Protandry in Aedes Sierrensis: The Significance of Temporal Variation in Female Fecundity

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PROTANDRY IN *AEDES SIERRENSIS*: THE SIGNIFICANCE OF TEMPORAL VARIATION IN FEMALE FECUNDITY[1]

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Abstract. Protandry, the early emergence of males into a seasonally breeding population, has been described mathematically as a mating strategy resulting from sexual selection on both sexes. A key implicit assumption in protandry models is that all matings contribute equally to a male's reproductive success. We build a simulation model of protandry based on field censuses and investigate the consequences of size-specific temporal variation in female fecundity for the optimal timing of protandry in the western treehole mosquito, *Aedes sierrensis*. We show that theoretical predictions of protandry are robust when differential female fecundity is incorporated into a model of protandry in *A. sierrensis*. In addition, we utilize field data and laboratory experiments to elucidate the selective forces acting on both sexes of this mosquito. Under conditions of reduced per capita resources, males minimized development time by pupating at lower mass; females maximized mass by delaying pupation. These gender-specific, homeostatic adjustments to food and density, which result in density-dependent protandry, indicate that protandry is the result of selection on independent fitness criteria in each sex.

Key words: Aedes sierrensis; fecundity; homeostasis; mosquito; protandry; reproductive success; tradeoffs; treehole.

INTRODUCTION

Protandry, the emergence of males before females into a seasonally breeding population, is a characteristic observed in many insects and other arthropods. Protandry has also been reported for some mammal populations that have restricted breeding seasons, such as mountain hares (Iason 1989), and ground squirrels (Michener 1983). Both Darwin (1871) and Wallace (1889) discussed the early seasonal appearance of male insects as an example of sexual selection due to increased mating opportunity of early emerging males. More recently, mathematical models of protandry have been developed that describe protandry as either a male mating strategy to maximize the number of matings (Wiklund and Fagerström 1977, Bulmer 1983, Iwasa et al. 1983, Parker and Courtney 1983) or a mating strategy of both sexes where females are under selective pressure to minimize the pre-reproductive period (Scott 1977, Fagerström and Wiklund 1982, Zonneveld and Metz 1991). Several authors provide evidence that protandry is not an incidental side effect of some other process; rather, protandry stems from sexual selection acting on both sexes (Singer 1982, Wiklund and Solbreck 1982, Wiklund et al. 1991, Nylin et al. 1993).

Although there are differences in mathematical treatment among protandry models, they all share several

major explicit assumptions: a genetic component to emergence time, female monogamy (or an advantage to mating with virgin females), the ability of males to mate with >1 female, and a discrete rather than continuous breeding season, or at least non-overlapping generations. In addition, a key implicit assumption in protandry models is that all matings contribute equally to a male's reproductive success. Singer (1971) noted that in the butterfly *Euphydryas editha,* females emerging early in the season have a higher reproductive value than females emerging later. Baughman et al. (1988) note that reproductive equality of all matings is unlikely to be a valid assumption. Still, this assumption has received relatively little investigation. Botterweg (1982), in a simulation model of protandry in the pine looper, included a factor to weight the success of each mating based on the age of the copulating moths; but, he found that the age of moths had no effect on the degree of stable protandry predicted by his model. In a theoretical model of protandry in butterflies, Zonneveld (1992) derived a weighting factor that took into account the decline in oviposition rate with age of the female. The qualitative results of his model led him to conclude that matings early in the flight season were more important than later ones.

We propose an additional factor to consider in models of protandry, that is, size-specific differential female fecundity. In many insects female fecundity is directly correlated with size at emergence (Lederhouse et al. 1982, Hawley 1985a, Bradshaw and Holzapfel 1992). Hawley (1985b) found that in field populations of the western treehole mosquito, *Aedes sierrensis* Lud-

low, both female fecundity and female survivorship increased with female size. Consequently, a sixfold variation in female size found in nature translates into a 30-fold variation in expected lifetime fecundity. Thus the simple abundance of females does not accurately reflect their value as a resource to males. Since *A. sierrensis* does not meet the implicit assumption of reproductive equality of females, the temporal mass-specific variation in female fecundity must be included in a model of protandry for this species. We agree that protandry is maintained by selection acting on both sexes, however, we propose that mosquito females are under selective pressure to maximize reproductive potential (size) rather than to minimize pre-reproductive time.

Herein, we build a simulation model of protandry based on field censuses and investigate the consequences of differential female fecundity on the optimal timing of protandry in *Aedes sierrensis*. In addition, we utilize field data and laboratory experiments to elucidate the selective forces acting on both sexes of this mosquito.

Aedes sierrensis occurs on the west coast of North America from southern California to British Columbia (Darsie and Ward 1981). The mediterranean climate in this region is characterized by mild, wet winters and hot, dry summers (Steinhauser 1979). *Aedes sierrensis* females lay eggs on treehole walls during the late spring and summer. When the treeholes fill with the autumn rains, the eggs hatch and larval development continues throughout the winter. Pupation begins in April and continues until treeholes dry up in early summer. Adult activity occurs from May to September (Hawley 1985b). Individuals of *Aedes sierrensis* enter a long-day induced aestival, embryonic diapause (Jordan 1980) and a short-day induced hibernal, larval diapause (Jordan and Bradshaw 1978); consequently, they are univoltine. Since mosquito females are monogamous and males are capable of multiple matings (Clements 1963), *A. sierrensis* is an appropriate species for testing the assumptions of protandry models.

MATERIALS AND METHODS

Protandry and female fecundity in nature

Treeholes in Alton Baker Park (44°03′ N; 123°04′ W; elevation 130 m), Eugene, Oregon were censused each year (1981–1983) beginning in autumn after the first heavy rainfall and continuing until pupal production stopped (as in Hawley 1985b). Censuses included measurement of water temperature and volume, and counting of immatures by stage. After determining the sex of all pupae, randomly selected live pupae were individually weighed to the nearest 0.1 mg after blotting on a paper towel. All individuals up to a maximum of 12 female pupae (1981) or 20 pupae of each sex (1982–1983) were weighed each census. Larval density for each treehole was calculated as the total number of

first instars to appear divided by the maximum observed treehole water volume for the season.

In addition, in 1983, adults were sampled daily at human bait from their first appearance in spring until their disappearance in the late summer. Since males of this species exhibit host attendance, both sexes were sampled. Wing length of each individual of both sexes was measured with an ocular micrometer to the nearest 0.05 mm. Females were frozen, then dissected within 3 d to determine parity by examination of ovarian tracheation (Hawley 1985b).

Protandry optimum

Our simulation model is based on that of Wiklund and Fagerström (1977) for organisms with monogamous females and discrete generations. Their theoretical model (1977) assumes that selection acts on the mean of the male emergence curve to produce an optimal degree of protandry where the maximum of the male fitness curve coincides with that of the male emergence curve. If protandrous males leave more offspring, then protandry would be expected to evolve through natural selection.

The Wiklund-Fagerström model makes the explicit assumptions that: (i) Eclosion time curves of males and females have a genetic basis; (ii) All females mate, only once, on the day of eclosion; (iii) Male mortality is constant and age-independent; (iv) Males can mate with more than one female; and (v) Mating occurs as an encounter probability. Wiklund and Fagerström (1977) argue that assumptions (i)–(v) are empirically justified for many species exhibiting protandry. Indeed, most of the assumptions hold for *Aedes sierrensis* populations. However, the model also contains the implicit assumption that all females are reproductively equal.

Stella software (High Performance Systems 1985) was used to build our simulation model. Due to the difficulty in handling a large number of cohorts with this dynamic modeling package, we tracked mosquitoes in cohorts corresponding to emergence over 3.75-d intervals (or eight time intervals per month) rather than tracking daily emergence cohorts. Protandry is calculated as the difference in median emergence date between males and females.

Our protandry model equates male fitness to the total lifetime number of offspring sired. Fitness is a function of a male's emergence time and the degree of protandry in the population. It is calculated as an encounter ratio based on the number of males and females alive at a given time. Field census data of *Aedes sierrensis* pupae and adults were used to generate emergence curves for 22 male cohorts and 32–36 female cohorts corresponding to consecutive 3.75-d intervals of adult emergence over the entire flight season. Our model generates the male fitness landscape for the flight season over a range of protandry using field-derived parameters for male mortality and female expected lifetime fecundity.

The fitness of an adult male emerging in male cohort

x of the flight season is given by (Wiklund and Fagerström 1977):

$$\text{fitness}_x = \sum_{t=1}^{45} \frac{(\text{cohort } x_t \cdot \text{offspring}_t) \div \text{total males}_t}{\text{initial size of cohort } x}, \quad (1)$$

where cohort x is all males emerging in the xth consecutive 3.75-d interval and cohort x_t is the number of males emerged in cohort x that are still alive at time t, given by:

$$\text{cohort } x_t = (\text{initial size of cohort } x)e^{-\lambda(t-t_1)},$$

$$t \geq t_1, \quad \text{and} \quad (2)$$

where λ is the constant age-independent male death rate. Total males$_t$ is the total number of males alive at time t given by:

$$\text{total males}_t = \sum_{x=1}^{22} \text{cohort } x_t, \quad (3)$$

and offspring$_t$ is the number of future offspring available to be sired by males, based on the number and size of females emerged at time t.

Variable resources

We conducted laboratory experiments to examine the combined effects of food and density on pupal mass, development time, and protandry in *Aedes sierrensis*. The experiments in this study all employ natural treehole sediment as a food source.

Water and sediment were collected in the fall of 1986 from a single 120-L rot-hole (as defined by Kitching 1971) in a large-leaf maple (*Acer macrophyllum* Pursch) in Alton Baker Park, Eugene, Oregon (treehole 1 of Fisher et al. 1990 and Hawley 1985b). This substrate was separated into leaf litter, coarse sediment, and fine sediment/soluble material as in Fisher et al. (1990). These components were dried and the empirical ratio of leaf : coarse : fine fractions was determined as 1:5:1. This ratio was used when setting up experiments. Leaves were torn into roughly 4-cm² pieces to make a more uniform litter layer in the experimental containers. All experiments were run in clear plastic dessert dishes that contained the appropriate aliquot of rehydrated dried treehole sediment as in Fisher et al. (1990). We did not add stemflow (Carpenter 1982) to the natural treehole sediment in this experiment for the reasons discussed in Fisher et al. (1990).

The *Aedes sierrensis* eggs used in this experiment were derived from a mass swarm of mosquitoes. Adults were collected as larvae from treeholes in Alton Baker Park, Eugene, Oregon, in 1984 and the population was in its fourth laboratory generation. Population sizes were maintained in the hundreds and all eggs collected from each generation were allowed to diapause, as in nature, before founding the next generation. Large population sizes and discrete generations were used to minimize unintentional artificial selection in the laboratory. Freshly hatched larvae were transferred to the exper-

TABLE 1. Sex ratio of first instar *Aedes sierrensis* collected from treeholes at various times of the year.

Date of collection	Number of males	Number of females	χ^{2*}
26 Jan 1982	258	269	0.23
27 Jan 1983	45	50	0.13
13 May 1983	46	49	0.09
25 Nov 1983	352	320	1.52

* Chi-square tests are for departure from the null hypothesis of a 1:1 sex ratio ($P > 0.05$ in all cases).

imental containers, with three replications at each food level (1.75, 3.50, or 7.00 g total sediment dry mass per dish) and at each density (10, 20, or 40 larvae per dish). All 27 containers were placed in an incubator at 22 ± 0.5°C with a 16:8 light : dark regime provided by a 4-W cool white fluorescent bulb. This regime provided unambiguous long-day photoperiod to promote direct development. The dishes were checked daily for pupae. Each pupa was gently blotted on tissue paper, weighed to the nearest 0.01 mg, and sexed. After 75 d, the number of larvae remaining in the dishes was low and the pupation rate was <1 pupa/week over all 27 containers. Consequently, the experiment was terminated.

The raw data were converted into the per dish values: median male and female pupal mass in milligrams, median time to pupation for males and females, and degree of protandry (difference in median time to pupation between males and females) in days. Base-10 logarithm transformations were performed to approximate normality of data and homogeneity of variance. Transformed life history traits (median value per dish) were subjected to two-way ANOVA with replication and were tested for significant effects of larval food level, larval density, and their interaction.

RESULTS

Protandry and female fecundity in nature

Collections of first instars taken from treeholes in different months and reared to the pupal stage in the laboratory in no case differed from a 1:1 sex ratio (Table 1), thus temporal variability in egg hatching is not related to sex. Since both the phenology and the sex ratio of the pupal and adult collections were consistent, the adult collections are assumed to be an unbiased sample of the adult population active during the season (Hawley 1985b).

Males and females emerged in discrete cohorts that were sampled during treehole censuses. Hawley (1985b: Fig. 4) found no relationship between adult survivorship and pupal mass of *Aedes sierrensis* males in the laboratory. Male wing length was not correlated with date during the period of maximum male abundance in the field ($P > 0.2$). Male survivorship was, therefore, assumed to be size and age independent. A computer spreadsheet was used to predict 1983 adult male abundance curves based on field-sampled 1983
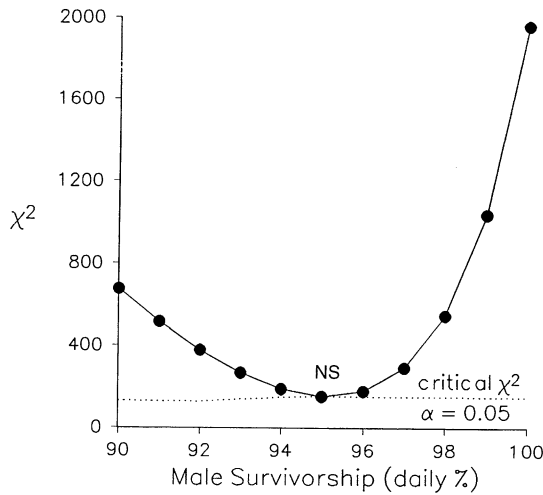
FIG. 1.   Chi-square values for goodness of fit of the field observed adult male abundance in 1983 to the adult male abundance predicted by each daily adult survival rate. ······· indicates the critical χ^2 value for each male survivorship rate at the 95% confidence level. The 95% daily male survivorship was the only rate tested that produced a nonsignificant χ^2 departure of observed adult male abundance from that predicted by survival rate.

male pupation, field-observed eclosion success, and daily survival rates from 90 to 100%. A chi-square goodness of fit value (Steel and Torrie 1980) was calculated for each daily survival rate tested. Fig. 1 shows that the male longevity of these cohorts producing a best fit with the observed pattern of male abundance is 20 d or a daily survivorship rate of 0.95.

Based on the relationships between expected lifetime fecundity and female size (larger females live longer and produce more eggs; Hawley 1985*b*,: Fig. 7) and female size and eclosion date (early emerging females are generally larger; Hawley 1985*b*,: Fig. 9), we calculated the expected number of offspring available to be sired by males throughout the flight season. Thus we were able to generate the expected lifetime fecundity of females or an "available future offspring" eclosion curve based on the 11-d running mean of field-sampled nulliparous females and mean female size (1983) or the 11-d running mean of field-sampled pupae and female pupal mass (1981–1983) for each eclosion period (Fig. 2A–D). When temporal, mass-specific variation of female fecundity is calculated, the median date of the available-future-offspring curve is shifted forward 0 d in 1981, 22 d in 1982 and 7 d in 1983
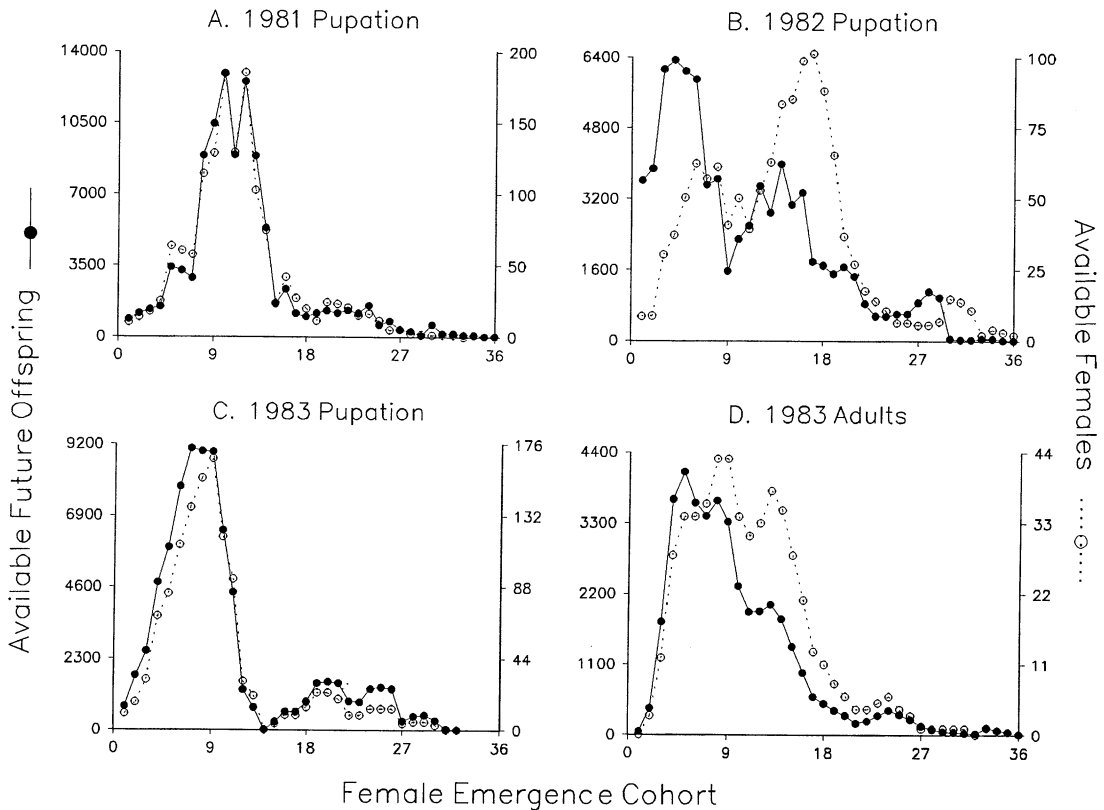

FIG. 2.   Female availability and future offspring available to be sired by *Aedes sierrensis* males throughout the flight season. Curves are based on the 11-d running mean of field-sampled pupae (1981–1983) or nulliparous females (1983 adults). The available-future-offspring curve was generated using the relationships between female mass and fecundity and female mass and eclosion time. Female emergence cohort is plotted in consecutive 3.75-d intervals starting with the appearance of the first female pupa or adult.
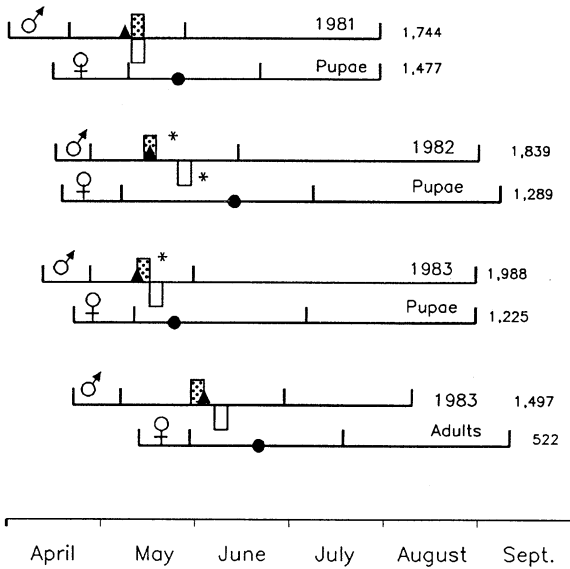
FIG. 3. Timing of pupation and adult emergence of *Aedes sierrensis* in treeholes in Oregon and protandry predicted by model simulations. The median date of field pupation or emergence is shown for males (▲) and females (●). Numbers at right of horizontal lines are numbers of individuals captured in the indicated year. Vertical lines show the 0%, 10%, 90%, and 100% pupation or emergence dates. The median date of male pupation or emergence predicted by the simulation based on mass-specific fecundity (stippled box above the line) or based on constant fecundity (open box below the line). Three simulations produced unstable protandry predictions due to higher fitness achieved by later emerging males (the median male's maximum fitness occurs at an unstable local peak rather than a stable saddle area in the male fitness landscape); these simulations are marked by an asterisk (*).

before the median date of female availability. When future available offspring are calculated from the size of flying, nulliparous adult females in the field (Fig. 2D), the peak in available future offspring occurs 7 d earlier than the peak in available females and a large secondary peak in female availability becomes a lower shoulder on the curve of available future offspring.

During three successive years, protandry measured in the field-collected pupae was 17, 28, and 12 d (Fig. 3). Protandry calculated in the 1983 field-sampled adults was 19 d (Fig. 3). When data from each year were combined, protandry was positively correlated with larval density in each respective treehole (Fig. 4).

Protandry optimum

We completed model simulations for each of three years of pupation data (1981–1983) and for the 1983 adult data. Two models were built for each of the four data sets. In one model the available future offspring curve was generated based on constant female fecundity. In the second model the available future offspring curve was generated based on temporal variation in mass-specific fecundity. Each model simulation produced a male fitness (lifetime offspring sired) land-

scape describing the relationships among male fitness, population protandry, and individual male emergence time. Fig. 5 shows the male fitness landscapes generated by the 1983 adult data. Levels of protandry are plotted, in time intervals of 3.75 d, on the x axis. We tested a range of population protandry from 3.75 to 33.75 d or 2 to 9 time intervals. The male emergence distribution is comprised of 22 cohorts. The y axis tracks the emergence time of these 22 male cohorts relative to the median female cohort emergence time which is fixed at time interval zero. Positive numbers represent male cohort emergence earlier (in time intervals of 3.75 d) than the median female cohort, and negative numbers represent emergence later than the median female cohort. Plotted at each level of protandry is the individual male fitness achieved by each of the 22 male emergence cohorts. As protandry increases from 2 to 9 time intervals (left to right on the x axis), the male emergence curve (plotted on the y axis) moves, relative to the median female emergence fixed at time interval zero, from late emergence (negative numbers) to early emergence (positive numbers). As population protandry increases, the change in relative emergence time and fitness of the median male emergence cohort is tracked by the solid circles and dotted line.

Fig. 5A presents the male fitness landscape generated by the simulation model using field-derived parameters and the assumption of equal female fecundity that is implicit in theoretical protandry models. Therefore, in the simulation for Fig. 5A, the available-future-offspring curve was generated based on constant fecundity per female. The median male cohort achieved its highest fitness at a protandry of four time intervals, corresponding to 11–15 d earlier than the median female. The assumption of equal female fecundity leads to an
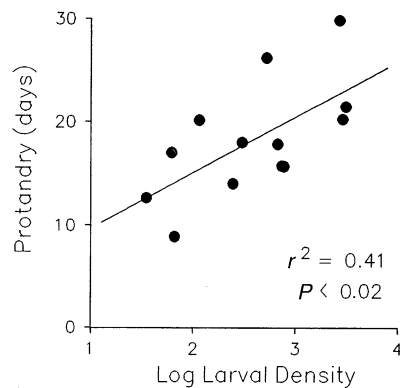

FIG. 4. Relationship between degree of protandry and larval density for treeholes that remained wet at least through June and produced a minimum of 10 pupae of each sex (1981–1983). Protandry was measured as the difference in median emergence date between males and females, larval density as numbers of first instars per unit treehole water volume, in mL.
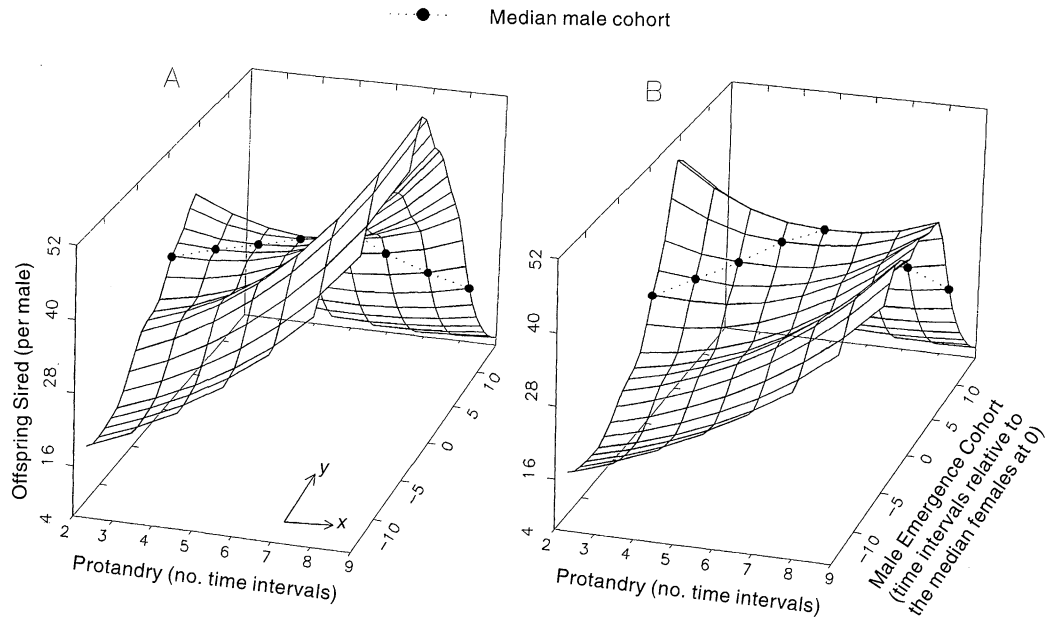
FIG. 5. *Aedes sierrensis* adult male fitness landscape generated by simulation models using 1983 field-derived parameters. Male fitness (z axis) is equated to lifetime offspring sired per male (Eq. 1). Simulation A is based on constant female fecundity. Simulation B is based on temporal variation in size-specific female fecundity. Protandry (x axis) is calculated as the difference in median emergence time between females and males. Each time interval represents 3.75 d. For each level of protandry, the y tracks emergence time of each of the 22 male cohorts comprising the male emergence distribution relative to the emergence of the median female cohort, which is fixed at time 0. Positive y values represent protandrous males and negative values represent males emerging later than the median females.

underestimation of the 19 d protandry exhibited by this 1983 adult population.

In Fig. 5B the available-future-offspring curve was based on the 11-d running mean of field-sampled nulliparous females and mean female size for each emergence interval. Thus, the model simulation in Fig. 5B incorporated temporal variation in mass-specific female fecundity. As protandry is increased along the x axis and the male cohorts emerge earlier (relative to median female emergence at time interval zero) along the y axis, maximum fitness moves from a high peak for early emerging males at low protandry, along a saddle of high fitness for median male cohorts at intermediate protandry, to a lower peak for late emerging males at high protandry. The predicted optimal degree of protandry, where the median male achieves the highest fitness, occurs in the saddle area, at protandry of six time periods, corresponding to the interval of 19 to 22 d. This interval closely approximates the protandry of 19 d observed in the field population of adults in 1983.

With this same simulation approach, we used the distribution of male and female pupation to predict optimal protandry in 1981–1983 (Fig. 3). In all cases, the addition of temporal mass-specific female fecundity either improves the protandry prediction (1982–1983) or does not change the prediction (1981). In 1981 the addition of mass-specific fecundity does not significantly change the shape or median of the available

future offspring curve (Fig. 2A). Simulations based on both constant and mass-specific female fecundity predict the same optimal protandry that is slightly less than protandry actually observed in the field (Fig. 3). Three simulations did not produce a stable optimal protandry. In these simulations later emerging males achieved a higher fitness than the maximum fitness achieved by the median male cohort. These results predict optimal protandry at an unstable, local peak in the male fitness landscape rather than at the more stable saddle area as in Fig. 5.

Variable resources

Both food level (substrate mass) and larval density affected development time (time to pupation), pupal mass, and protandry in laboratory cohorts of *Aedes sierrensis* (Table 2). Of the 27 original cohorts, the three at the highest density and lowest food level failed to produce any pupae and one of the remaining 24 cohorts produced only male pupae. Two-way ANOVA of log (cohort median) pupal mass, development time, and protandry was therefore performed using Type III sums of squares in the General Linear Models procedure (SAS Institute 1985). Consistently, pupal mass of both sexes increased with increasing food and decreasing density; development time of both sexes and protandry increased with decreasing food and increasing density. There was a significant food × density interaction effect only on female development time and pro-

TABLE 2. Effect of density and food (natural treehole substrate) on pupal mass, development time (time to pupation, in days), and protandry in laboratory microcosms of *Aedes sierrensis*.*

	Food	Density	Interaction	R^2 (%)
♂ Pupal mass	+ + + +	− − − −	1.84	89
♀ Pupal mass	+ + +	− − − −	1.47	92
♂ Development time	−	+ + + +	0.86	77
♀ Development time	− − − −	+ + + +	+	94
Protandry	+ + + +	+ +	+ +	87

* Entries in the table are the results of 2-way ANOVA. If the associated probability did not indicate significance ($P >$ 0.05), the actual F value is shown; if the F value was significant, the level of significance (1–4 plus or minus signs showing $P < 0.05$, $P < 0.01$, $P < 0.001$, and $P < 0.0001$, respectively) and the sign of the effect on the criterion variable are shown. R^2 provides reduction in total sums of squares attributable to both independent variables and their interaction.

tandry. These results show that declining per-capita resources resulted in smaller pupae, in retarded development, and in increasing protandry. The significant interaction effects on female but not male development time and on protandry indicate that males and females differ in their response to variable food and density. Median pupal mass per dish was inversely correlated with median development time per dish (Fig. 6) for both males and females in all treatments. ANCOVA of pupal mass with development time as a covariate and sex as a fixed effect revealed significant heterogeneity of regression coefficients ($F_{1,44} = 10.39$, $P < 0.01$). Significant heterogeneity of regression coefficients persisted if development time was used as the dependent variable and pupal mass as the covariate ($F_{1,44} = 14.63$, $P < 0.001$). The regression coefficient (b, in Fig. 6) was steeper for males than females, showing that, under suboptimal conditions, females conserved pupal mass more than development time and males conserved development time more than pupal mass.

DISCUSSION

Both Bulmer (1983) and Iwasa et al. (1983) found that the Wiklund-Fagerström model underestimated the observed protandry in the butterfly populations that they tested, as do our simulations based on the assumption of constant female fecundity (Fig. 3). When we include differential female fecundity in our calculation of the available-future-offspring curve in the 1983 adult population (Fig. 2D), the median date of the future-offspring curve is shifted forward 7 d. When this time is added to the prediction of the Wiklund-Fagerström model (based on constant fecundity) of 11–15 d protandry, this prediction approximates the observed field protandry of 19 d (Fig. 3). The addition of mass-specific fecundity similarly affects the protandry predictions based on pupation data in 1982 and 1983. In 1981 there is no significant temporal difference between constant and mass-specific fecundity and

both models predict a close approximation of field measured protandry (Fig. 3). Thus, once differential fecundity is incorporated into the theoretical model of protandry proposed by Wiklund and Fagerström (1977), the model is robust for *Aedes sierrensis*. The shape of the male fitness landscape (Fig. 5) suggests that protandry will tend to stabilize at the intermediate levels where the median male cohort attains the highest fitness values, rather than at the extreme levels of protandry where only the very early or very late emerging males achieve highest fitness. We conclude that the assumption of equal female fecundity can lead to predicting optimal protandry that is less than that measured in the field. In addition, the difference in mass-specific fecundity and field-observed protandry between the pupal and adult collections in 1983 indicates the importance of assessing preemergence mortality (Iwasa et al. 1983) or adult mortality before sexual maturation, if pupation data are used to predict protandry in the adult population.

Zonneveld and Metz (1991) developed a model of protandry in butterflies that predicts an increase in protandry with an increase in density. The causative factor in their model was mate competition due to an increase in mate encounter rate as a consequence of high density. We observed an increase in protandry with increased larval density in treeholes (Fig. 4) and with increase in density or decrease in food in laboratory microcosms (Table 2). Although our results are consistent with the predictions of Zonneveld and Metz (1991), we propose that mate competition is not the sole cause for density-dependent protandry; in addition, density-dependent protandry may also be an incidental consequence of natural selection acting differently on males and females. Steinwascher (1982) proposed that, in mosquitoes, female fitness is propor-
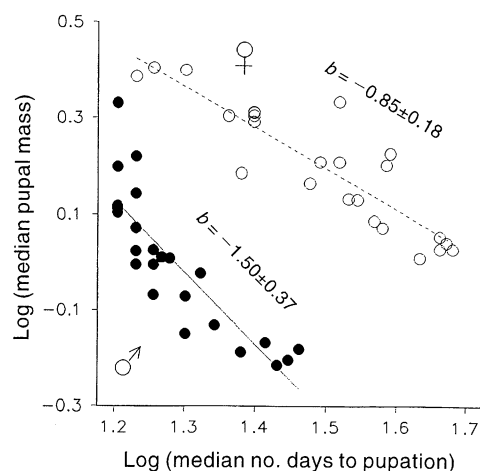

FIG. 6. Relationship between pupal mass (measured to 0.01 mg) and time to pupation of *Aedes sierrensis* males and females exposed to varying levels of larval density and food (natural treehole substrate) in laboratory microcosms (Table 2). Regression coefficients (b) are shown as mean ± 2 SE.

tional to female fecundity while male fitness is proportional to the number of females mated. Size at metamorphosis is an accurate predictor of lifetime fecundity in female mosquitoes (Hawley 1985a, Bradshaw and Holzapfel 1992), but can have much less of an impact on lifetime offspring sired in male mosquitoes (Benjamin and Bradshaw 1994). Under conditions of reduced per-capita resources, female larvae should then delay metamorphosis in order to accumulate mass and, therefore, maximize future fecundity. Under any conditions, males will miss opportunity to mate with the largest, most fecund females if they delay development. Under conditions of reduced per-capita resources, males should still minimize development time in order to maximize access to the smaller number of highly fecund females, even if early metamorphosis can be accomplished only at a smaller size. In *Aedes sierrensis,* the increase in protandry with density is due to an increase in female development time relative to males, i.e., a response to the physiological limitation of size-dependent reproductive potential, rather than to selection for a particular mating strategy. Thus, even in monandrous species for which the Wiklund-Fagerström model is robust, mate competition is not the sole cause of protandry.

Nylin et al. (1993) have considered the relative role of sexual vs. natural selection contributing to protandry. They propose that if protandry is largely or entirely a consequence of sexual selection, then protandry may itself be under some form of sexual selection. In that case, protandry should be relatively stable across a range of environments as it is in the butterfly *Pararge aegeria* (Nylin et al. 1993). In *Aedes sierrensis,* however, protandry varies across levels of per capita resource (Fig. 6) and reflects the significant effect of food × density interaction (Table 2). Males minimize development time by pupating at lower mass; females maximize body mass by delaying pupation. These gender-specific, homeostatic adjustments to larval food and density result in density-dependent protandry. Hence, protandry has not evolved solely as a mating strategy of males or females. Rather, protandry is the result of selection on independent fitness criteria in each sex.

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