RESEARCH ARTICLE

Modelling evolutionarily stable strategies in oviposition site selection, with varying risks of predation and intraspecific competition

Arik Kershenbaum · Matthew Spencer · Leon Blaustein · Joel E. Cohen

Abstract   Many ovipositing mosquitoes, as well as other species, can detect biotic factors that affect fitness. However, a female mosquito seeking a high quality oviposition site (e.g. one with low risk of predation and competition to her progeny) must often balance the competing risk of increasing probability of mortality to herself while she continues to search, against increased probability of finding a high quality site. Such oviposition site selection may affect adult population size. We examined a female mosquito's expected strategy of oviposition site selection under conditions of varying predator prevalence and adult mortality risk, by combining a detailed structured population model with a Markov chain implementation of the adult behavioural process. We used parameter values from the specific mosquito-predator system, *Culiseta longiareolata-Notonecta maculata*, although the overall results can be generalised to many mosquito species. Our model finds the evolutionarily stable strategy of oviposition site selection for different parameter combinations. Our model predicts that oviposition strategy does not vary smoothly with varying environmental risk of adult mortality, but that certain oviposition strategies become unstable at some parameter values. Mosquitoes will distribute their reproductive effort between breeding sites of varying predation risk only when adult mortality is low or larval competition high. Our model predicts that females will continue searching for predator-free pools, rather than oviposit in the first site encountered, regardless of the risk of mortality to the adult. The ecological basis for a reproductive strategy with alternative behaviours is important for understanding the effect of biotic factors on the population dynamics of

A. Kershenbaum (✉) · L. Blaustein
Department of Evolutionary and Environmental Biology, Faculty of Natural Sciences, and the Institute of Evolution, University of Haifa, Haifa, Israel
e-mail: arik.kershenbaum@gmail.com

M. Spencer
School of Environmental Sciences, University of Liverpool, Liverpool, England, UK

J. E. Cohen
Laboratory of Populations, Rockefeller University and Columbia University, New York, NY, USA

ⓢ Springer

mosquitoes, and for the development of biological control strategies, such as the dissemination of predator-cue chemicals.

Introduction

Natural selection should favour a strategy of habitat selection that maximises fitness (Fretwell and Lucas 1969). For example, selection of foraging sites should be influenced by density-dependent effects to avoid intraspecific competition. Predation risk also may influence habitat selection, with individuals preferring sites either with lower predator densities (Silberbush and Blaustein 2011), or with habitat features such as structural complexity that reduce predation risk (Sadeh et al. 2009). Many species of arthropods and amphibians deposit progeny (eggs or larvae) that are constrained to the breeding habitat until metamorphosis, so that the choice of oviposition site is very important. In choosing sites for oviposition, females have to consider multiple—and possibly conflicting—factors to arrive at a site selection strategy that will optimise their own fitness (Blaustein 1999). The site selection strategy may have consequences at the population level, as natural selection favours strategies maximising surviving offspring, thereby increasing population size, and this could be important in interpreting and designing biological pest control experiments, e.g. Spencer et al. (2002a), Shaalan and Canyon (2009), since manipulation of predator distributions could bring about reduction in pest population sizes.

Many oviparous species avoid oviposition in habitats with high risk of predation to their larvae, including mosquitoes (Blaustein et al. 2004; Reguera and Gomendio 2002; Rieger et al. 2004; Vonesh and Blaustein 2010), anurans (Binckley and Resetarits 2002; Rieger et al. 2004), terrestrial bugs (Reguera and Gomendio 2002) and mites (Choh and Takabayashi 2010). However, exclusive avoidance of habitats in which a larval predator is present could lead to overcrowding of predator-free habitats, and could result in negative density-dependent effects on offspring fitness. In addition, continuing to search for preferred sites incurs additional risk of adult mortality (Ward 1987). We expect a three-way tradeoff among larval predation, larval density, and adult mortality (Fig. 1).

In an environment that is riskier to an ovipositing female, females might be expected to oviposit in the first habitat encountered, regardless of the fitness it confers.

An alternative possibility is that when the overall environmental adult mortality is high, adult population size becomes low, and so larval density is low across all sites. Pools free of conspecific prey larvae and predators then become more desirable and worth continuing to search for. Therefore, a species that can detect predators and conspecific density might be expected to adopt a "mixed oviposition strategy", in which it distributes its reproductive effort among alternative reproductive behaviours (Austad 1984): it lays some eggs in predator-free environments and some in predator-inhabited ones.

One kind of reproduction-distributing strategy is "stochastic", sensu Dawkins (1980): the probability of choosing a habitat is positively related to the perceived fitness benefit of that habitat. This probabilistic outcome is in contrast to that of an ideal-free distribution (Fretwell and Lucas 1969) in which the forager knows the habitat qualities of each patch. The stochastic strategy would evolve within the population to an evolutionarily stable strategy (ESS) (Dawkins 1980; Maynard Smith and Price 1973), so that when the entire population adopts the ESS, a deviant strategy with a different proportion of eggs in each
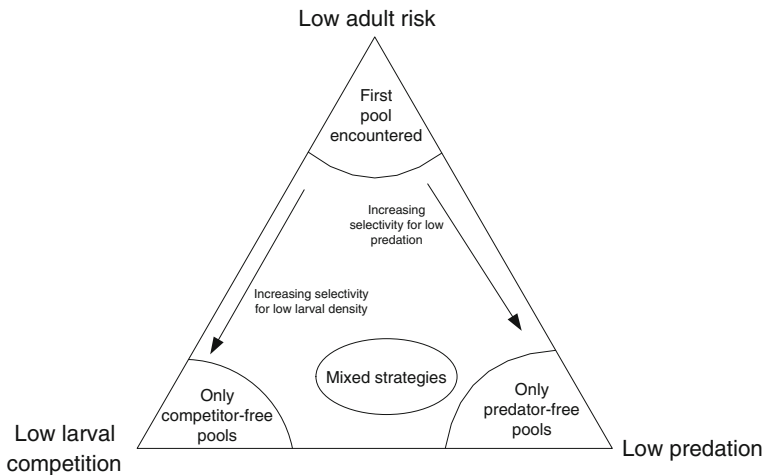
Fig. 1 Qualitative schematic diagram of the three-way tradeoff among larval competition, predation, and adult survival. Pure strategies minimise adult mortality (*top apex*) by ovipositing in the first pool encountered, minimise predation (*right apex*) by ovipositing only in predator-free pools, and minimise larval competition (*left apex*). Mixed strategies in the *bottom half* of the triangle, where adults are selective about oviposition site, balance predation against larval competition

type of habitat would gain no fitness benefit over the common strategy and would not spread through the population.

Numerous arthropod and amphibian species adopt a mixed oviposition strategy, including mosquitoes (Blaustein et al. 2004), golden egg bugs (Reguera and Gomendio 2002), treefrogs (Binckley and Resetarits 2002), cherrybugs (Nakajima and Fujisaki 2010), and others, reviewed in Mayhew (1997).

Larvae and pupae of the mosquito *Culiseta longiareolata* are highly vulnerable to predation by the backswimmer *Notonecta maculata* (Blaustein 1998). Conspecific larval density can strongly influence larval survival (Kiflawi et al. 2003a; Munga et al. 2006) and adult fitness (Reiskind and Lounibos 2009). Therefore, a tradeoff would be expected between the advantage of avoiding habitats with high predation risk and the disadvantage of high larval density. *C. longiareolata* females may use chemical cues to detect and avoid high larval conspecific density (Blaustein and Kotler 1993; Kiflawi et al. 2003a, b) and risk of predation by *N. maculata* (Blaustein et al. 2004; Silberbush and Blaustein 2011).

Using a nonlinear stage-structured population model Spencer et al. (2002a) predicted that *C. longiareolata* should always oviposit in pools without *N. maculata* to maximise individual fitness, and if it did so, adult population size would increase. Spencer et al. (2002a) considered two types of habitat: pools where *N. maculata* was present, and pools where they were absent, which were assumed to occur in equal proportions.

We extended the Spencer et al. model to incorporate a varying prevalence of *N. maculata* pools in the environment, and varying adult mosquito daily survival. We explicitly modelled the tradeoff between continuing to search for "higher quality" pools and the risk of mortality while searching, and we investigated the resulting qualitative changes in reproductive strategy. Pool "quality" was determined by both predator presence or absence (an environmental factor), and larval crowding, which is a function of the mosquito's site selection strategy.

Predator density is correlated with mosquito success in surviving to emergence as an adult (Eitam and Blaustein 2004; Murdoch et al. 1984). When given pair-wise choices,

female mosquitoes can quantify predation risk (Silberbush and Blaustein 2011). In a mosaic of different *Notonecta* densities, *Culiseta* mosquitoes treat the pools as either predator-free or predator-present (Eitam and Blaustein 2004).

We expected that the competing risks of *N. maculata* predation and larval density-dependent competition, together with adult search mortality, will cause mosquitoes to display a mixed oviposition strategy, where the female sometimes lays her eggs in predator-free pools, and sometimes in predator-inhabited pools. Some data support this hypothesis (Blaustein and Whitman 2009; Kiflawi et al. 2003a). Site preference (i.e. selectivity) should depend on maternal mortality risk, as well as predator prevalence and larval density. We expect adult mortality risk to be the main determining factor on oviposition strategy, and we investigate whether a mixed strategy is more or less likely when the mortality risk to adult mosquitoes is high.

Methods

We simulated mosquito oviposition using a hybrid model, combining two different techniques to capture two different aspects of the system: a structured population projection matrix to describe the population dynamics, and a Markov chain to describe the behaviour of adult mosquitoes in response to environmental cues. We use *C. longiareolata* and *N. maculata* as our model system, in particular because many parameter values have been measured, though this model could be adapted to other mosquitoes and other predators. In canyon pools in the deserts of the Middle East, *C. longiareolata* is by far the most abundant organism (Blaustein and Margalit 1995; Blaustein et al. 1995), and is subject to conspecific density dependent effects (Kiflawi et al. 2003a). *C. longiareolata* is often without influential competitors for months after the rainy season begins, before some pools are colonised by tadpoles of its competitor *Bufo viridis* (Blaustein and Margalit 1995; Blaustein and Margalit 1996; Stav et al. 2010).

Our models simulated a system with eggs laid into two pool types in the environment, predator pools and predator-free pools. Eggs hatch into larvae, which are subject to predation and density-dependent intraspecific competition. After larvae metamorphose into pupae and then into adults, the adults (after a blood meal and egg development) seek oviposition sites and lay eggs according to a strategy that takes into account both predator presence/absence, and existing larval density.

We simulated the population dynamics separately in each pool type using the structured population projection matrix. This model calculated the number of individuals in each stage of the mosquito lifecycle in each pool type, and we then used a Markov chain model to calculate the predicted oviposition rates in the different types of pools, given behavioural parameters. These two combined models calculated the equilibrium adult population size and the relative fitness of individuals who used the two types of pools.

Population dynamics

The projection matrix technique was based on that used by Spencer et al. (2002a) and described in detail in Cushing (1996). We considered eight population compartments: eggs (e), larvae (l), pupae (m), and adults (u), for each of the two types of pools: predator-free pools (f), and "predator" pools where predators are present (p). The state of the system at any time was given by the vector $\mathbf{j} = [e_f, l_f, m_f, u_f, e_p, l_p, m_p, u_p]^T$, where subscripts indicate

the type of pool. The state after one time step (one day, in our simulation) was calculated as:

$$\mathbf{j}(t+1) = \mathbf{A} \cdot \mathbf{j}(t) \tag{1}$$

where $\mathbf{A}$ is the projection matrix defined in (2). The elements of the projection matrix specify the contribution per individual from each (column) compartment to each (row) compartment.

	Predator-free				Predator			
	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults

$$A = \begin{bmatrix} 1-H & 0 & 0 & K_f & 0 & 0 & 0 & K_f \\ H & \Pi_f & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \Delta_f & 1-M & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & M & \Sigma & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & K_p & 1-H & 0 & 0 & K_p \\ 0 & 0 & 0 & 0 & H & \Pi_p & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \Delta_p & 1-M & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & M & \Sigma \end{bmatrix} \tag{2}$$

A description of all the symbols is given in Table 1. Three of the values in the projection matrix, Σ (the survival of adults), and K_f, K_p (the numbers of eggs laid per adult in the predator-free and predator pools respectively), depend on the behavioural response of adult mosquitoes to the presence of predators in the pool (Fig. 2), and will be derived from the Markov chain. H represents the proportion of eggs that hatch to become larvae each day, and M represents the proportion of pupae that emerge to become adults each day. H, M, and Σ are independent of the presence or absence of predators, since *Notonecta* feeds only on larvae, not on *Culiseta* eggs, pupae, or adults. Π and Δ are nonlinear growth functions that describe the density-dependent effects on larvae within the pool, as defined in Spencer et al. (2002a). We describe them here in brief: Let v_i be the proportion of larvae that survives each day in pools of type i, $i \in \{f, p\}$:

$$v_i = \exp(-\mu - \beta l_i/P_i - \gamma N) \tag{3}$$

where μ is the instantaneous mortality rate of larvae at low density in the absence of predators, β is the per capita effect of number of larvae on larval death rate per day (due to cannibalism and competition), l_i is number of larvae in pools of type i, P_i is the proportion of pools of type i (l_i/P_i therefore being a measure of larval density in pools of type i), γ is the per capita effect of predators on larval mortality per day, and N is the number of predators in a predator pool. Let w_i be the proportion of survivors that becomes pupae each day,

$$w_i = d \, \exp(-\alpha l_i/P_i) \tag{4}$$

where d is the proportion of larvae developing into pupae per day at low density and α is the effect of each additional larva on development rate (per larva). Then $\Delta = vw$ and $\Pi = v(1 - w)$.

For the population model, we used the assumptions detailed and justified in Spencer et al. (2002a), summarised below:

1. All pools in a region are available to every adult female mosquito, and the fitness of larvae in these pools is affected only by the presence or absence of predators and the

Table 1 Symbols used in the model and their meanings

Symbol	Description	Estimated value
a	Probability of ovipositing in an encountered predator-free pool	0–1
a_0	Probability of ovipositing in an encountered predator-free pool with no larvae present	1
b	Probability of ovipositing in an encountered predator pool	0–1
b_0	Probability of ovipositing in an encountered predator pool with no larvae present	0–1
d	Proportion of immatures developing into adults per day at low density	1/14
e_f, e_p	Number of eggs in the predator-free and predator pools respectively	–
F	Number of eggs laid per adult per day	–
G	Gestation period	6 days
H	Proportion of eggs that hatch each day	½
i	Pool type, "predator-free" or "predator"	f, p
K_f, K_p	Number of eggs laid per adult each day in the predator-free and predator pools respectively	–
l_f, l_p	Number of larvae in the predator-free and predator pools respectively	–
M	Proportion of pupae that emerge each day	½
N	Number of predators in a pool	2
P_f, P_p	Proportion of pools that are predator-free and predator pools respectively	0–1
S	Proportion of adults that survive each day on average	0.5–1
S_b	Proportion of adults that survive the search for a blood meal	0.25–1
S_g	Proportion of adults that survive one day of gestation	0.7–1
S_s	Proportion of adults that survive the search for a single oviposition pool	0.38–1
T	Time (measured in days)	1–4,000 days
u_f, u_p	Number of adults in the predator-free and predator pools respectively	–
V	Proportion of immatures that survive each day	–
W	Proportion of immatures that become adult each day	–
Δ_f, Δ_p	Proportion of immatures that survive and become adult in the next day in the two types of pools	–
Π_f, Π_p	Proportion of immatures that survive to the next day but do not become adult in the two types of pools	–
Σ	Proportion of adults that survive to lay eggs	–
Ω	Expected adult life span	–
α	Effect of each additional immature on development rate (per immature)	2.1×10^{-4}
β	Effect of number of immatures on death rate per immature per day (due to cannibalism and competition)	2×10^{-3}
γ	Per capita effect of predators on immature survival per predator per day	0.23
μ	Instantaneous mortality rate of immatures at low density in the absence of predators	1.7×10^{-2}
ω	Effect of larvae already in pool on the oviposition decision of an adult	2.3×10^{-3}

number of mosquito larvae. Temporary rock pools in Israel often occur in wadis or exposed areas of bedrock, with many similar pools in areas of a few hundred square meters (Kiflawi et al. 2003c; Spencer et al. 2002b). Maximum flight distances of many mosquitoes are several kilometres (Service 1976), so all pools in a small area are likely to be available to any female.

Fig. 2 The structured population model. Each pool (predator and predator-free) was simulated separately, with progression from eggs to larvae to pupae to adults. Individuals moved from pool to pool only in the adult stage, where the parameters of pool selection (K) are determined by the Markov chain model
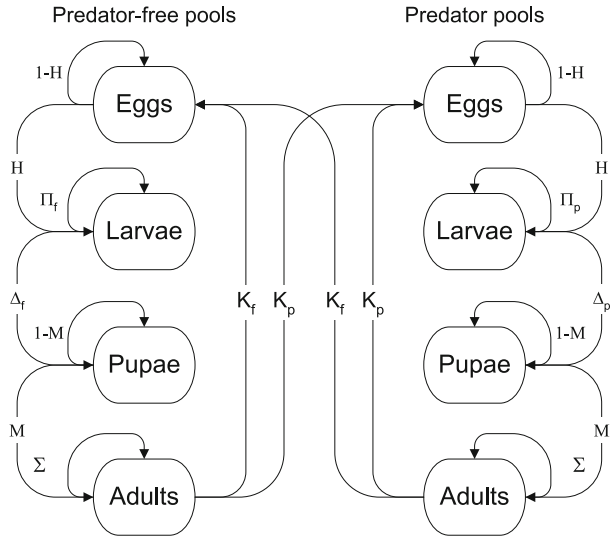
2. All females produce egg rafts with a constant number of eggs. The mean number of eggs per field-collected egg raft is 280 and eggs of *C. longiareolata* are rarely laid singly in the laboratory (Van Pletzen and Van Der Linde 1981). Our model did not explicitly group eggs into rafts.

3. Oviposition occurs only once in each 24-h period. This assumption allowed us to use a discrete-time structured population model with a time step of one day. *C. longiareolata* oviposits only at night (Van Pletzen and Van Der Linde 1981).

4. Predators do not move from pool to pool and their numbers remain constant over time. *N. maculata* larvae are wingless (adults can fly but are much less abundant than larvae). We assumed predator numbers remained constant, because other *Notonecta* species have much longer generation times than mosquitoes (Murdoch et al. 1984; Murdoch et al. 1985). When *C. longiareolata* densities are manipulated in artificial pools, *N. maculata* does not colonise these pools in response to *Culiseta* densities (Hill and Blaustein, unpublished data). Thus, we do not expect a numerical response of *Notonecta* in a given pool to *Culiseta* densities.

5. All predator pools are assumed to have the same density of predators and the distribution of predator pools is homogeneous in the environment.

6. The rate at which predators consume larvae is a linear function of the number of larvae 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 (Blaustein et al. 1995; Blaustein 1998).

7. *N. maculata* predation on egg rafts is rare or does not occur (Blaustein, unpublished data) and predation on adults does not occur. Female *C. longiareolata* alight on the water surface when ovipositing, but remain above the surface film and are therefore unlikely to be vulnerable to attack by *N. maculata*, which feeds below the surface film.

8. We do not consider changes in abiotic conditions such as temperature throughout the whole simulation.

A two-patch model does not capture the dynamics of flow between adjacent patches in a spatially structured array of patches, such as a chain of islands or 2-dimensional array;

rather, it approximates the properties of an array in which every patch is equally accessible from every other patch. We choose, however, to use the two-patch configuration since mosquitoes are considered to range widely and have access to all pools (assumption 1). The condensation of multiple patches into a stereotyped example of each patch type, making no assumptions about the nature of adjacent patches, is a well established technique (e.g. Abrams et al. 2007; Holt 1985). However, if flight search range is limited and restricts the pools to which an individual female has access, and if pools are not homogeneously distributed, then the patchiness of predator pool presence might affect the results of the simulation. In a sensitivity test, we varied the homogeneity of pool distribution under the assumption that every patch is equally accessible from every other patch, and observed no significant effect on the simulation results (see Supplementary Material).

Behavioural model

The number of eggs deposited in each type of pool depends on the behaviour of adult mosquitoes. Lifespan and the preference for each type of pool determine the average number and location of oviposition events for each adult female. To calculate these, we represented the adult part of the life cycle as a Markov chain (Fig. 3). The transition probabilities from one state to another are conditional on an event having occurred. We now define each assumption in this model and its parameters: S, S_b, S_g, S_s, P_f, a, and b.

Assumptions

1. Female *Culiseta* mosquitoes mate soon after emergence. We began our model with a mated adult female.
2. The mated female searches for a blood meal. We denoted the probability of survival to a gravid state by S_b. We assumed that the search for a blood meal always ends in a single day either in success or mortality, and that the female becomes gravid on taking a blood meal.
3. After taking a blood meal, the mosquito gestates for G days. During this time, the overall probability of survival (not daily) is S_g. The value of G is used later in the model to calculate the expected life span.
4. The mosquito searches for an oviposition site.
5. Pools have one of two predator statuses: predator-free pools which are encountered with probability P_f, and predator pools which are encountered with probability $P_p = 1 - P_f$.
6. Having found a pool of one or the other type, the mosquito chooses whether to oviposit according to the predator status and the larval density in the pool. We assumed that pools of the same predator status have identical larval density.
7. If the mosquito chooses not to oviposit, it continues to search, i.e. returns to step 4. We made the simplifying assumption that the search always ends with either oviposition or mortality. That is, a mosquito may be choosy during the course of a single day, but it does not retain its eggs for a second day. There is some evidence (Kiflawi et al. 2003a; Silberbush and Blaustein 2011; Silberbush et al. 2010) that if only poor conditions are available, mosquitoes will not oviposit at all; i.e. will continue to search until they die.
8. A mosquito does not become less choosy if it initially encounters only predator pools and does not oviposit, i.e. there is no change in the "motivation" to oviposit if
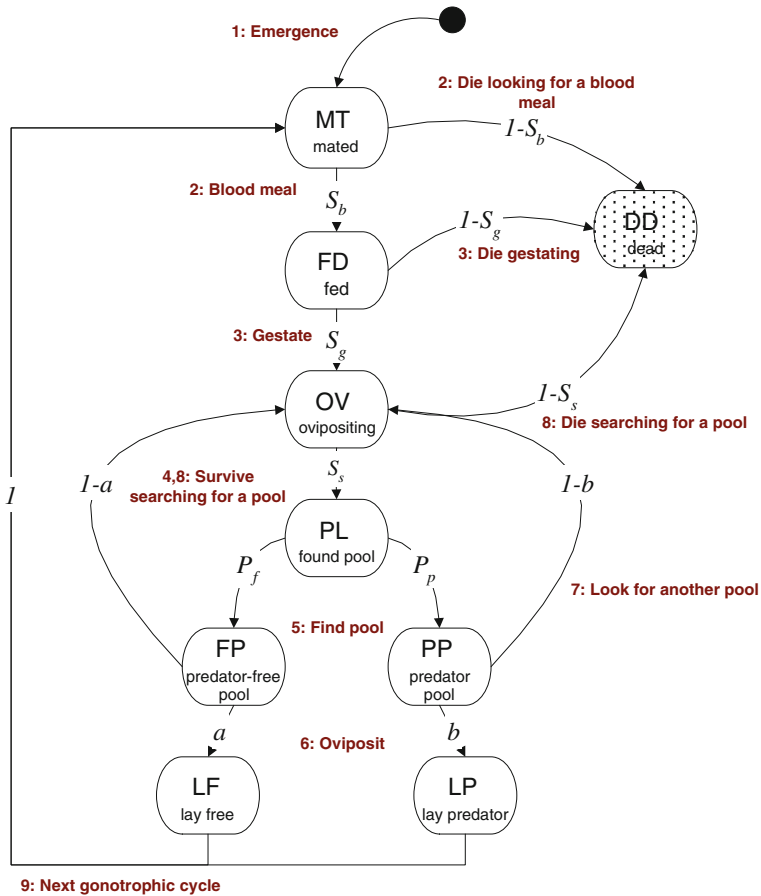
Fig. 3 Markov chain representing the adult mosquito's reproductive life cycle

predator-free pools are not encountered, and the "preference" for predator-free pools also remains constant (Root and Kareiva 1984).

9. The mosquito is exposed to a risk of mortality $1 - S_s$ each time it searches for a pool. Choosing not to oviposit in an encountered pool therefore incurs additional risk of mortality.
10. If a mosquito survives the search and oviposits, it returns to the mated state; female mosquitoes store sperm in their spermatheca and we assumed that no further mating is required to take another blood meal and lay another batch of eggs (Spielman et al. 2001, p. 12).

Survival probabilities

No studies estimate adult mortality rates associated with different activities such as feeding versus gestation. However, many studies have attempted to estimate general daily adult survival probability, denoted here by S. Daily mortality could reflect a number of environmental conditions, such as inter-pool distances (affecting flight time while searching),

the effects of species that prey on adult mosquitoes, or human intervention such as insecticide spraying (Roitberg and Mangel 2010). In our simulations, we varied S between realistic extremes to cover a wide range of environments with different adult mortality (for empirical estimates, see Kiszewski et al. 2004), and gave only a qualitative relationship between S and the activity-specific survival rates, S_b and S_g. Although some mosquito species may venture out and take sugar meals during gestation (Manda et al. 2007), the gestation period is still a relatively sedentary activity, and therefore the adult is less exposed to predation, so we assumed $S_g > S_b$, i.e. that the probability of surviving the gestation period of G days is greater than the probability of surviving the search for a single blood meal. We performed a sensitivity analysis in which S_b and S_g were varied by 10% for constant S, and observed that the results obtained were qualitatively similar (for brevity, they are not reported here). Although we had no estimate of the mortality while searching for oviposition sites, we assumed that it too is less risky than searching for a blood meal (as the mosquitoes are not exposed to defensive reactions of host animals), but riskier than the daily average, i.e. $S_b < S_s < S$. Reiskind and Wund (2009) showed a 32% reduction in oviposition events in the presence of a predator of adult mosquitoes (long-eared bats, *Myotis septentrionalis*). We applied this mortality risk each time the mosquito searches for a pool, i.e. more "pickiness" increases the risk of mortality while searching. Searching survival rate (S_s) could be considered a proxy for pool abundance, since if pools are closely spaced, continuing to search for a superior oviposition site is less risky than if long flights are needed to find alternative sites.

Oviposition probability

Mosquitoes can use two criteria for choosing to oviposit in a pool (as opposed to continuing to search for a "better" pool): the presence or absence of predators, and the density of mosquito larvae in the pool (Munga et al. 2006). We denoted the probability that a mosquito will oviposit in a predator-free pool as *a(l)*, and the probability that it will oviposit in a predator pool as *b(l)*, where *a(l)* and *b(l)* are functions of the number of larvae *l* currently in the pool. We modelled the dependence of *a* and *b* on *l* as exponential, i.e.:

$$a(l_f) = a_0 e^{-\omega l_f}$$
$$b(l_p) = b_0 e^{-\omega l_p} \tag{5}$$

where a_0 and b_0 are the probabilities of ovipositing in predator-free and predator pools respectively when there are no larvae present, and ω is the effect of larvae already in the pool on the oviposition decision of an adult. We assume this to be the same constant for predator-free and predator pools, as it seems plausible that behavioural responses could evolve more rapidly than life history characteristics. Kiflawi et al. (2003a) showed that more than 1,000 *C. longiareolata* larvae in a 36-litre pool resulted in reduction of almost 90% in the probability of oviposition. We therefore selected a value of $\omega = 2.3 \times 10^{-3}$ which is consistent with the above observations, and also varied ω around this value. We further assumed that $a_0 = 1$, since a pool without predators and without other larvae represents the optimal oviposition habitat (all other factors being equal), and a gravid mosquito should oviposit immediately in such a pool.

As with Spencer et al. (2002a), we assumed that in a population at equilibrium, the values of a_0 and b_0 represent an evolutionarily stable strategy (ESS). This means that no alternative strategy of a_0' and b_0' can spread through the population. Since we assumed above that $a_0 = 1$, the oviposition strategy is defined solely by the parameter b_0. We found this stable

strategy using the Bishop–Cannings theorem (Bishop and Cannings 1978): if an ESS mixed strategy b_0* exists, then the fitnesses of a deviant adopting the two pure strategies ($b_0 = 0$ and $b_0 = 1$) will be equal. At such a point, if it exists, a deviant with an alternative oviposition strategy gains no advantage over the common strategy. Using the results of Cushing (1996) we derived the expected fitnesses of deviants with strategies $b_0 = 0$ and $b_0 = 1$, namely,

$$F_0 = \Omega_0 K_f^0 \frac{\Delta_f}{1 - \Pi_f}$$
$$F_1 = \Omega_1 \left[K_f^1 \frac{\Delta_f}{1 - \Pi_f} + K_p^1 \frac{\Delta_p}{1 - \Pi_p} \right]$$

$$(6)$$

where the nonlinear growth functions Δ and Π are functions of larval density and hence of the common strategy b_0*. Ω_0 and Ω_1 are the expected lifespans of individuals adopting the $b_0 = 0$ and $b_0 = 1$ strategies respectively, and K_f^0, K_f^1, K_p^1 are the number of eggs laid in the different types of pools by the 0 and 1 strategies. Note that a strategy of $b_0 = 1$ still results in some eggs being laid in predator-free pools. To determine the values of these functions, we simulated the full model to convergence for each value of b_0. We found the ESS value of b_0, if one existed, by finding where $|F_0 - F_1| = 0$ using standard iterative minimisation algorithms (*fminbnd()*, Matlab, v7.1). If the fitness of one pure strategy is always higher than that of the other for all values of b_0 in [0, 1], then the expression $F_0 = F_1$ does not hold for any value of b_0, and no mixed ESS exists: the only stable strategy is one of the two pure strategies.

Once the parameters of this Markov chain were defined, we calculated the expected number of oviposition events in the two types of pools, predator-free and predator. The transition matrix **T** based on Fig. 3 is:

$$
\mathbf{T} =
\begin{array}{c|ccccccccc}
 & MT & FD & OV & PL & FP & PP & LF & LP & DD \\
\hline
MT & 0 & S_b & 0 & 0 & 0 & 0 & 0 & 0 & 1 - S_b \\
FD & 0 & 0 & S_g & 0 & 0 & 0 & 0 & 0 & 1 - S_g \\
OV & 0 & 0 & 0 & S_s & 0 & 0 & 0 & 0 & 1 - S_s \\
PL & 0 & 0 & 0 & 0 & P_f & P_p & 0 & 0 & 0 \\
FP & 0 & 0 & 1 - a & 0 & 0 & 0 & a & 0 & 0 \\
PP & 0 & 0 & 1 - b & 0 & 0 & 0 & 0 & b & 0 \\
LF & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
LP & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
DD & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\end{array}
$$

$$(7)$$

Abbreviations of the states are defined in Fig. 3. Defining **Q** as the top left quadrant of **T** obtained by omitting the row and column of the absorbing state, *DD*:

$$
\mathbf{Q} =
\begin{bmatrix}
0 & S_b & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & S_g & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & S_s & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & P_f & P_p & 0 & 0 \\
0 & 0 & 1 - a & 0 & 0 & 0 & a & 0 \\
0 & 0 & 1 - b & 0 & 0 & 0 & 0 & b \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{bmatrix}
$$

$$(8)$$

The fundamental matrix **J** is given by $\mathbf{J} = (\mathbf{I} - \mathbf{Q})^{-1}$. The expected number of visits to *LF* and *LP* are given by $\mathbf{J}_{MT \to LF}$ and $\mathbf{J}_{MT \to LP}$ respectively, and these represent the number of oviposition events in each type of pool.

To calculate the average number of eggs laid per day, we estimated the expected lifetime of an adult, Ω, by summing the result of the element-by-element multiplication (Hadamard product) of the fundamental matrix $\mathbf{J}$ by the number of days of each step: i.e. $\{MT \rightarrow FD, \, OV \rightarrow LF, \, LP\}$ = one day, $\{FD \rightarrow OV\} = G$ days. Assuming 280 eggs per oviposition event (Van Pletzen and Van Der Linde 1981), and a 50:50 ratio of males to females, the average number of female eggs laid per day per adult female mosquito (F) in predator-free and predator pools is:

$$F_f = 140\,\frac{\mathbf{J}_{MT \rightarrow LF}}{\Omega}$$
$$F_p = 140\,\frac{\mathbf{J}_{MT \rightarrow LP}}{\Omega} \tag{9}$$

Numerical solution

We iterated the projection matrix $\mathbf{A}$, beginning from a state of two adults in a predator-free pool, until the populations of all compartments in both types of pools converged (relative change $<10^{-5}$ per time step). At this point, we calculated the total adult population as $u_f + u_p$, and the oviposition probabilities (a & b), as well as the larval populations sizes for each pool type. We obtained numerical solutions for varying predator prevalence (P_p) and varying daily adult survival rate S. We fixed the values of other parameters to those found in previous studies. Spencer et al. (2002a) varied the density-dependent mortality of larvae (β) between what they considered reasonable values, but more recent studies, e.g. Maciá (2009), have shown that a higher estimate may be appropriate. We chose $\beta = 2 \times 10^{-3}$ which is the maximum value used by Spencer et al. (2002a). These researchers also varied the mean number of eggs per adult per day (F), whereas we used a fixed gestation period $G = 6$ days to derive F from the Markov section of the model.

Results

An ESS does not exist for all values of daily adult survival S and predator pool prevalence P_p. At low daily adult survival, the fitness of the pure strategy $b_0 = 0$ is higher than that of $b_0 > 0$ for all common strategies, implying that under these circumstances, the gravid mosquito should never lay eggs in a predator pool with no larvae present. As the daily adult survival increases, the fitness of the $b_0 = 0$ strategy falls (Fig. 4), and eventually intersects the $b_0 = 1$ fitness curve, for some value of the common b_0. This point then represents an ESS, since when $F_0 = F_1$, no benefit can be gained by switching oviposition strategy. This behaviour is characteristic of a saddle-node bifurcation, and indicates the loss of stability of the mixed oviposition ESS when the daily adult survival is decreased; or the loss of stability of the exclusive predator-free pool oviposition strategy when the adult survival increases beyond the critical value. Figure 5 shows the ESS mixed strategy b_0^* for varying predator prevalence (P_p) and daily adult survival (S) when $\beta = 2 \times 10^{-3}$. Remembering that $a_0 = 1$, the probability of ovipositing in predator pools (b_0) defines the oviposition strategy overall. Distributing egg rafts between predator-free and predator pools is a stable strategy only for high daily adult survival rates, and is gradually lost when S falls below around $S \approx 0.6$, although eggs are still laid in predator pools at lower adult survival, when predator pools are very common.
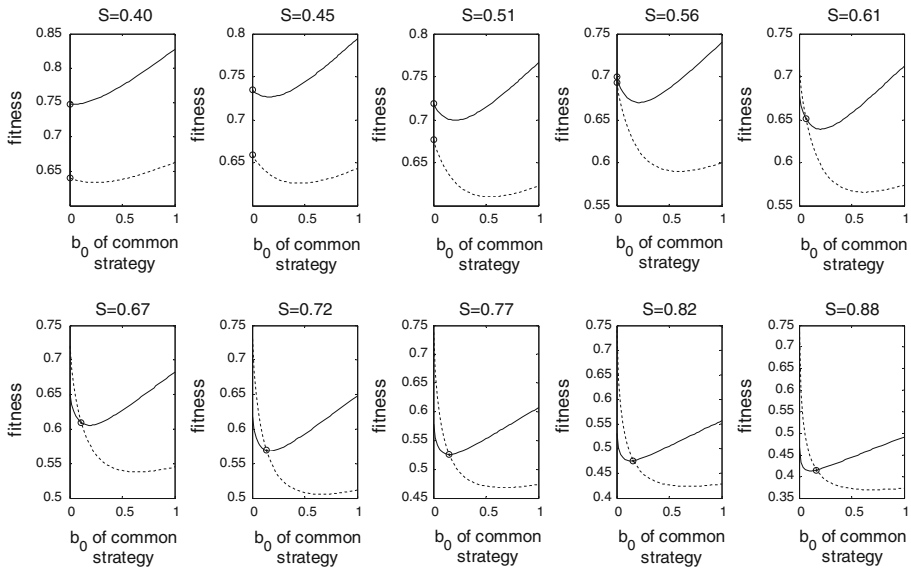
Fig. 4 Saddle node bifurcation of oviposition strategy with daily adult survival (*S*) as the control parameter. Each graph represents a different value of *S*, and shows the fitness on the *y*-axis, against the common strategy b_0 on the *x*-axis. The *two lines* represent the two types of pure strategy, $b_0 = 0$ (ovipositing in predator-free pools) as a *solid line*; and $b_0 = 1$ (ovipositing in predator pools) as a *broken line*. The *circle* indicates the location of the ESS. When the curves intersect, an evolutionarily stable mixed strategy is possible

Due to the non-linear form of the density dependent response (Eqs. 3, 4), it was not possible to derive a closed-form solution for the location of the bifurcation. Graphically, the probability of oviposition in predator pools rises with the proportion of predator pools in the environment, and the bifurcation occurs at much lower *S* when predator pools are very common.

Daily adult survival S affects the equilibrium adult mosquito population size more than the proportion P_p of predator pools (Fig. 6), although when adult survival is high, increasing the prevalence of predators in the environment can reduce adult mosquito population size by about half.

The probabilities of ovipositing in the two types of pools, *a(l)* and *b(l)*, are functions of the density of larvae already in the pool (Eq. 5). At low probabilities of adult survival, mosquitoes readily oviposit in predator-free pools (Fig. 7a, b), but at high adult survival rates, when larval density is high (Fig. 7c, d), the probability of ovipositing in predator-free pools falls to near zero when predator-free pools are common, although the number of eggs in these pools rises (Fig. 7e). The probability of ovipositing in predator pools (Fig. 7b) also falls somewhat as they become more common in the environment and the larval population in them becomes greater, but rises sharply at high predator prevalence as adult survival decreases.

The magnitude of the larval density-dependent effect, *β*, has a strong effect on the location of the bifurcation, i.e. the daily adult survival S at which the ESS destabilises. When larval density-dependent effects are weak, the mixed oviposition strategy is only stable at very high adult survival, but this threshold value of *S* falls rapidly when larval

Fig. 5 Probability of ovipositing in an encountered predator pool, with no larvae present (b_0), as a function of daily adult survival (S) and the proportion of predator pools in the environment (P_p)
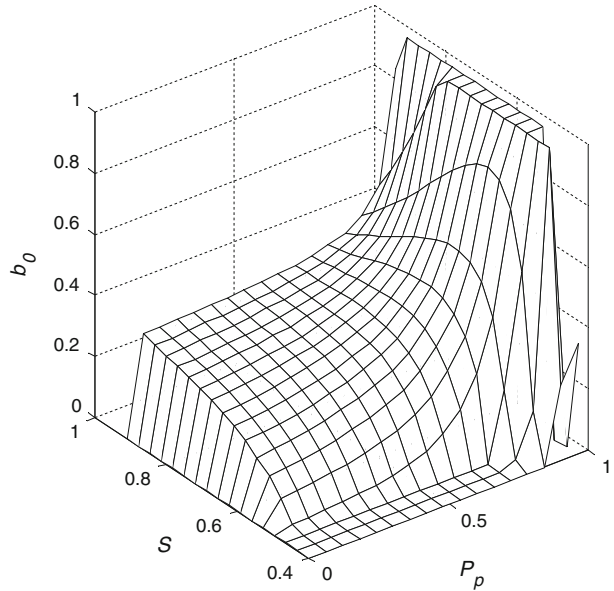

Fig. 6 Equilibrium adult population size, as a function of daily adult survival (S) and the proportion of predator pools in the environment (P_p)
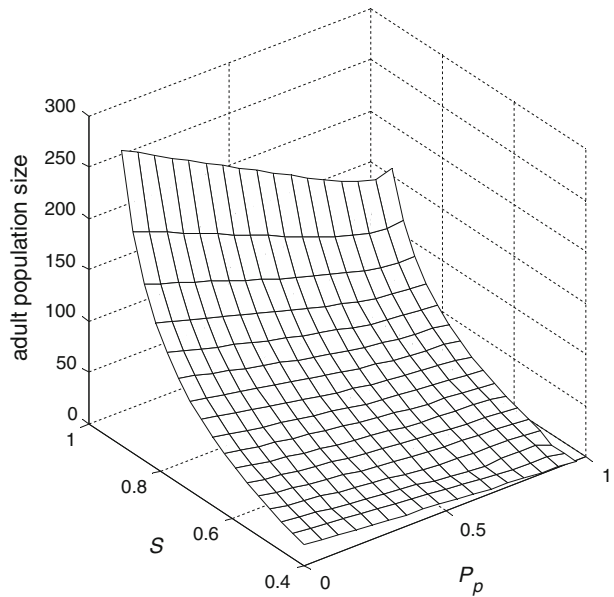

density effects increase (Fig. 8). This indicates that strong larval density-dependent effects are important for the existence of a mixed oviposition strategy.

Varying the value of ω, the response of adult mosquitoes to the existing density of mosquito larvae, did not qualitatively change the results of the simulation, although for extreme values of ω, the mixed strategy was restricted to only the highest values of S (data not shown).
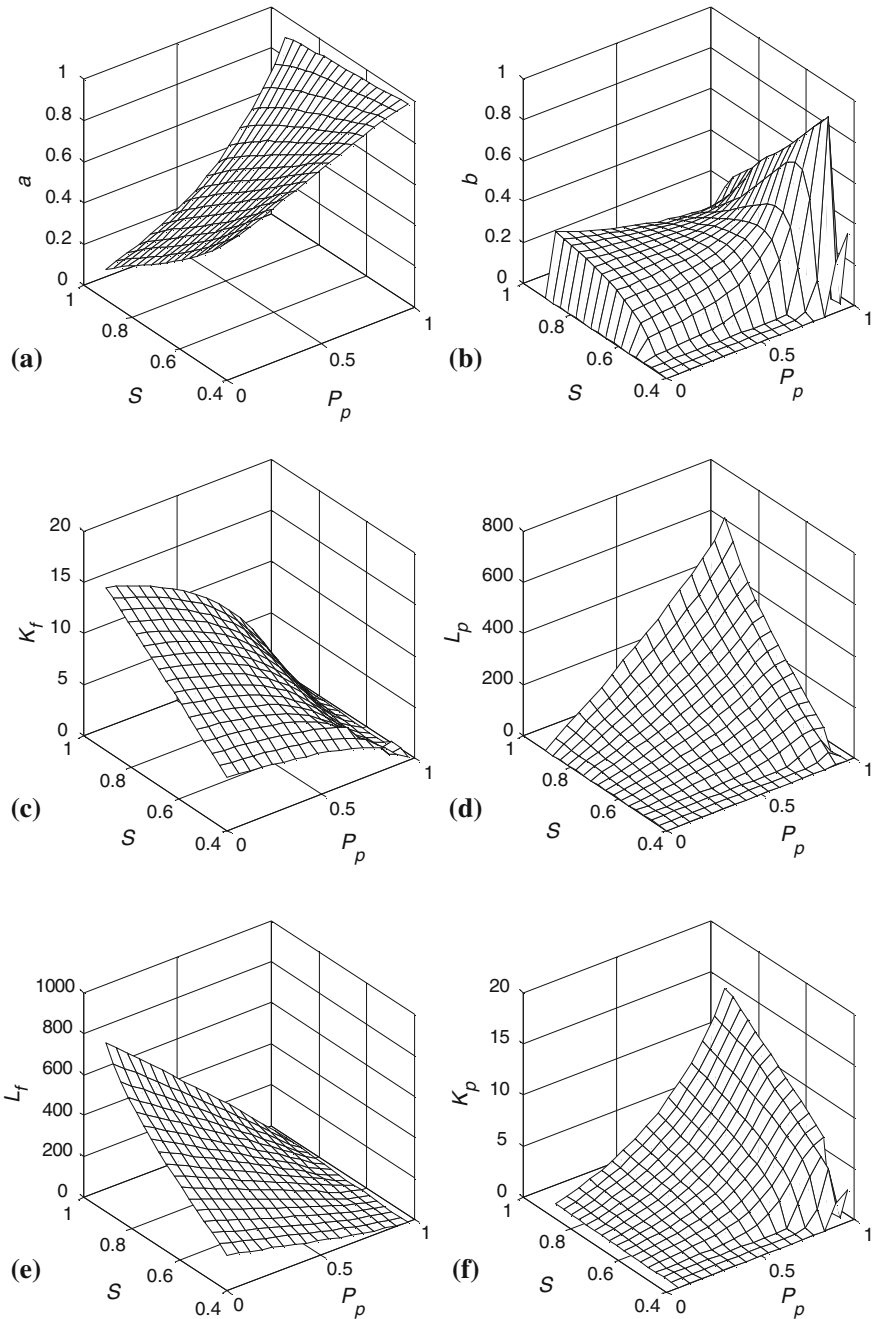
Fig. 7 Larval density and oviposition probability as functions of daily adult mosquito survival (S) and the proportion of predator pools in the environment (P_p). **a** and **b** show the probability of oviposition in predator-free and predator pools respectively, corrected for the existing density of larvae in the pools (Eq. 5). **c** and **d** show the larval population size in the two pool types. **e** and **f** show the number of eggs deposited in each type of pool per adult per day

Fig. 8 Threshold daily adult survival, S, below which a mixed strategy does not exist, for varying larval density dependent effect, β, when $P_p = 0.5$
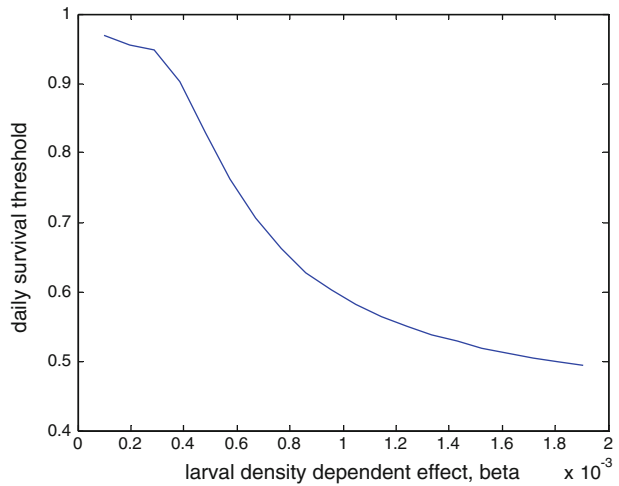
Discussion

Our model has shown that distribution of oviposition is a behaviour which does not exist below a critical larval density. Below that density, mosquitoes can be expected to lay all their eggs in predator-free pools. Above that density, mosquitoes distribute their eggs between predator and predator-free pools. A mixed reproductive strategy is evolutionarily stable only when the density-dependent effect of larval overcrowding balances the effect of predation. Since the strategy becomes unstable as the daily adult survival decreases, this qualitative change in adult mosquito behaviour is a form of saddle-node bifurcation. It appears that the bifurcation occurs as a result of population size changes (larval density), and only indirectly in response to altered daily adult survival, which determines larval population size.

This mechanism also explains an unexpected result: at low daily adult survival rates, mosquitoes are expected to ignore predator pools completely, unless very few predator-free pools exist in the environment ($P_p \approx 1$). It could be argued that when daily adult survival is low, mosquitoes should readily oviposit in the first pool they encounter in order to gain some fitness benefit before falling victim to the high mortality rate. However, on the contrary, our model predicted that, at low daily adult survival when the total adult population size is low, larval density in predator-free pools is low and so the relative advantage of a predator-free pool over a predator pool is much higher. A deviant mosquito that oviposits in predator pools at low daily adult survival cannot compensate for the lower fitness of a predator pool by avoiding overcrowding in predator-free pools, as the low overall population size means that these pools are not crowded.

At high adult survival rates and low predator prevalence, the probability of ovipositing in a predator-free pool fell to near zero in our model. This is because mosquitoes continue searching for low density pools, rejecting almost every predator-free but crowded pool that they encounter, until they die. If predator pools are rare, mosquitoes are unlikely to find such low density pools, but since adult daily survival is high, the adults can continue searching for a very long time. Clearly this assumption is at odds with findings of mosquito senescence (Styer et al. 2007), but this unexpected behaviour occurs only at the extremes of our parameter space.

Black and Dodson (1990) and Austad (1984) recognised that a tradeoff may exist in the selection of reproductive habitat. Mangel and Clark (1988) developed modelling tools to predict the optimal reproductive strategy using dynamic programming techniques, and Ward (1987) demonstrated that time-limited reproducers may choose suboptimal habitats for reproduction to avoid mortality while searching. Many studies have shown that mosquitoes avoid oviposition in habitats with predators present (Angelon and Petranka 2002; Blaustein et al. 2004; Chesson 1984; Eitam et al. 2002), and mosquitoes also avoid habitats overcrowded with conspecific larvae (Kiflawi et al. 2003a; Munga et al. 2006). The population consequences of this tradeoff have been modelled for a number of species, such as peacock wrasse (Warner et al. 1995), checkerspot butterflies (Singer et al. 1992), and tree frogs (Resetarits et al. 2004).

Our study consisted of a general modelling approach, and the results highlighted qualitative features of mosquitoes' reproductive strategy. Although our emphasis was on making qualitative predictions, some results agree well with quantitative studies. When presented with equal numbers of predator-free and predator pools, a number of studies showed that $\sim 10\%$ of *Culiseta* egg rafts are laid in predator pools (reviewed in Blaustein and Whitman 2009). We were not able to make quantitative predictions of adult population size due to a number of simplifying assumptions in building the model. First, the values of the mortality risk during different activities (feeding, ovipositing, gestating) were chosen arbitrarily, although the magnitude relationship between them was realistic. It is not easy to make empirical measurements of the mortality risk to mosquitoes during different activities in the wild. Second, our model ignored the activity of gestating females to take sugar meals. Taking sugar meals lowers gestating females' survival because it exposes them to predation (Manda et al. 2007; Stone et al. 2009). However, gestation while taking sugar meals remains less risky than taking blood meals or ovipositing. Third, our model does not consider the effect of mosquito size at metamorphosis as a predictor of reproductive success. Larger larvae may have a greater probability of survival as adults (Manoukis et al. 2006). Overcrowding is likely to affect adult mosquito population dynamics by pathways more complex than just larval mortality. This connection could be a useful direction for future research. Fourth and finally, although most parameters of the model were taken from empirical studies where possible (see Spencer et al. 2002a), in a number of cases where empirical data were unavailable and assumptions could be simplified, we preferred to simplify the model rather than assign arbitrary values to ecological parameters. For example, we assumed that similar pools have identical larval density, rather than a probability distribution. Our consideration of an ESS solution implicitly assumes that reproductive strategy is a heritable trait, an assumption discussed critically in Austad (1984).

Tradeoffs exist in all ecological systems. Understanding how these tradeoffs affect individual behaviour is necessary to predict ecological responses to environmental disruption, such as changes in daily adult survival caused by increased scarcity of oviposition sites. When qualitative changes in behaviour occur as the result of a small change in environmental parameters (bifurcation), it is particularly important to understand what behavioural changes are expected and under what circumstances. Bifurcations can cause catastrophic changes such as extinctions or population outbreaks (Strogatz 1994). Behavioural reproductive decisions cannot be ignored when investigating population dynamics, since individuals attempt to maximise their own reproductive fitness, rather than maximise overall population size (Smith et al. 2000). However, in our model, the effect on adult population size of behavioural bifurcations (when mosquitoes begin to deposit eggs in predator pools) appears to be small.

Although *C. longiareolata* is not considered an important disease vector, extension of this work to other mosquito species could be important for the control of medically relevant mosquito species. Spencer et al. (2002a) and Shaalan and Canyon (2009) proposed that it might be possible to control the population size of disease vectors by dispersing chemical cues of predators (predator-released kairomones) in the environment. Supplying the adult mosquitoes with false environmental cues may cause them to adopt a non-optimal oviposition strategy, and thus reduce overall mosquito population size. In particular, placing predator-released kairomones in potential oviposition sites might cause females to avoid these sites, leading to higher larval density in the remaining, non-kairomone pools, and therefore more density-dependent mortality. However, such a control strategy would be effective only if female mosquitoes use a mixed strategy, as appears to be the case with Culiseta (Blaustein and Whitman 2009). Our findings are important because they indicate that this occurs only in a limited region of parameter space (high adult survival). We are currently building models to investigate the efficiency of spreading one or more kairomones for mosquito control.

References

Abrams PA, Cressman R, Křivan V (2007) The role of behavioral dynamics in determining the patch distributions of interacting species. Am Nat 169:505–518

Angelon KA, Petranka JW (2002) Chemicals of predatory mosquitofish (*Gambusia affinis*) influence selection of oviposition site by *Culex* mosquitoes. J Chem Ecol 28:797–806

Austad SN (1984) A classification of alternative reproductive behaviors and methods for field-testing ESS models. Am Zool 24:309

Binckley CA, Resetarits WJ (2002) Reproductive decisions under threat of predation: squirrel treefrog (*Hyla squirella*) responses to banded sunfish (*Enneacanthus obesus*). Oecologia 130:157–161

Bishop D, Cannings C (1978) A generalized war of attrition. J Theor Biol 70:85–124

Black AR, Dodson SI (1990) Demographic costs of *Chaoborus*-induced phenotypic plasticity in *Daphnia pulex*. Oecologia 83:117–122

Blaustein L (1998) Influence of the predatory backswimmer, *Notonecta maculata*, on invertebrate community structure. Ecol Entomol 23:246–252

Blaustein L (1999) Oviposition habitat selection in response to risk of predation: consequences for populations and community structure. In: Wasser SP (ed) Evolutionary processes and theory: modern perspectives. Kluwer Academic Publishers, pp 441–456

Blaustein L, Kotler BP (1993) Oviposition habitat selection by *Culiseta longiareolata*: effects of immature conspecifics, tadpoles and food levels. Ecol Entomol 18:104–108

Blaustein L, Margalit J (1995) Spatial distributions of *Culiseta longiareolata* (Culicidae: Diptera) and *Bufo viridis* (Amphibia: Bufonidae) among and within desert pools. J Arid Environ 29:199–211

Blaustein L, Margalit J (1996) Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. J Anim Ecol 65:77–84

Blaustein L, Whitman DW (2009) Behavioral plasticity to risk of predation: oviposition site selection by a mosquito in response to its predators. In: Whitman D, Ananthakrishnan TN (eds) Phenotypic plasticity of insects: mechanisms and consequences. Science Pub Inc, Plymouth, pp 263–280

Blaustein L, Kotler BP, Ward D (1995) Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. Ecol Entomol 20:311–318

Blaustein L, Kiflawi M, Eitam A, Mangel M, Cohen JE (2004) Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. Oecologia 138:300–305

Chesson J (1984) Effect of notonectids (Hemiptera: Notonectidae) on mosquitoes (Diptera: Culicidae): predation or selective oviposition. Environ Entomol 13:531–538

Choh Y, Takabayashi J (2010) Predator avoidance by phytophagous mites is affected by the presence of herbivores in a neighboring patch. J Chem Ecol 36:614–619

Cushing J (1996) Nonlinear matrix equations and population dynamics. In: Structured-population models in marine, terrestrial, and freshwater systems. Kluwer Academic Publishers, pp 205–243

Dawkins R (1980) Good strategy or evolutionarily stable strategy? In: Barlow GW, Silverberg J (eds) Sociobiology: beyond nature/nurture?

Eitam A, Blaustein L (2004) Oviposition habitat selection by mosquitoes in response to predator (*Notonecta maculata*) density. Physiol Entomol 29:188–191

Eitam A, Blaustein L, Mangel M (2002) Effects of *Anisops sardea* (Hemiptera: Notonectidae) on oviposition habitat selection by mosquitoes and other dipterans and on community structure in artificial pools. Hydrobiologia 485:183–189

Eitam A, Norena C, Blaustein L (2004) Microturbellarian species richness and community similarity among temporary pools: relationships with habitat properties. Biodivers Conserv 13:2107–2117

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36

Holt RD (1985) Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theor Popul Biol 28:181–208

Kiflawi M, Blaustein L, Mangel M (2003a) Oviposition habitat selection by the mosquito *Culiseta longiareolata* in response to risk of predation and conspecific larval density. Ecol Entomol 28:168–173

Kiflawi M, Blaustein L, Mangel M (2003b) Predation-dependent oviposition habitat selection by the mosquito *Culiseta longiareolata*: a test of competing hypotheses. Ecol Letters 6:35–40

Kiflawi M, Eitam A, Blaustein L (2003c) The relative impact of local and regional processes on macroinvertebrate species richness in temporary pools. J Anim Ecol 72:447–452

Kiszewski A, Mellinger A, Spielman A, Malaney P, Sachs SE, Sachs J (2004) A global index representing the stability of malaria transmission. Am J Trop Med Hyg 70:486–498

Maciá A (2009) Effects of larval crowding on development time, survival and weight at metamorphosis in *Aedes aegypti* (Diptera: Culicidae). Revista de la Sociedad Entomológica Argentina 68:107–114

Manda H, Gouagna LC, Foster WA, Jackson RR, Beier JC, Githure JI, Hassanali A (2007) Effect of discriminative plant-sugar feeding on the survival and fecundity of *Anopheles gambiae*. Malar J 6:113

Mangel M, Clark CW (1988) Dynamic modeling in behavioral ecology. Princeton University Press, Princeton

Manoukis NC, Touré MB, Sissoko I, Doumbia S, Traoré SF, Diuk-Wasser MA, Taylor CE (2006) Is vector body size the key to reduced malaria transmission in the irrigated region of Niono, Mali? J Med Entomol 43:820

Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79:417–428

Maynard Smith J, Price GR (1973) The logic of animal conflict. Nature 246:15–18

Munga S, Minakawa N, Zhou G, Barrack OOJ, Githeko AK, Yan G (2006) Effects of larval competitors and predators on oviposition site selection of *Anopheles gambiae* sensu stricto. J Med Entomol 43:221–224

Murdoch WW, Scott MA, Ebsworth P (1984) Effects of the general predator, *Notonecta* (Hemiptera) upon a freshwater community. J Anim Ecol 53:791–808

Murdoch WW, Chesson J, Chesson PL (1985) Biological control in theory and practice. Am Nat 125:344–366

Nakajima Y, Fujisaki K (2010) Fitness trade-offs associated with oviposition strategy in the winter cherry bug, *Acanthocoris sordidus*. Entomol Exp Appl 137:280–289

Reguera P, Gomendio M (2002) Flexible oviposition behavior in the golden egg bug (*Phyllomorpha laciniata*) and its implications for offspring survival. Behav Ecol 13:70–74

Reiskind M, Lounibos L (2009) Effects of intraspecific larval competition on adult longevity in the mosquitoes *Aedes aegypti* and *Aedes albopictus*. Med Vet Entomol 23:62–68

Reiskind MH, Wund MA (2009) Experimental assessment of the impacts of northern long-eared bats on ovipositing *Culex* (Diptera: Culicidae) mosquitoes. J Med Entomol 46:1037–1044

Resetarits WJ, Rieger JF, Binckley CA (2004) Threat of predation negates density effects in larval gray treefrogs. Oecologia 138:532–538

Rieger JF, Binckley CA, Resetarits WJ (2004) Larval performance and oviposition site preference along a predation gradient. Ecology 85:2094–2099

Roitberg BD, Mangel M (2010) Mosquito biting and movement rates as an emergent community property and the implications for malarial interventions. Isr J Ecol Evol 56:297–312

Root RB, Kareiva PM (1984) The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. Ecology 65:147–165

Sadeh A, Mangel M, Blaustein L (2009) Context-dependent reproductive habitat selection: the interactive roles of structural complexity and cannibalistic conspecifics. Ecol Lett 12:1158–1164

Service MW (1976) Mosquito ecology: field sampling methods. Applied Science

Shaalan EAS, Canyon DV (2009) Aquatic insect predators and mosquito control. Trop Biomed 26:223–261

Silberbush A, Blaustein L (2011) Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. Funct Ecol 25:1091–1095

Silberbush A, Markman S, Lewinsohn E, Bar E, Cohen JE, Blaustein L (2010) Predator-released hydrocarbons repel oviposition by a mosquito. Ecol Lett 13:1129–1138

Singer MC, Vasco D, Parmesan C, Thomas CD, Ng D (1992) Distinguishing between 'preference' and 'motivation' in food choice: an example from insect oviposition. Anim Behav 44:463–471

Smith C, Reynolds JD, Sutherland WJ (2000) Population consequences of reproductive decisions. Proc R Soc Lond B Biol Sci 267:1327

Spencer M, Blaustein L, Cohen JE (2002a) Oviposition habitat selection by mosquitoes (*Culiseta longiareolata*) and consequences for population size. Ecology 83:669–679

Spencer M, Schwartz SS, Blaustein L (2002b) Are there fine-scale spatial patterns in community similarity among temporary freshwater pools? Global Ecol Biogeogr 11:71–78

Spielman A, D'Antonio M, Wallace B (2001) Mosquito: a natural history of our most persistent and deadly foe. Faber and Faber, London

Stav G, Kotler BP, Blaustein L (2010) Foraging Response to Risks of Predation and Competition in Artificial Pools. Isr J Ecol Evol 56:9–20

Stone C, Taylor R, Roitberg B, Foster W (2009) Sugar deprivation reduces insemination of *Anopheles gambiae* (Diptera: Culicidae), despite daily recruitment of adults, and predicts decline in model populations. J Med Entomol 46:1327

Strogatz SH (1994) Nonlinear dynamics and chaos: with applications to physics, biology, chemistry, and engineering. Westview Press, Cambridge

Styer LM, Carey JR, Wang JL, Scott TW (2007) Mosquitoes do senesce: departure from the paradigm of constant mortality. Am J Trop Med Hyg 76:111

Van Pletzen R, Van Der Linde TCDK (1981) Studies on the biology of *Culiseta longiareolata* (Macquart) (Diptera: Culicidae). Bull Entomol Res 71:71–79

Vonesh J, Blaustein L (2010) Predator-induced shifts in mosquito oviposition site selection: a meta-analysis and implications for vector control. Isr J Ecol Evol 56:263–279

Ward SA (1987) Optimal habitat selection in time-limited dispersers. Am Nat 129:568–579

Warner RR, Wernerus F, Lejeune P, Van Den Berghe E (1995) Dynamics of female choice for parental care in a fish species where care is facultative. Behav Ecol 6:73
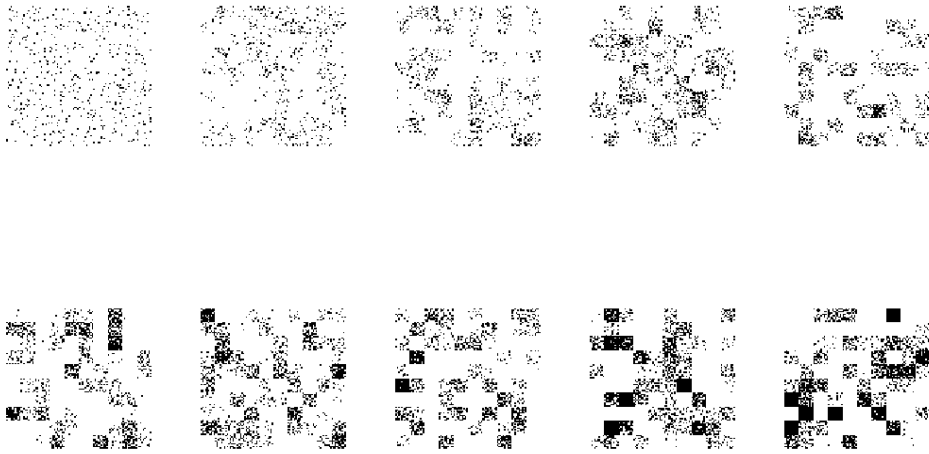
(a)
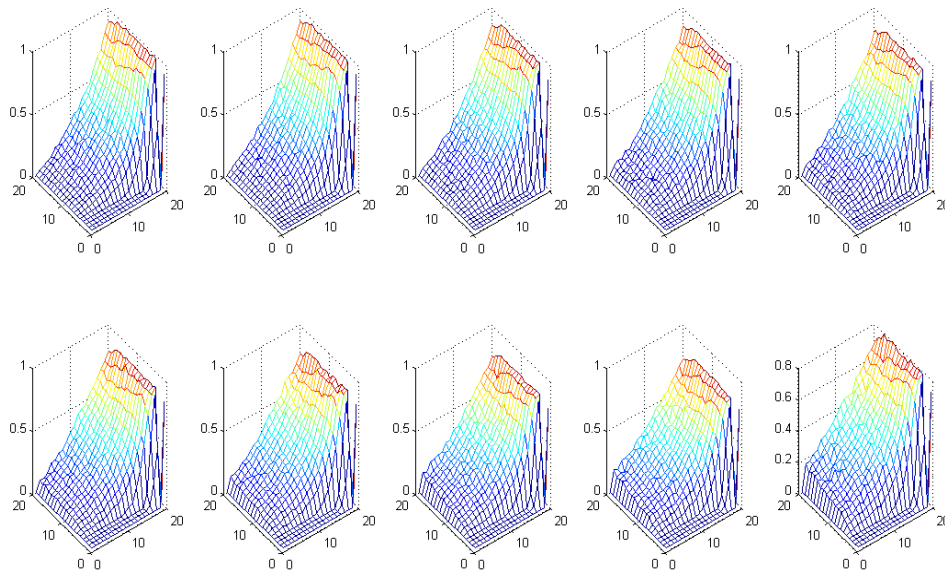
(b)

Figure S1: Simulations of varying levels of homogeneity of pool distribution. (a) The distribution

of pools in different simulations varying from homogeneous (top left) to highly patchy (bottom

right). (b) The number of eggs laid in predator pools for each of the spatial arrangements shown

in (a). No significant difference is found for different spatial configurations, under the assumption that every patch is equally accessible from every other patch.