CON), population (AL, ME), and selection-by-population interaction (all with df = 1, 16).

RESULTS

Mean egg size (Fig. 1) was positively correlated with latitude of population origin ($F_{1,8} = 13.39$, $P = 0.006$). The regression of egg size on latitude was steeper for populations having been reared at 20 than at 40 larvae per leaf ($F_{1,8} = 6.74$, $P = 0.032$), but there was no significant main treatment effect of density ($F_{1,8} = 2.53$, $P = 0.150$). These results show that egg size varied across latitudes and showed plastic responses to larval density.

After 10 generations of selection, egg sizes (Fig. 2a) were larger in the northern than southern population ($F_{1,16} = 128.64$, $P < 0.001$), were smaller in the selected than control lines ($F_{1,16} = 73.98$, $P < 0.001$), and the effect of selection was greater in the northern than southern population ($F_{1,16} = 7.18$, $P = 0.008$). Egg maturation time (Fig. 2b) did not differ between the northern and southern population ($F_{1,16} = 1.64$, $P = 0.22$), but was shorter in the selected than control lines ($F_{1,16} = 7.24$, $P = 0.02$), regardless of population ($F_{1,16} = 0.62$, $P = 0.44$). Fecundity (Fig. 2c) did not differ between the northern and southern population ($F_{1,16} = 0.64$, $P = 0.44$) or between selected lines ($F_{1,16} = 0.03$, $P = 0.87$), regardless of population ($F_{1,16} = 0.05$, $P = 0.82$). Similarly, fertility (Fig. 2d) did not differ between the northern and southern population ($F_{1,16} = 1.67$, $P = 0.21$) and did not differ between selected lines ($F_{1,16} = 2.11$, $P = 0.17$), regardless of population ($F_{1,16} = 0.55$, $P = 0.47$). These results show that 10 generations of selection at high temperature and low food caused a reduction in egg size, a decrease in egg maturation time, and had no effect on fecundity or fertility in selected lines relative to the control lines.

DISCUSSION

In *W. smithii,* egg size increases with increasing latitude of population origin (Fig. 1), implying that natural selection, presumably temperature, has influenced this trait's evolution over the climatic gradient of eastern North America. This implication is reinforced by the evolution of smaller egg size (Fig. 2a) after 10 generations of chronic exposure to high temperature and low food (conditions more similar to southern than northern habitats). In our experiments, we imposed low food concurrently with high temperature. There is no evidence for a trade-off between performance at high and low densities either within (Bradshaw and Holzapfel 1996) or among (Bradshaw and Holzapfel 1989) populations of *W. smithii.* Consequently, we assumed that the combined conditions of low food and high temperature during our selection experiment imposed primarily heat stress on developing and adult mosquitoes.

Low per capita food encountered during preadult development results in smaller egg size than high per capita food (Fig. 1). Thus, phenotypically plastic responses of egg size to density in the laboratory reflect evolved differences in egg size among populations over a latitudinal density gradient in nature and during 10 generations of selection under thermal- and nutrient-limiting stress in the laboratory.

Most models of evolution involving propagule size consider the critical trade-offs to occur between the number and rate of propagule production (see introduction) or between propagule number and propagule size (or some component of offspring performance related to propagule size; Harvey 1977; Capinera 1979; Kaplan 1980; Reznick 1981, 1982; Travis 1981, 1983, 1984; Parker and Begon 1986; Nakasuji

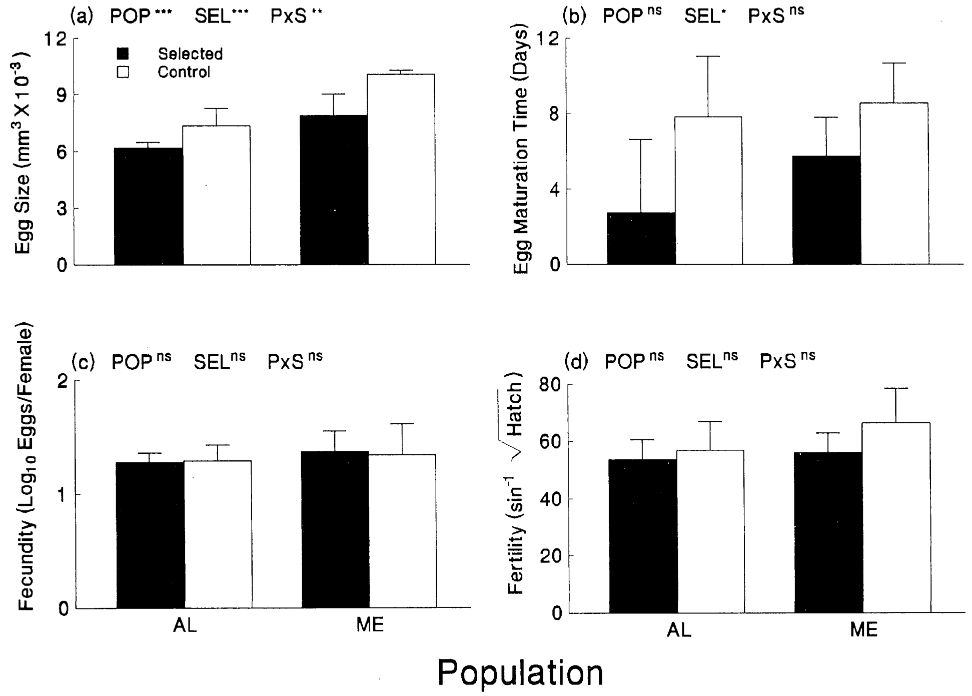

FIG. 2. Reproductive allocation to (a) egg size, (b) egg maturation time, (c) fecundity, and (d) fertility of *Wyeomyia smithii* in populations from Alabama (AL) and Maine (ME). Selected lines (closed square) persisted through 10 generations of chronic heat stress and low food; control lines (open square) were maintained under near optimal conditions (see text). Bars represent means (±2 SE). Results of ANOVA given at the top of each plot indicate effects of population (POP), selection (SEL), and population-by-selection interaction (P × S). $^{\mathrm{ns}}P > 0.05$, $^{*}P < 0.05$, $^{***}P < 0.001$.

1987; Wicklund et al. 1987; Solbreck et al. 1990; Roff 1992; Fox and Czesak 2000). Theory predicts that as environmental quality deteriorates, selection should favor investment in larger progeny that presumably have greater ability to survive, grow, and develop in harsh environments (Fox and Czesak 2000). In contrast, in *W. smithii* selection has resulted in populations that produce smaller eggs in harsher southern latitudes (Fig. 1), where temperatures are higher and resources scarcer than at northern latitudes, and in selected rather than control lines having persisted through 10 generations of chronic heat stress and high larval densities (Fig. 2a).

Several authors have suggested that aspects of maternal performance such as locomotor activity (Berrigan 1991) or foraging efficiency (Bernardo 1996) might trade off with propagule size and therefore constrain its evolution. In *W. smithii,* there are no indications that under conditions of chronic thermal and food stress egg size (Fig. 2a) or egg maturation time (Fig. 2b) trades off with fecundity (Fig. 2c), with fertility (Fig. 2d), or with other components of fitness that include preadult survivorship or development time (Armbruster et al. 1999). The trade-off we did observe between egg size (Fig. 2a) and egg maturation time (Fig. 2b) is the first of which we are aware demonstrating an evolutionary trade-off between propagule size (Fig. 2a) and rate of propagule production (Fig. 2b). Our results provide a new and different example of maternal performance as a factor constraining the evolution of egg size.

Several studies have demonstrated evolutionary changes in egg size as a correlated response to direct selection on other traits. Correlated increases in egg size have been observed after direct selection for egg desiccation-resistance in the mosquito *Aedes albopictus* (Sota 1993) or for fast larval development in *D. melanogaster* (Bakker 1969). The decline in egg size after chronic exposure to thermal- and nutrient-limiting stress (Fig. 2a) may also be a correlated response. Adult *W. smithii* are able to fly and therefore can thermoregulate behaviorally, unlike the larvae, which are captive within the water-filled pitcher-plant leaves. Identical thermal conditions imposed on adults and larvae during selection could have been more stressful and imposed a stronger selection differential on the normally mobile adults than on the effectively sedentary larvae. Faster egg maturation by the adults having persisted through 10 generations of chronic heat stress may then be the direct response that effectively reduces the more hazardous adult stage of a complex life cycle (Istock 1967), with reduced egg size its correlated response.

Our results bear a striking resemblance to those of Azevedo et al. (1996), who documented (1) an increase in egg size with latitude of population origin in *D. melanogaster* from South America and Australia; (2) parallel evolutionary changes in egg size in replicated lines of *D. melanogaster* maintained in the laboratory at 16.5°C and 25°C; and (3) no evidence for a trade-off between egg size and fecundity in their laboratory-selected lines. Azevedo et al. (1996) did not test for the selective effect of the thermal environment on egg maturation time. As in *W. smithii,* the evolutionary changes in egg size of *D. melanogaster* in response to temperature in the laboratory clearly implicate temperature as a selective factor affecting the evolution of egg size over latitudinal (temperature) gradients, but do not necessarily establish egg size as the direct target of that selection. In both species, the evolution of egg size may be the correlated response to direct selection on another component of reproductive allocation.

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