

OVIPOSITION HABITAT SELECTION BY MOSQUITOES (*CULISETA LONGIAREOLATA*) AND CONSEQUENCES FOR POPULATION SIZE

MATTHEW SPENCER,^{1,3} LEON BLAUSTEIN,¹ AND JOEL E. COHEN²

¹Community Ecology Laboratory, Institute of Evolution, University of Haifa, Haifa 31905 Israel

²Laboratory of Populations, Rockefeller University, 1230 York Avenue, Box 20, New York, New York 10021-6399 USA
and Columbia University, USA

Abstract. Many kinds of adaptive behavior, including responses to risk of predation, have been documented, but there have been few attempts to translate these behaviors into consequences for populations. We present one of the first models to predict the consequences of adaptive behavior for population size in a specific natural system. Larvae of the mosquito *Culiseta longiareolata* (Diptera: Culicidae) develop in freshwater pools. They are vulnerable to predation by the backswimmer *Notonecta maculata* (Hemiptera: Heteroptera), and to intraspecific competition. Adult female *C. longiareolata* usually avoid ovipositing in pools that contain *N. maculata*. This is presumably an adaptive response that increases individual fitness, but it is also likely to affect the size of the population. We take a novel approach to understanding the relationship between adaptive behavior and population dynamics in *C. longiareolata*. We use a nonlinear stage-structured population model to predict the evolutionarily stable oviposition strategy and its consequences for the size of the *C. longiareolata* population. Our model predicts that female *C. longiareolata* should always avoid ovipositing in pools with *N. maculata*. Such avoidance will increase the equilibrium size of the *C. longiareolata* population, relative to a population in which oviposition is indiscriminate with respect to *N. maculata*. The qualitative effect on population size is the same even if, as observed, *C. longiareolata* occasionally oviposit in pools containing *N. maculata*. These predictions have important practical implications for assessing the effectiveness of predators as biological control agents.

Key words: adaptive oviposition behavior; biological control; *Culiseta longiareolata*; evolutionarily stable strategy; habitat selection; *Notonecta maculata*; population dynamics; risk of predation; stage-structured population model.

INTRODUCTION

Adaptive behavior is generally believed to have important consequences for population dynamics (Sutherland 1996, Fryxell and Lundberg 1998). Behavioral assumptions are implicit in the parameters of most population dynamic models (Hassell and May 1985), and models in which individuals are allowed to modify their behavior so as to maximize their fitness can show very different dynamics from models in which behavior is fixed (Parker 1985). For example, optimal foraging by predators affects the functional response linking prey density to consumption rate (Chesson and Rosenzweig 1991). Host selection behavior may be an important factor in the effectiveness of parasitoids as biological control agents (Luck 1990). Many empirical studies have shown that behavioral changes such as reduced foraging activity in response to increased risk of predation can alter per capita interaction strengths in food webs (e.g., Peacor and Werner 1997, Anholt et al. 2000). Population regulation in mammals is likely to

be profoundly influenced by social behavior, through its effects on competition for resources (Clutton-Brock and Albon 1985). However, only a few attempts have been made to model adaptive behavior and population dynamics in specific natural systems. Diehl et al. (2000) showed that in a model of an open system containing predators, grazers, and producers, reduced foraging and increased emigration by grazers in response to increased predator densities (assumed to be adaptive responses) could result in increased producer biomass. These predictions were in broad agreement with the results of an artificial stream study using trout, invertebrate grazers, and benthic algae. Smith et al. (2000) developed a model for the population dynamics of a fish (the bitterling) whose larvae are parasitic on freshwater mussels, and predicted that avoidance of already-parasitized mussels by ovipositing females would reduce the total fish population relative to a model with nondiscriminatory oviposition, while maximizing the fitness of individual fish. Here, we develop a model for the population dynamics of a mosquito able to choose adaptively between oviposition sites with and without predators.

Many insects, including mosquitoes, have a dispersing adult stage and nondispersing immature stages. The habitats in which immature insects develop are often

Manuscript received 5 June 2000; revised 30 March 2001; accepted 9 April 2001.

³Present address: Department of Biochemistry, University of Cambridge, Tennis Court Road, Cambridge, CB2 1QW, England. E-mail: ms379@cam.ac.uk



PLATE 1. Adult backswimmers (*Notonecta maculata*) are common predators of mosquito larvae in temporary pools in Israel. Photograph by Leon Blaustein and Eden Orion.

discrete, for example, separate water bodies for mosquitoes, and fruit, fungi, or carrion for other species. When habitat patches differ in their suitability for immature growth and survival, adult females may choose the patches in which they oviposit to maximize their fitness. Several vertebrate and invertebrate taxa, including mosquitoes, have been shown to avoid ovipositing in patches that contain predators (reviewed by Blaustein 1999). We define oviposition habitat selection (OHS) as a pattern of oviposition that is selective with respect to some measurable attribute(s) of the habitat. Like many other aspects of behavior, OHS is likely to be influenced by selection acting on individual organisms, but to have consequences at the level of the population.

The mosquito *Culiseta longiareolata* Macquart (Diptera: Culicidae) is common and abundant in temporary pools in the Middle East and Africa (van Pletzen and van der Linde 1981, Ward and Blaustein 1994). The larvae are extremely vulnerable to predation by the aquatic hemipteran (backswimmer) *Notonecta maculata* Fabricius (Hemiptera: Heteroptera), which is also common in temporary pools (see Plate 1). *C. longiareolata* avoids ovipositing in pools containing *N. maculata* (Blaustein et al. 1995, Blaustein 1998). Oviposition rates may be slightly lower in pools already containing *C. longiareolata* larvae, and adding nutrients (increasing the growth of microorganisms and algae on which larvae feed, and thus potentially reducing exploitation competition) increases oviposition (Blaustein and Kotler 1993). It seems plausible that natural selection played some role in the evolution of this OHS behavior.

Here, we describe a simple population model for *C. longiareolata* in a system of pools with and without *N. maculata*. We address the question: if females oviposit so as to maximize their fitness, and OHS is explained

by natural selection, what behavior would we expect (Parker and Maynard Smith 1990, Orzack and Sober 1994)? To answer this question, we estimate parameters for the model from a range of experiments and observations. We then use the model to predict the evolutionarily stable oviposition strategy (ESS) at equilibrium, and its sensitivity to changes in parameter estimates. We compare the predicted ESS strategy with the observed strategy in an experiment. We predict the consequences of both the ESS strategy and the observed strategy for the equilibrium adult population size, relative to a strategy in which female *C. longiareolata* do not discriminate between pools with and without predators when ovipositing.

METHODS

Assumptions

1) Several separate pools of equal quality (apart from differences in the numbers of predators and immature *C. longiareolata* they contain) are available to ovipositing females. Temporary rockpools in Israel often occur in wadis or exposed areas of bedrock, with many pools in an area of a few hundred square meters. Maximum flight distances of most mosquitoes are several kilometers (Service 1993), so all pools in a small area are likely to be available to any female.

2) Females choose oviposition sites so as to maximize their fitness. We define fitness as the number of offspring surviving to adulthood under equilibrium conditions. Fitness decreases as the numbers of predators and *C. longiareolata* larvae in a pool increase. Female *C. longiareolata* are less likely to oviposit in pools with predators than pools without predators (Blaustein et al. 1995, Blaustein 1998, Stav et al. 1999). The presence of predators (*Notonecta maculata*) reduces survival of larval *C. longiareolata* (Blaustein

1998). High larval densities of *C. longiareolata* are likely to reduce survival and increase development time as they do in the congeneric *Culiseta incidunt* (Barr 1985) and many other mosquitoes (e.g., Chambers 1985, Mogi et al. 1985, Roberts 1998). Older larvae of *C. longiareolata* are also cannibalistic on younger larvae (L. Blaustein, *personal observation*).

3) When estimating parameters, we assume that females produce egg rafts containing a constant number of eggs (which we take to be the mean number of eggs observed in field-collected egg rafts). *C. longiareolata* only rarely lays single eggs in the laboratory (van Pletzen and van der Linde 1981). In the model we do not explicitly group eggs into rafts.

4) Oviposition occurs only at a single time in each 24-h period. This assumption allows us to use a discrete-time model with a time step of one day. *C. longiareolata* oviposits only at night (van Pletzen and van der Linde 1981).

5) Predators do not move between pools. Their numbers remain constant within each pool over time, but may differ between pools. We are interested in predation by *N. maculata*, whose larvae are wingless (*N. maculata* adults are able to fly but are much less abundant than larvae). We assume predator numbers remain constant, because other *Notonecta* species have much longer generation times than mosquitoes (Murdoch et al. 1984, 1985). Most pools also have abundant alternative prey (insect larvae and crustacea), which will support *N. maculata* in the absence of *C. longiareolata* larvae.

6) The rate (per unit of time) at which an individual *N. maculata* consumes immature *C. longiareolata* is a linear function of the number of immature *C. longiareolata* alone. *N. maculata* strongly prefers *C. longiareolata* over other potential prey (Blaustein 1998), and predator saturation is unlikely to be important at the relatively low numbers of immature *C. longiareolata* that co-occur with predators in nature.

7) Aquatic predators do not kill adult *C. longiareolata* or prey on egg rafts (L. Blaustein, *unpublished data*). Adults must visit pools when ovipositing, but they remain above the surface film and are therefore unlikely to be vulnerable to attack by *N. maculata*, which feeds below the surface film.

8) For simplicity, we assume that abiotic conditions such as temperature remain constant over time.

Model structure

The model employs a nonlinear projection matrix with a time step of one day. The model groups individuals into three life stages (eggs, larvae/pupae, and adults). If there is only one pool, we use the projection matrix

$$\begin{bmatrix} e_{t+1} \\ l_{t+1} \\ u_{t+1} \end{bmatrix} = \begin{bmatrix} 1 - H & 0 & F \\ H & P & 0 \\ 0 & D & S \end{bmatrix} \begin{bmatrix} e_t \\ l_t \\ u_t \end{bmatrix} \quad (1)$$

where e , l , and u are the numbers of eggs, immatures (including both larvae and pupae), and adults respectively, at times indicated by subscripts. H is the proportion of eggs that hatches each day (dimensionless, and assumed to be always greater than zero), F is the number of eggs laid per adult each day (dimensionless), and S is the proportion of adults that survives each day (dimensionless). P is the proportion of immatures that survives to the next day but does not become adult (dimensionless), and D is the proportion of immatures that survives and becomes adult in the next day (dimensionless). P and D are nonlinear functions, which we will describe later, of the numbers of immatures and predators in a pool. We approximate the time delay between oviposition and egg hatching by assuming that a constant proportion of eggs hatches each day. Similarly, we group all immatures into a single stage and assume that a certain proportion (which depends on the number of immatures in the pool) becomes adult each day, whereas in reality no immatures below a certain threshold age can become adults. Preliminary investigations of more complex models with time delays in egg hatching and development of immature individuals showed that the three-stage model is a reasonable approximation.

We now describe the functions P and D . The proportion of immatures that survives each day is

$$v = \exp(-\mu - \beta l - \gamma N) \quad (2)$$

where μ is the instantaneous mortality rate of immatures at low density in the absence of predators (d^{-1}), β is the effect of number of immatures on death rate per immature per day (due to cannibalism and competition), l is number of immatures, γ is the per capita effect of *N. maculata* on immature survival per predator per day, and N is the number of *N. maculata* in a pool. The proportion of survivors that becomes adult each day is

$$w = d \exp(-\alpha l) \quad (3)$$

where d is the proportion of immatures developing into adults per day at low density (dimensionless) and α is the effect of each additional immature on development rate (per immature). Then $D = vw$ and $P = v(1 - w)$.

The reproductive number n is the number of surviving offspring with which each adult replaces itself. The reproductive number can be calculated from the projection matrix in Eq. 1 (Cushing 1997):

$$n = \frac{F}{1 - S} \sum_{i=1}^2 \frac{D_i a_i}{1 - P_i} \quad (4)$$

where $F/(1 - S)$ is the number of eggs an adult produces over its lifetime, $D_i/(1 - P_i)$ is the proportion of eggs that become adult in pool i (although if the population is not at equilibrium, D_i and P_i change over time), and the relative attractiveness a_i is the proportion of eggs laid in pool i . If $n = 1$ constantly over time,

TABLE 1. Parameter estimates and data sources used in the population model for the mosquito *Culiseta longiareolata*.

Symbol	Meaning	Dimensions	Estimate	Source
H	daily proportion of eggs hatching	dimensionless	1/2	van Pletzen (1981), van Pletzen and van der Linde (1981), G. Stav, <i>unpublished data</i> [laboratory and field observations]
d	proportion of immatures developing per day at low density	dimensionless	1/14	van Pletzen (1981), van Pletzen and van der Linde (1981); mean of two laboratory studies
α	effect of immature numbers on development rate	per immature	2.1×10^{-4}	Blaustein and Margalit (1996): artificial pool experiment
μ	basic immature mortality rate	per day	1.7×10^{-2}	Blaustein and Margalit (1996): artificial pool experiment
γ	per capita effect of <i>N. maculata</i> on immature survival	per predator per day	0.23	Blaustein (1998): artificial pool experiment
β	effect of immature numbers on death rate of immatures	per immature per day	$0-2 \times 10^{-4}$	no source
S	daily adult survival	dimensionless	0.8	Service (1993): mean of 14 field estimates from subfamily Culicinae
F	daily eggs per adult	dimensionless	0 to 20	van Pletzen and van der Linde (1981): laboratory experiment

and not merely in transition from $n < 1$ to $n > 1$ or vice versa, then the population is at equilibrium. To examine the effects of OHS on population dynamics, we consider three cases for a system in which half the pools have no predators, and half have a constant number of predators. Assuming that all pools of a given kind are identical, we treat this as a two-pool system with relative attractiveness a_a if predators are absent, and relative attractiveness $a_p = 1 - a_a$ if predators are present. The three cases are: (1) the ESS value of a_a when the population is at equilibrium, (2) typical values of a_a observed in experiments, and (3) no discrimination between pools with and without predators ($a_a = 0.5$).

For each case, we estimate the expected equilibrium adult population size. When the population is at equilibrium, $D_i/(1 - P_i)$ is the relative fitness of an egg raft laid in pool i . We find the ESS value of a_a by minimizing the absolute difference in $D_i/(1 - P_i)$ at equilibrium between pools with zero and with three predators. We chose three predators because the experiments with which we compared the model predictions used three predators. In all cases, we estimated the equilibrium by numerical iteration (over 1000–4000 d, with initially two adult *C. longiareolata* per pool and no *C. longiareolata* larvae or pupae), using Matlab version 4.2d for Macintosh (The Mathworks, Natick, Massachusetts). The equilibrium was stable for all parameter values used here, although cycles were possible using unrealistically high fecundity.

Parameter estimates

We estimate all parameters from data on *C. longiareolata* unless otherwise stated. We scale all estimates to apply to a pool volume of 36 L (reasonable for natural temporary pools, and the size of artificial pool in which we have carried out many experiments). We

summarize the data sources and parameter estimates in Table 1. The most important feature of these estimates is that we remain uncertain of the values of two parameters, β (the effect of immatures on survival) and F (eggs per adult per day). For these parameters, we examine a range of plausible values.

H (proportion of eggs hatching per day).—Eggs hatch in ~2 d (van Pletzen 1981, van Pletzen and van der Linde 1981; G. Stav, *unpublished data*), so H is 1/2.

d (proportion of immatures developing per day at low density).—Larvae reared individually and fed daily took ~15 d to become adults at 22°C (van Pletzen 1981). In another experiment, larvae reared at a density of 70 individuals/L with daily feeding (and thus unlikely to experience food shortages) took ~12.5 d to become adults at 23°C (van Pletzen and van der Linde 1981). The average development time is 14 d, so d is 1/14.

α (effect of number of immatures on development rate).—Larvae raised at densities of 25 and 50 individuals/L in 2 L of water (corresponding to 900 and 1800 larvae per 36-L pool) had all either pupated or died by age 16 d (Blaustein and Margalit 1996). The proportion of surviving larvae that had pupated at age 12 d was 0.58 at 25 larvae/L and 0.52 at 50 larvae/L. If 12-d-old individuals are in their first day as pupae, and average pupal duration is 2.5 d (van Pletzen 1981, van Pletzen and van der Linde 1981), these individuals would become adults at age 14.5 d. In our model, the proportion of survivors that have not reached adulthood after t days is $(1 - w)^t$. With $t = 14.5$ d, this gives estimates of w of 0.058 at 900 larvae per 36-L pool and 0.050 at 1800 larvae per 36-L pool. At zero larvae per pool, w is equal to d . We estimate α from these three data points by least-squares regression through the origin, using the equation

$$\ln w - \ln d = -\alpha t \quad (5)$$

which gives $\alpha = 2.1 \times 10^{-4}$ immatures $^{-1}$, with a standard error of 9×10^{-6} ($F_{1,2} = 474$, $P = 0.002$).

μ (larval mortality rate at low density).—There was no consistent difference in survival between larval densities of 25 and 50 larvae/L in 2-L pools (Blaustein and Margalit 1996; mean survival 0.77 over 15 d). This suggests that these densities are low enough to estimate death rate at low density. Assuming a constant mortality rate, $\mu = -\ln(0.77)/15 = 1.7 \times 10^{-2}$ d $^{-1}$.

γ (per capita effect of *N. maculata* on survival).—We estimate the per capita effect of *N. maculata* from the average numbers of egg rafts and larvae in 36-L pools with two *N. maculata* per pool (Blaustein 1998). There were an average of 55 eggs (0.2 egg rafts, assuming 280 eggs per raft; van Pletzen and van der Linde 1981) and 1.2 third and fourth instar larvae per pool (averaged over three weeks, beginning one week after the introduction of predators). Third and fourth instar larvae are between 6 and 12 d old (van Pletzen 1981). Taking the midpoint, survival over nine days was roughly 0.02. This survival results from natural mortality (approximately μ , as larval density is low) and mortality due to predators

$$0.02 = \exp(-(\mu + \gamma N)t). \quad (6)$$

Rearranging and substituting $\mu = 1.7 \times 10^{-2}$ d $^{-1}$ (Table 1), this gives $\gamma = 0.23$ per predator per day.

β (effect of immatures on survival).—An artificial pool experiment found no significant difference in survival between single cohorts of *C. longiareolata* larvae at densities corresponding to 900 or 1800 individuals per 36-L pool (Blaustein and Margalit 1996), which suggests $\beta = 0$. However, larger larvae may have stronger competitive effects on smaller larvae, including cannibalism (Livdahl 1982, Livdahl and Koenekoop 1985 for other mosquito species; L. Blaustein, personal observation for *C. longiareolata*). Thus, survival may depend more strongly on number of larvae when larvae of many different ages are present in a pool. We consider a range of values between 0 and 2×10^{-4} , giving 77% and 5% survival respectively over 15 d at a constant density of 900 larvae per 36-L pool (with μ from Table 1). We think β is unlikely to fall outside this range.

S (daily adult survival).—Field estimates of daily adult survival from 14 studies on the subfamily Culicidae (which contains *Culiseta*, although these estimates are from the genera *Culex*, *Mansonia*, and *Aedes*) have a mean of 0.8 and a standard deviation of 0.05 (Service 1993). We set S to 0.8.

F (eggs per adult per day).—Females probably need a blood meal before developing eggs, although this may not be true of all populations of *C. longiareolata* (van Pletzen and van der Linde 1981). The length of time between blood feeding and oviposition (G , the effective length in days of the gonotrophic cycle) varies from 4 to at least 18 d in the laboratory (van Pletzen and van

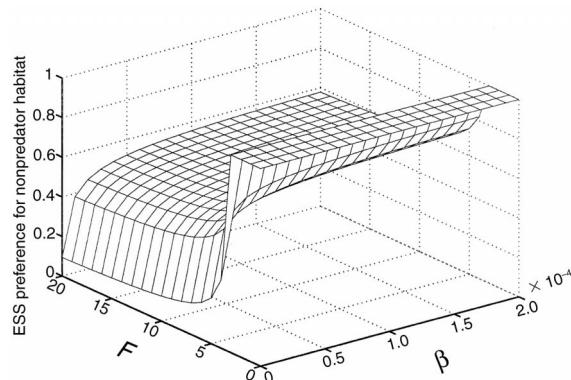


FIG. 1. ESS (evolutionarily stable strategy) proportion of eggs laid in pools without predators (a_e) at equilibrium in a system with equal numbers of pools with zero and three predators per pool, for a range of values of adult fecundity (F) and effect of immature numbers on mortality (β). Parameter values are given in Table 1.

der Linde 1981), perhaps because females can hold developed eggs for some time (Day et al. 1990). We calculate an upper limit on F , assuming that the probabilities of finding a mate, finding a blood meal, developing eggs, and finding an oviposition site are close to 1, and that almost all eggs hatch. If daily survival of females is S and the gonotrophic cycle lasts G days, then the proportion of females surviving from blood feeding to oviposition is S^G . The expected number of egg rafts a female will produce in her lifetime is

$$E = \frac{1}{1 - S^G} - 1 \quad (7)$$

(the -1 is because the first gonotrophic cycle must be completed before an egg raft can be produced). The expected number of eggs per adult (or female eggs per female adult) over the entire lifetime is then $E \times 0.5 \times 280$, because the sex ratio is ~ 0.5 and each raft contains an average of 280 eggs (van Pletzen and van der Linde 1981). In our model, expected eggs per lifetime is $F/(1 - S)$, so with $S = 0.8$ (see above), F may range from 0.5 (if G is 18 d) to 19 (if G is 4 d). We will consider a range of F from 0 to 20.

RESULTS

Predicted ESS oviposition strategy

The ESS proportion of eggs laid in nonpredator pools at equilibrium (a_e , Fig. 1) ranges from 0.09 (with $F = 20$ and $\beta = 0$) to 1 (with $F \leq 3$). The equilibrium total number of eggs per two pools increases with increasing F , and has a maximum at low but nonzero values of β (Fig. 2a). The numbers of immatures in pools with and without predators increase with increasing F and decreasing β , although there are no immatures in predator pools at low values of F (Fig. 2b, c). The relationship of the total number of adults per two pools to F and β is more complicated (Fig. 2d). With low values of β ,

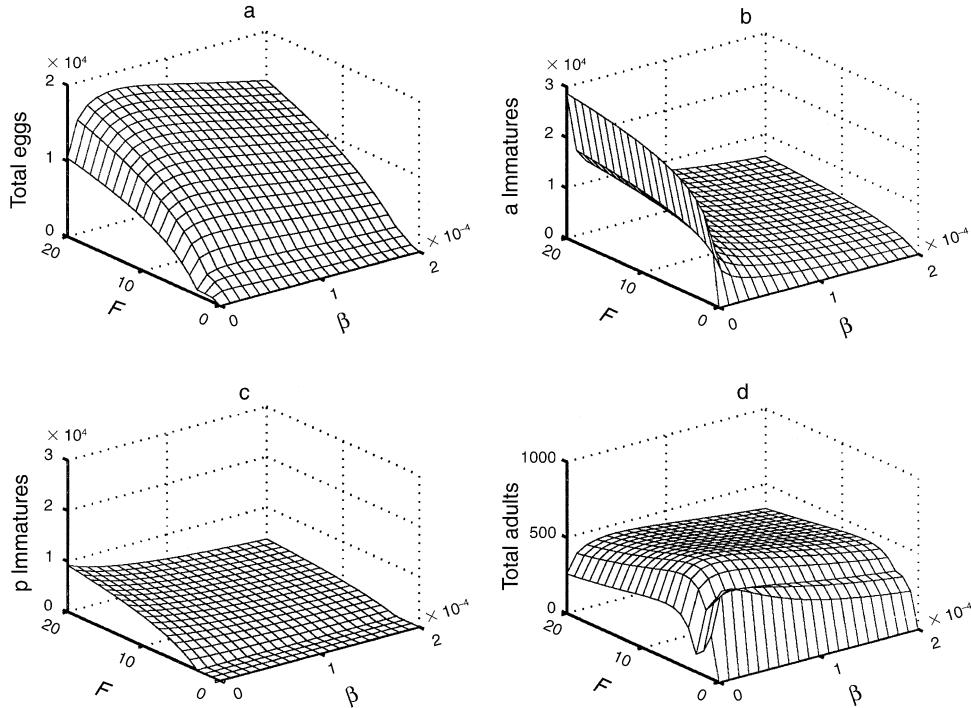


FIG. 2. Equilibrium numbers of (a) eggs per two pools, (b) immatures in pools from which predators are absent (a Immature), (c) immatures in pools in which predators are present (p Immature), and (d) adults per two pools. The figure presents numerical iterations of a system with equal numbers of pools with zero and three predators per pool, for a range of values of adult fecundity (F) and effect of immature numbers on mortality (β). Parameter values are given in Table 1.

the total number of adults has a local maximum at very low F , and a local minimum at slightly higher F . For higher values of β , the relationship is smoother, with a single maximum at intermediate F . For all values of β , increasing fecundity above ~ 10 has little effect on the total adult population, presumably because of strong density dependence in the immature stage.

The relationship between β (the per-capita effect of larval density on larval mortality) and a_a (the ESS proportion of eggs laid in nonpredator pools) is counter-intuitive. As β increases, a_a also increases (Fig. 1). One might expect that high values of β would result in high larval mortality in pools without predators, and thus reduce the ESS preference for pools without predators. However, the equilibrium population size and stable age structure also change with β . Fig. 2b and 2c shows that increasing β reduces the equilibrium number of larvae in pools with and without predators. Thus, although the per-capita effect of larval density on larval mortality is higher at high β , the total effect is lower.

To determine the ESS strategy predicted by this model, we need to set F and β to values that give a plausible equilibrium population size (measured as eggs rather than adults, as we have no data on adult population sizes). We estimated the average number of eggs per two pools from an artificial pool experiment (L. Blaustein, M. Spencer, and T. Fahima, *unpublished data*) that was not used to estimate parameters. Wild *C. lon-*

giareolata were allowed to oviposit in a set of 32 artificial pools (36 L each), of which 15 pools contained three *N. maculata* each and 17 pools contained no *N. maculata*. To reduce the importance of initial conditions, we used data only from the final period of the experiment (from 17 May to 7 June 1998), which ran for ~ 2 mo in total. In this final period, we observed a total of 39 newly oviposited *C. longiareolata* egg rafts by visual counts on eight different sample dates. Assuming that egg rafts take two days to hatch and contain 280 eggs each (van Pletzen and van der Linde 1981), this corresponds to an equilibrium of ~ 170 eggs per two pools (counting both newly laid and older eggs). We do not correct for the small difference in proportions of pools with and without predators, but we show below that even a fourfold error in this estimate of the equilibrium number of eggs per two pools does not affect our predicted ESS strategy.

Fig. 3 shows combinations of F and β giving small integer multiples of 170 eggs per two pools at equilibrium. Contours connecting combinations of F and β giving a range of ESS preferences for nonpredator pools are overlaid. Plausible equilibrium numbers of eggs per two pools for this experiment (up to three times the observed number) occur only at $F < 2$. For F as low as this, the ESS strategy is always to oviposit in pools without predators, if pools with and without predators are equally available. The model predicts

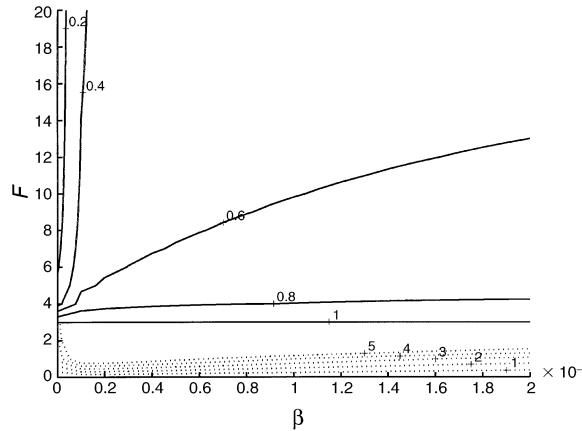


FIG. 3. Plausible combinations of adult fecundity (F) and effect of immature numbers on mortality (β), and the corresponding ESS preference for pools without predators (a_a). Dotted lines are contours connecting combinations of F and β giving small integer multiples of the observed number of eggs per two pools (1×170 , 2×170 , and so on, labeled as 1, 2, and so on). Solid lines are contours connecting combinations of F and β giving values of a_a from 0.2 to 1.0 (labeled with their values of a_a). Parameter values are given in Table 1.

ESS values of a_a as low as 0.2 for populations having five times as many eggs at equilibrium as we observed, although this is extrapolating far outside the range of population sizes used to estimate parameters.

Sensitivity analysis

We estimated the sensitivity of the ESS preference for nonpredator pools, and the total numbers of eggs and adults per two pools, to changes of $\pm 10\%$ in each parameter relative to the values given in Table 1. We did this for 22 combinations of F and β giving approximately the observed number of eggs per two pools. In all cases, the ESS preference for nonpredator pools was unchanged ($a_a = 1$). The mean proportional effects on the equilibrium number of adults over all 22 combinations of F and β are shown in Table 2. Varying adult survival (S) has by far the largest effects on the total adult population, followed by the proportion of immatures becoming adult each day at low density (d) and adult fecundity (F). The coefficient of variation among the published estimates of S we used (see *Methods*) was 6%, which is large enough to have substantial effects on the predicted number of adults. The range of the two estimates of d we obtained (see *Methods*) is $\sim 10\%$ of the mean estimate, so improving the precision of d would also be worthwhile. It is difficult to determine how large the errors in other parameter estimates might be, given the diversity of sources from which they were obtained. The relatively high sensitivity of adult numbers to F highlights the importance of obtaining an estimate for this parameter under realistic conditions. The sensitivity of adult numbers to the daily proportion of eggs hatching (H) is zero be-

cause we assume no egg mortality (Eq. 1). Altering H thus alters the rate at which eggs turn into immatures, but not the proportion of eggs that survives to adulthood (provided $H > 0$). The sensitivity of adult numbers to the per capita effect of *N. maculata* on immature survival is zero for all the parameter combinations used to generate Table 2, because for these combinations, the ESS is always to avoid pools containing *N. maculata*. The proportional effects on eggs were very similar, except that the absolute mean effects of F (0.56, standard deviation 0.16) and H (-0.20, standard deviation 0.00) were larger.

We also estimated the ESS oviposition strategy for 1100 random combinations of parameters. We sampled each parameter independently from a uniform distribution with range $\pm 50\%$ around our best estimate (for F and β , we sampled 50 times around each of 22 combinations giving approximately the observed number of eggs, as above). We did not find any random combinations of parameters for which sometimes ovipositing in pools with predators was an ESS, except where the total number of eggs was more than seven times greater than observed.

Observed oviposition strategy

In the artificial pool experiment described previously (L. Blaustein, M. Spencer, and T. Fahima, *unpublished data*), 33 of 39 egg rafts were oviposited in the 17 of 32 pools without predators. The preference a_a for pools without predators was $(33/17)/(33/17 + 6/15) = 0.83$ (standard error ~ 0.06). The probability of the observed distribution given the predicted ESS ($a_a = 1$) is zero.

TABLE 2. Sensitivity analysis for equilibrium number of mosquito adults per two pools.

Parameter	Mean proportional change	Standard deviation
S	2.56	0.35
d	0.38	0.03
F	0.36	0.17
β	-0.15	0.02
μ	-0.06	0.04
α	-0.06	0.02
H	0	0
γ	0	0

Notes: For each of 22 combinations of F and β giving approximately the observed number of eggs per two pools, we varied each parameter in turn by $\pm 10\%$ and estimated the equilibrium number of adults by numerical iteration. Proportional changes in number of adults are expressed as $(u_{+10} - u_{-10})/u_{base}$, where u_{+10} is the number of adults with the parameter increased by 10%, u_{-10} is the number of adults with the parameter decreased by 10%, and u_{base} is the number of adults with the original value of the parameter. The table gives the mean and sample standard deviation of proportional change over all 22 combinations of F and β in descending order of absolute magnitude.

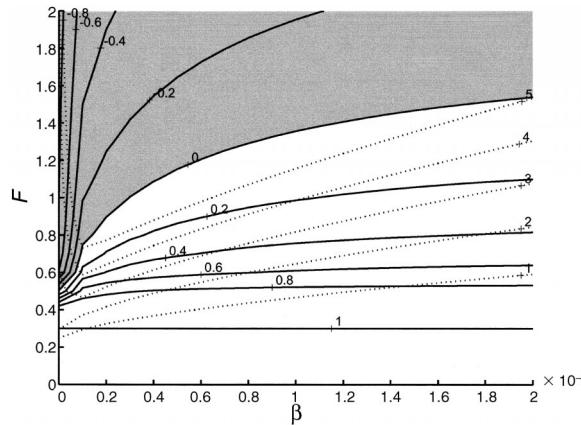


FIG. 4. Consequences of the predicted ESS oviposition strategy ($a_a = 1$) for adult population size, compared to a nondiscriminatory strategy ($a_a = 0.5$). The shaded region is the region of parameter space in which the population is predicted to be lower under the ESS strategy than under a nondiscriminatory strategy. Dotted lines are contours connecting combinations of F and β giving small integer multiples of the observed number of eggs per two pools (1×170 , 2×170 , and so on, labeled as 1, 2, and so on) under the ESS strategy. Solid lines are contours connecting combinations of F and β giving equal values of the proportional difference in equilibrium adult population (labeled with these proportional differences). The proportional difference in equilibrium adult population is expressed as $(\text{adults}_1 - \text{adults}_{0.5})/\text{adults}_1$, where subscripts refer to the value of a_a . Only a subset of the range of F used in numerical iterations is shown for clarity, as higher values did not give plausible equilibrium numbers of eggs per two pools (Fig. 3). Parameter values are given in Table 1.

Effects of oviposition strategies on adult population size

For most combinations of F and β giving up to three times as many eggs per two pools as observed, the predicted ESS oviposition strategy ($a_a = 1$) results in a higher predicted equilibrium adult population size than a strategy ($a_a = 0.5$) in which ovipositing females do not discriminate between pools with and without predators (Fig. 4, unshaded region). For combinations of F and β giving the observed number of eggs per two pools, a nondiscriminatory strategy gives an equilibrium adult population from >60% to 100% lower. At very low values of F (<0.3), a population using the ESS strategy might persist where a population using the nondiscriminatory strategy would not persist. At relatively high values of F (>0.5, giving a predicted equilibrium egg population under the ESS strategy three or more times higher than observed), the predicted ESS oviposition strategy may actually result in a lower equilibrium adult population size than a nondiscriminatory strategy (Fig. 4, shaded region). For plausible equilibrium numbers of eggs per two pools, this only occurs at relatively low values of β (<1 $\times 10^{-5}$).

With the observed oviposition strategy ($a_a = 0.83$),

the contour connecting values of F and β giving the observed number of eggs per two pools again lies entirely in the region in which the equilibrium adult population size is greater than with a nondiscriminatory strategy (Fig. 5). A nondiscriminatory strategy gives a predicted equilibrium adult population from >40% lower to >80% lower. For combinations of F and β giving the observed number of eggs under the observed strategy, the predicted ESS strategy always gives a higher equilibrium adult population than the observed strategy (Fig. 6). Combinations of F and β that give other than the observed number of eggs per two pools are not relevant, because we do not know what oviposition strategy would have been used at these numbers.

DISCUSSION

The high consumption rate of *C. longiareolata* larvae by *N. maculata* in the laboratory (Blaustein 1998) and in artificial pools (L. Blaustein and B. P. Kotler, *unpublished data*) suggests that predation has the potential for dramatic effects on mosquito populations. This predation may favor the evolution of avoidance of predators by ovipositing mosquitoes (Blaustein 1999). Many experiments with *C. longiareolata* and other mosquitoes have found that oviposition is not random with respect to predators and conspecifics (e.g., Chesson 1984, Blaustein et al. 1995, Onyabe and Roitberg 1997, Blaustein 1998, Edgerly et al. 1998, Stav et al. 1999). For combinations of parameters giving realistic numbers of eggs per two pools, our model predicts that female *C. longiareolata* should always avoid ovipos-

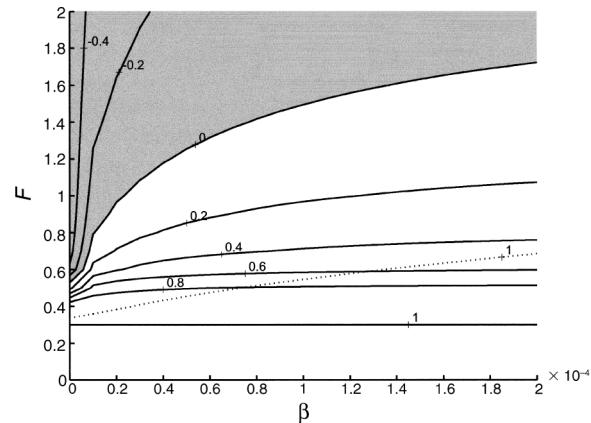


FIG. 5. Consequences of the observed oviposition strategy ($a_a = 0.83$) for adult population size, compared to a nondiscriminatory strategy ($a_a = 0.5$). The dotted line is a contour connecting combinations of F and β giving the observed number of eggs per two pools (1×170 , labeled as 1) under the observed oviposition strategy. Solid lines are contours connecting combinations of F and β giving equal values of the proportional difference in equilibrium adult population (labeled with these proportional differences). The proportional difference in equilibrium adult population is expressed as $(\text{adults}_{0.83} - \text{adults}_{0.5})/\text{adults}_{0.83}$, where subscripts refer to the value of a_a .

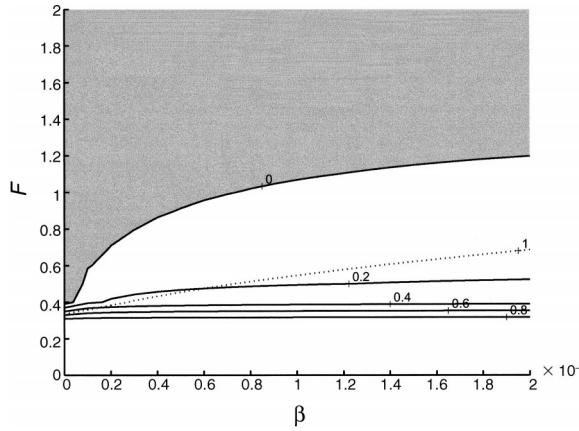


FIG. 6. Consequences of the ESS oviposition strategy ($a_e = 1$) for adult population size, compared to the observed strategy ($a_e = 0.83$). The dotted line is a contour connecting combinations of F and β giving the observed number of eggs per two pools (1×170 , labeled as 1) under the observed oviposition strategy. Solid lines are contours connecting combinations of F and β giving equal values of the proportional difference in equilibrium adult population (labeled with these proportional differences). The proportional difference in equilibrium adult population is expressed as $(\text{adults}_1 - \text{adults}_{0.83})/\text{adults}_1$, where subscripts refer to the value of a_e .

iting in pools containing predatory *N. maculata*, if pools with and without predators are equally available (Fig. 3). In fact, female *C. longiareolata* avoided ovipositing in pools with *N. maculata* 83% of the time, in the experimental data reported here. Over these data, three comparable experiments in artificial pools (Blaustein et al. 1995, Blaustein 1998; L. Blaustein, unpublished data) and one experiment in natural pools (M. Kiflawi, A. Eitam, and L. Blaustein, unpublished data), the median proportion of *C. longiareolata* egg rafts laid in pools without *N. maculata* was 0.83 (range 0.79 to 0.95).

The discrepancy between our predicted ESS and the observed strategy thus appears fairly small but consistent. Either natural selection was not the only important factor in the evolution of this behavior, or our model does not include all the important details of its action. Our aim is to determine the consequences of a particular set of assumptions, of which one is that females adopt an OHS strategy that maximizes their fitness (Parker and Maynard Smith 1990). Given the discrepancy, our model cannot explain the observed behavior completely (Orzack and Sober 1994), although different sets of plausible assumptions might. There are many plausible constraints that we did not include. For example, adult *C. longiareolata* may sometimes fail to detect the presence of *N. maculata*. A similar explanation has been proposed for apparently suboptimal oviposition behavior in the pitcher plant mosquito *Wyeomyia smithii* (Heard 1994). The dispersal rate of *N. maculata* appears to be low relative to the time scale of *C. longiareolata* population dynamics, but the risk

of *N. maculata* arriving in a pool after oviposition by *C. longiareolata* could reduce the benefit of choosing *N. maculata*-free pools. There may also be constraints on the amount of time that a female *C. longiareolata* can spend searching for an oviposition site. If a *C. longiareolata* fails to find an *N. maculata*-free pool within her limited search time, she may be forced to accept a pool containing *N. maculata*. Errors in the structure or parameter estimates of our demographic model are possible, although our sensitivity analysis suggests that these errors would have to be large to obtain an ESS in which some *C. longiareolata* oviposit in *N. maculata* pools. *C. longiareolata* larvae reared at high densities are smaller than those reared at low densities (M. Kiflawi, L. Blaustein and M. Mangel, unpublished manuscript). If smaller adults have lower survival and/or fecundity, the cost of intraspecific larval competition might be considerably higher than we estimated. It is also possible that our fitness measure is inappropriate: a problem of currency rather than constraint (Haccou and van der Steen 1992). We estimated fitness at equilibrium, but different results might occur with changing population sizes. Some or all of these factors might be needed to explain the observed behavior.

Despite the discrepancy between observed and predicted oviposition strategies, we can make a clear qualitative prediction about the effect of OHS on the size of the *C. longiareolata* population. We expect a larger population of adult *C. longiareolata* if females select oviposition sites so as to maximize their fitness than if females oviposit indiscriminately (Fig. 4). The same qualitative result holds if females follow the observed oviposition strategy (Fig. 5). This is not the only possible outcome: oviposition that maximizes individual fitness may reduce population size in some species (Smith et al. 2000). We cannot make a quantitative prediction about the magnitude of the effect on population size, because we do not have precise estimates of two demographic parameters (adult fecundity, F , and the effect of immature numbers on the death rate of immatures, β). The next steps will be to obtain better estimates of F and β , use them to make a quantitative prediction about the effects of adaptive oviposition on population size, and test this prediction experimentally. One obvious approach is to manipulate oviposition behavior in replicated enclosed populations (Anholt 1997).

The potential importance of habitat selection for population dynamics has been recognized in many different contexts. Density dependence can arise from the interaction between environmental heterogeneity and behavior (Chesson and Rosenzweig 1991). Abstract models of breeding site selection suggest that the details of behavioral interaction (ideal free vs. ideal preemptive) can be important for management decisions such as the size and spatial arrangement of habitat that should be conserved (Pulliam and Dan-

ielson 1991). Predator avoidance can lead to nonlinear relationships between predation risk and the proportion of total mortality due to predation (Houston and McNamara 1997). Predators may therefore regulate prey abundance without directly killing many prey (Brown et al. 1999). Sutherland (1996) reviews models linking ESS foraging and breeding site selection and equilibrium population size, mainly in vertebrates. However, there are very few demonstrations of the link between behavior and population dynamics in realistic models (Fryxell and Lundberg 1998). Our study is novel in that we have attempted to predict the consequences of adaptive behavior for population size in a specific natural population, rather than an abstract model. Our results also have practical importance. Many experimental assessments of predators on larvae as potential biological control agents for mosquitoes implicitly assume nonselective oviposition (e.g., Walton and Mulla 1991, Homski et al. 1994). If mosquitoes are ovipositing selectively, these experiments may radically overestimate the effectiveness of predators in reducing mosquito populations. Understanding the interaction between OHS and population size in mosquitoes is therefore important both for making correct management decisions, and for advancing the conceptual unification between behavioral ecology and population biology.

ACKNOWLEDGMENTS

Marc Mangel contributed ideas and criticism at all stages of this work. We are also grateful to Yehuda Braverman, Phil Crowley, Moshe Kiflawi, Uriel Kitron, Gil Stav, and Bill Walton for comments and suggestions, and to Burt Kotler, Matthew Liebold, Cynthia Lord, Phil Lounibos, and two anonymous referees for reviewing earlier versions of the manuscript. Edward F. Connor and two anonymous referees improved the manuscript by their constructive comments. This work was supported by United States-Israel Binational Science Foundation grant no. 95-305 to L. Blaustein and J. E. Cohen and grant no. 98-390 awarded to L. Blaustein, J. E. Cohen, and M. Mangel. J. E. Cohen was supported in part by US NSF grants DEB-9207293 and DEB-9981552, and by the hospitality of Mr. and Mrs. William T. Golden.

LITERATURE CITED

- Anholt, B. R. 1997. How should we test for the role of behaviour in population dynamics? *Evolutionary Ecology* **11**: 633–640.
- Anholt, B. R., E. Werner, and D. K. Skelly. 2000. Effect of food and predators on the activity of four larval ranid frogs. *Ecology* **81**:3509–3521.
- Barr, A. R. 1985. Population dynamics of immature *Culiseta incidunt*. Pages 147–154 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Blaustein, L. 1998. Influence of the predatory backswimmer, *Notonecta maculata*, on invertebrate community structure. *Ecological Entomology* **23**:246–252.
- Blaustein, L. 1999. Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. Pages 441–456 in S. P. Wasser, editor. *Evolutionary theory and processes: modern perspectives, papers in honor of Eviatar Nevo*. Kluwer Academic Dordrecht, The Netherlands.
- Blaustein, L., and B. P. Kotler. 1993. Oviposition habitat selection by the mosquito, *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. *Ecological Entomology* **18**:104–108.
- Blaustein, L., B. P. Kotler, and D. Ward. 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. *Ecological Entomology* **20**:311–318.
- Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larvae–toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* **65**:77–84.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**:385–399.
- Chambers, R. C. 1985. Competition and predation among larvae of three species of treehole-breeding mosquitoes. Pages 25–53 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Chesson, J. 1984. Effect of notonectids (Hemiptera: Notonectidae) on mosquitoes (Diptera: Culicidae): predation or selective oviposition? *Environmental Entomology* **13**:531–538.
- Chesson, P., and M. Rosenzweig. 1991. Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* **72**:1187–1195.
- Clutton-Brock, T. H., and S. D. Albon. 1985. Competition and population regulation in social mammals. Pages 557–575 in R. M. Sibly and R. H. Smith, editors. *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Scientific, Oxford, UK.
- Cushing, J. M. 1997. Nonlinear matrix equations and population dynamics. Pages 205–243 in S. Tuljapurkar and H. Caswell, editors. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York, USA.
- Day, J. F., G. A. Curtis, and J. D. Edman. 1990. Rainfall-directed oviposition behavior of *Culex nigripalpus* (Diptera: Culicidae) and its influence on St. Louis encephalitis virus transmission in Indian River County, Florida. *Journal of Medical Entomology* **27**:43–50.
- Diehl, S., S. D. Cooper, K. W. Kratz, R. M. Nisbet, S. K. Roll, S. W. Wiseman, and T. M. Jenkins, Jr. 2000. Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *American Naturalist* **156**:293–313.
- Edgerly, J. S., M. McFarland, P. Morgan, and T. Livdahl. 1998. A seasonal shift in egg-laying behaviour in response to cues of future competition in a treehole mosquito. *Journal of Animal Ecology* **67**:805–818.
- Fryxell, J. M., and P. Lundberg. 1998. *Individual behavior and community dynamics*. Chapman and Hall, London, UK.
- Haccou, P., and W. J. van der Steen. 1992. Methodological problems in evolutionary biology. IX. The testability of optimal foraging theory. *Acta Biotheoretica* **40**:285–295.
- Hassell, M. P., and R. M. May. 1985. From individual behaviour to population dynamics. Pages 3–32 in R. M. Sibly and R. H. Smith, editors. *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Scientific, Oxford, UK.
- Heard, S. B. 1994. Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*). *Evolutionary Ecology* **8**:493–502.
- Homski, D., M. Goren, and A. Gasith. 1994. Comparative evaluation of the larvivorous fish *Gambusia affinis* and

- Aphanius dispar* as mosquito control agents. *Hydrobiologia* **284**:137–146.
- Houston, A. I., and J. M. McNamara. 1997. Patch choice and population size. *Evolutionary Ecology* **11**:703–722.
- Livdahl, T. P. 1982. Competition within and between hatching cohorts of a treehole mosquito. *Ecology* **63**:1751–1760.
- Livdahl, T. P., and R. K. Koenekoop. 1985. The nature of egg hatching in *Aedes triseriatus*: ecological implications and evolutionary consequences. Pages 439–458 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Luck, R. F. 1990. Evaluation of natural enemies for biological control: a behavioral approach. *Trends in Ecology and Evolution* **5**:196–199.
- Mogi, M., M. Horio, I. Miyagi, and B. D. Cabrera. 1985. Succession, distribution, overcrowding and predation in the aquatic community in aroid axils, with special reference to mosquitoes. Pages 95–119 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. *American Naturalist* **125**:344–366.
- Murdoch, W. W., M. A. Scott, and P. Ebsworth. 1984. Effects of the general predator, *Notonecta* (Hemiptera) upon a freshwater community. *Journal of Animal Ecology* **53**:791–808.
- Onyabe, D. Y., and B. D. Roitberg. 1997. The effect of conspecifics on oviposition site selection and oviposition behaviour in *Aedes togoi* (Theobold) (Diptera: Culicidae). *Canadian Entomologist* **129**:1173–1176.
- Orzack, S., and E. Sober. 1994. Optimality models and the test of adaptationism. *American Naturalist* **143**:361–380.
- Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. Pages 33–58 in R. M. Sibly and R. H. Smith, editors. *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Scientific, Oxford, UK.
- Parker, G. A., and J. Maynard Smith. 1990. Optimality theory in evolutionary biology. *Nature* **348**:27–33.
- Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* **78**:1146–1156.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* **137**Supplement:S50–S66.
- Roberts, D. 1998. Overcrowding of *Culex sitiens* (Diptera: Culicidae) larvae: population regulation by chemical factors or mechanical interference. *Journal of Medical Entomology* **35**:665–669.
- Service, M. W. 1993. *Mosquito ecology. Field sampling methods*. Second edition. Elsevier, London, UK.
- Smith, C., J. D. Reynolds, and W. J. Sutherland. 2000. Population consequences of reproductive decisions. *Proceedings of the Royal Society of London Series B* **267**:1327–1334.
- Stav, G., L. Blaustein, and J. Margalith. 1999. Experimental evidence for predation risk sensitive oviposition by a mosquito, *Culiseta longiareolata*. *Ecological Entomology* **24**:202–207.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford, UK.
- van Pletzen, R. 1981. Larval and pupal behaviour in *Culiseta longiareolata* (Macquart, 1838) (Culicidae, Diptera). *Journal of the Limnological Society of South Africa* **7**:24–28.
- van Pletzen, R., and T. C. d. K. van der Linde. 1981. Studies on the biology of *Culiseta longiareolata* (Macquart) (Diptera: Culicidae). *Bulletin of Entomological Research* **71**:71–79.
- Walton, W. E., and M. S. Mulla. 1991. Integrated control of *Culex tarsalis* larvae using *Bacillus sphaericus* and *Gambusia affinis*: effects on mosquitoes and nontarget organisms in field mesocosms. *Bulletin of the Society for Vector Ecology* **16**:203–221.
- Ward, D., and L. Blaustein. 1994. The overriding influence of flash floods on species-area curves in ephemeral Negev Desert pools: a consideration of the value of island biogeography theory. *Journal of Biogeography* **21**:595–603.