

The role of resource availability and state-dependence in the foraging strategy of blood-feeding mosquitoes

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ABSTRACT

Background: Blood-feeding female mosquitoes are omnivores that face trade-offs and constraints between taking blood meals, sugar meals, and ovipositing their eggs.

Questions: (1) How does a mosquito allocate her time and energy to blood and sugar feeding? (2) How does the availability of sugar and/or blood influence her decisions?

Methods and key assumptions: We use a dynamic state variable model to address this question. The model is parameterized from primary literature using *Anopheles gambiae* for reference where possible. The model assumes that female mosquitoes have evolved to make decisions that maximize their lifetime reproductive success.

Conclusions: Blood and sugar have important roles in the life history of blood-feeding female mosquitoes. In the presence of blood hosts, the decision to search for a blood meal is almost always chosen over the search for sugar. However, away from the blood host microhabitat, sugar is readily used. Survivorship and fecundity are increased with an increase in sugar availability. Frequency of blood feeding, mosquito fecundity, and survivorship are only marginally decreased with decreases in blood availability.

Keywords: *Aedes aegypti*, *Anopheles gambiae*, dynamic state variable model, foraging behaviour, mosquitoes, omnivores, resource availability, state-dependence, vector-borne disease control.

INTRODUCTION

Organisms that consume more than one resource are faced with the dilemma of what to eat and when to eat it. In nature, we see many different ways of solving the problem of diet selection and have come to understand that there are many factors responsible for the different decisions an organism makes about how to forage for resources. For instance, patchy resources (MacArthur and Pianka, 1966), predator foraging inaccuracies (Fryxell and Lundberg, 1998), time-lagged predator responses (Ma *et al.*, 2003), and diet balancing (Pulliam, 1975; Westoby, 1978) may all play a role in changing the way an individual chooses to forage. One interesting life history that does not fall under any of these typical diet choice scenarios is that of

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blood-feeding female mosquitoes, which require a blood meal before they are capable of laying eggs.

Blood-feeding female mosquitoes are omnivores that exploit two disparate food sources, namely sugar and blood, and therefore must decide how to allocate time and energy between acquiring the two resources. Sugar, predominately obtained from floral nectaries (Foster, 1995) and extra-floral nectaries (Gary and Foster, 2004), provides a source of readily available energy for flight and for the accumulation of adult nutritional reserves (Clements, 1955; Nayar and Sauerman, 1975). Blood, on the other hand, is primarily used as a source of protein required for the production of eggs. However, blood can also be used as a source of energy reserves but at a lower efficiency than a sugar meal (Van Handel, 1965). Clearly, sugar is the more profitable resource for the accumulation of energy reserves, and blood meals can be used for the accumulation of energy reserves but only at the expense of egg production.

To produce offspring, a female must take a blood meal, develop eggs, and lay her eggs at a suitable oviposition site. For many species of mosquitoes, blood hosts and oviposition sites are spatially segregated; thus, a mosquito must travel from one habitat to another to successfully lay eggs (Kauffmann and Briegel, 2004; Le Menach *et al.*, 2005). Furthermore, there is a physical trade-off for abdominal space between blood in the midgut and sugar in the crop; that is, a replete blood meal excludes the possibility of a replete sugar meal and vice versa (Foster and Eischen, 1987; Takken *et al.*, 2001; Fernandes and Briegel, 2005), which is further complicated by spatial constraints imposed by fully developed eggs (Klowden, 1981). Blood feeding is associated with a higher risk of death than sugar feeding because of host defensive behaviour (Walker and Edman, 1985). Engorged mosquitoes are heavier, thereby limiting their ability to fly (Nayar and Sauerman, 1971; Foster, 1995), escape predators (Roitberg *et al.*, 2003), and ultimately to acquire resources.

Feeding decisions of a female mosquito are affected by her physiological state (Briegel, 2003), and studies on the nutritional status of a mosquito are of importance when thinking about the trade-off between blood and sugar feeding. Small-bodied mosquitoes face relatively higher energetic deficits, and therefore may behave very differently from large-bodied, energy-rich conspecifics (Takken *et al.*, 1998b), and starved mosquitoes are more likely to approach a host than well-fed mosquitoes (Klowden, 1986).

Resource availability may also affect the decisions of a mosquito. Sugar feeding depends on the seasonal availability of floral nectaries (Andersson, 1990), but there has been little work done on how varying sugar availability might affect the trade-off between blood and sugar feeding of mosquitoes.

In light of our understanding of the trade-offs and constraints on blood and sugar feeding as well as the state-dependence of these feeding decisions, the biological complexity associated with diet choice in blood-feeding female mosquitoes is not easily elucidated. For instance, decreasing the supply of blood should lead to, on average, a decrease in the blood meals taken by a population of female mosquitoes; however, mosquitoes with fewer opportunities to blood feed may decide to feed at increased frequency relative to scenarios where blood meals are readily available (i.e. increased biting rate). Furthermore, decreasing the supply of sugar should lead to, on average, an increase in blood meals taken by a population of female mosquitoes because blood may be used to fuel somatic maintenance in the absence of readily available sugar sources (Takken *et al.*, 1998b).

To better understand the interaction between foraging for these disparate resources, we present a dynamic state variable model of mosquito foraging behaviour where the trade-offs, constraints, and state-dependence of feeding decisions are explicit (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000). We apply the model to

answer two questions of interest: (1) Under what physiological conditions should a female mosquito undertake a particular feeding decision? (2) How does the availability of sugar and/or blood influence these feeding decisions?

THE MODEL

We construct a dynamic state variable (DSV) model of female mosquito feeding decisions over her lifetime. This type of model allows us explicitly to explore the importance of individual physiological states on flexible decision-making policies (Clark and Mangel, 2000). We assume that a female mosquito has evolved to make decisions that maximize her lifetime reproductive success given a particular combination of physiological states. Specifically, the physiological states we consider are blood in the midgut (B), sugar in the crop (S), nutritional reserves (R), and egg reserves (E). Additionally, we include a location state (L) because we consider a situation where resource availability is dependent on location – indoors or outdoors.

The activities that the female mosquito can decide to undertake are (1) search for a blood host (denoted as the subscript *blo*), (2) search for a sugar host (*sug*), (3) search for an oviposition site (*ovip*), (4) rest (*rest*), or (5) leave her current location (*leave*). The outcome of a particular decision is denoted as either failure (= 0) or success (= 1) based on a probability, $\lambda_{k,m}$, of finding resource k in the location m . There is no $\lambda_{k,m}$ term associated with the decision to rest, as we assume that if an individual chooses to rest, it can do so at any time. For each decision (i) and outcome (j), there is an associated metabolic cost, $a_{i,j}$, and time cost, $\tau_{i,j}$.

A mosquito acquires energy from the environment only when blood or sugar feeding; the volume of blood or sugar taken on a feeding bout is drawn from a binomial distribution ($n = 10$, $P = 0.7$). Sugar can only be used to produce energy reserves, but blood can be used to produce eggs and/or nutritional reserves. Ingested sugar (S) enters the crop, where it is transferred to nutritional reserves (R) at a constant rate (σ). Similarly, blood is transferred to nutritional reserves at a constant rate β_r and to eggs at β_e . Blood and sugar are converted into reserves with conversion efficiencies of c_b and c_s respectively. Blood is converted into eggs as a decelerating function of blood state (Anderson and Roitberg, 1999; Roitberg and Gordon, 2005). For each foraging decision made, the mosquito also decides how to allocate her existing blood energy between reserves at a proportion ψ or egg production at a proportion $(1 - \psi)$ to maximize her lifetime reproductive success. Thus, the general form of the basic flow of energy into and between states, which is the same regardless of activity, is described by equations (1a–d):

$$B(t + \tau_{i,j}) = B(t) - \psi\beta_r B(t) - (1 - \psi)\beta_e B(t) \quad (1a)$$

$$S(t + \tau_{i,j}) = S(t) - \sigma S(t) \quad (1b)$$

$$R(t + \tau_{i,j}) = R(t) + c_b\psi\beta_r B(t) + c_s\sigma S(t) \quad (1c)$$

$$E(t + \tau_{i,j}) = E(t) + (1 - \psi)\beta_e B(t) \quad (1d)$$

Furthermore, if a female chooses to leave her current location (L), then her state is updated to the other patch (e.g. if $L = \text{indoors}$ and the individual decides to leave, then $L' = \text{outdoors}$).

There are several restrictions placed on the state values. Each state is bounded by a ceiling (X_{\max}) and floor value (X_{\min}), where X represents a generic state variable. The floor value for all states is set to $X_{\min} = 0$. In addition, to account for the trade-off between midgut and crop space in the abdomen, we make the maximum volume of both blood (B_{lim}) and sugar (S_{lim}) that can be ingested functions of the current blood and sugar volumes. We additionally assume that B_{lim} is a linearly decreasing function of egg load because the presence of mature eggs imposes a small physical limitation on available midgut space (Klowden, 1981). The limit for blood and sugar for a given feeding event are expressed using equations (2a, b) respectively:

$$B_{lim} = B_{0max} - (1 - \nu) S(t) - B(t) - E(t) \quad (2a)$$

$$S_{lim} = S_{0max} - (1 - \nu/\gamma) B(t) - S(t) \quad (2b)$$

where B_{0max} and S_{0max} represent the capacity for blood in an empty midgut and sugar in an empty crop respectively, ν represents the maximum proportion of midgut size available with a full crop, and γ represents the size ratio of the midgut and the crop. Finally, we assume that a critical level of egg production (E_{crit}) must be reached for egg maturation, below which the mosquito is assumed to have immature ovarian follicles, and therefore cannot lay eggs (Briegel, 1990).

Basic mortality is modelled as a linearly increasing function of weight (Roitberg *et al.*, 2003), which in turn is a linearly increasing function of current resource states. The basic mortality associated with flight in location m to undertake decision i , including leaving, is represented by $\mu_i(b, s)$ (equation 3):

$$\mu_i(b, s) = \left(\frac{\mu_{\max,i,m} - \mu_{\min,i,m}}{\gamma B_{0max} + S_{0max}} (\gamma b + s) + \mu_{\min,i,m} \right) \quad (3)$$

where $\mu_{\max,i,m}$ and $\mu_{\min,i,m}$ represent the probability of dying at maximum and minimum weight respectively. Mortality is applied each time step in a geometric fashion. An additional mortality cost, $\mu'(b, s)$, is associated with blood feeding that is due to the defensive behaviour of the blood host. This function follows the same form as equation (3) but uses μ'_{\max} and μ'_{\min} .

An individual female mosquito's expected fitness, $F(b, s, r, e, l, t)$, can be decomposed into two components: the direct contribution to fitness between times t and $t + 1$, and the expected contribution to fitness from time $t + 1$ onwards (i.e. future fitness) given that the mosquito survives to until that time (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000). Because of the spatial nature of the model, fitness indoors and outdoors mirror one another and are calculated independently of one another. The only decision that returns a direct contribution to fitness is the decision to oviposit, with a conversion of egg state into eggs of c_e . The fitness from blood feeding, sugar feeding, and resting is based on the expected contribution to fitness after time $t + 1$ onwards given that the mosquito survives. The fitness from leaving is based on the best choice from the other habitat from time $t + 1$ onwards weighted by the probability of surviving the flight from one location to the other.

The basic change in state variables described in equations (1a–d) are used below as $B(t - \tau_{i,j}) = b'$, $S(t - \tau_{i,j}) = s'$, $R(t - \tau_{i,j}) = r'$, and $E(t - \tau_{i,j}) = e'$. The expected future fitness values are weighted by the probability of that activity occurring ($\lambda_{i,j}$) as well as the probability of surviving that activity ($\mu_i(b, s)$). Furthermore, during each activity, the individual

maximizes fitness by allocating blood energy between energy reserves or egg production based on the proportion ψ . The fitness gain for each activity is given, for a location m , below.

(1) *Search for a blood host.* A successful blood meal will increase the blood state (B) by $\varepsilon(b)$, the expected blood meal size, which is drawn from a binomial distribution and bounded between 0 and B_{lim} . The fitness value from seeking a blood host is

$$\begin{aligned} V_{blo}(b, s, r, e, l, t) = & \\ & \max_{\psi} [\lambda_{blo,m} (1 - \mu_{blo}(b, s))^{\tau_{blo,1}} (1 - \mu'(b, s)) F(b' + \varepsilon(b), s', r' - \alpha_{blo,1}, l, t + \tau_{blo,1}) \\ & + (1 - \lambda_{blo,m}) (1 - \mu_{blo}(b, s))^{\tau_{blo,0}} F(b', s', r' - \alpha_{blo,0}, e', l, t + \tau_{blo,0})] \end{aligned} \quad (4a)$$

(2) *Search for a sugar host.* If the individual is successful at finding a sugar host, the sugar state (S) is increased by the expected sugar meal size, $\varepsilon(s)$, which is bounded between 0 and S_{lim} . The fitness value from seeking a sugar host is

$$\begin{aligned} V_{sug}(b, s, r, e, l, t) = & \\ & \max_{\psi} [\lambda_{sug,m} (1 - \mu_{sug}(b, s))^{\tau_{sug,1}} F(b', s' + \varepsilon(s), r' - \alpha_{sug,1}, e', p, t + \tau_{sug,1}) \\ & + (1 - \lambda_{sug,m}) (1 - \mu_{sug}(b, s))^{\tau_{sug,0}} F(b', s', r' - \alpha_{sug,0}, e', p, t + \tau_{sug,0})] \end{aligned} \quad (4b)$$

(3) *Search for an oviposition site.* Successful oviposition differs from the other actions because successful oviposition means that there is a direct contribution to fitness through egg production, where $c_e E$ is the number of eggs produced. When a successful oviposition has occurred, the egg state $E = 0$ because all reproductive energy has gone to egg production. The fitness value for seeking an oviposition site is

$$\begin{aligned} V_{ovip}(b, s, r, e, l, t) = & \\ & \max_{\psi} [\lambda_{ovip,m} (c_e e' + (1 - \mu_{ovip}(b, s))^{\tau_{ovip,1}} F(b', s', r' - \alpha_{ovip,1}, 0, l, t + \tau_{ovip,1})) \\ & + (1 - \lambda_{ovip,m}) (1 - \mu_{ovip}(b, s))^{\tau_{ovip,0}} F(b', s', r' - \alpha_{ovip,0}, e', l, t + \tau_{ovip,0})] \end{aligned} \quad (4c)$$

(4) *Rest.* There are no probabilities associated with resting – if an individual decides to rest, she will rest. The fitness value of resting is

$$\begin{aligned} V_{rest}(b, s, r, e, l, t) = & \\ & \max_{\psi} [(1 - \mu_{rest}(b, s))^{\tau_{rest}} F(b', s', r' - \alpha_{rest}, e', l, t + \tau_{rest})] \end{aligned} \quad (4d)$$

(5) *Leave.* If an individual successfully leaves its current location, the location state, l , is updated to be l' . The fitness value of leaving the current habitat is

$$\begin{aligned} V_{leave}(b, s, r, e, l, t) = & \\ & \max_{\psi} [\lambda_{leave,m} (1 - \mu_{leave}(b, s))^{\tau_{leave,1}} F(b', s', r' - \alpha_{leave,1}, e', l', t + \tau_{leave,1}) \\ & + (1 - \lambda_{leave,m}) (1 - \mu_{leave}(b, s))^{\tau_{leave,0}} F(b', s', r' - \alpha_{leave,0}, e', l, t + \tau_{leave,0})] \end{aligned} \quad (4e)$$

Lifetime reproductive success is maximized via choosing the best activity and allocation decisions at each time step for each state combination, yielding

$$F(b, s, r, e, l, t) = \max[V_{blo}, V_{sug}, V_{ovip}, V_{rest}, V_{leave}]. \quad (5)$$

The optimal decision is calculated by backwards induction from a terminal fitness function $F(b, s, r, e, l, t, T) = 0$ for all combinations of states (Clark and Mangel, 2000). We use a large value for our time horizon that is well beyond the expected lifetime of an individual mosquito ($T = 2500$), and allow the model to converge to stationary states. Our convergence criterion is that the decisions for each combination of states do not change for the last 25 time steps. For non-integer state values, we use a four-state linear interpolation to calculate fitness (Clark and Mangel, 2000).

The solution to the DSV assumes that the mosquito has evolved to maximize lifetime reproductive success in a given environment with known resource availability. We use Monte Carlo simulations to determine how mosquitoes that have evolved in that environment might behave in novel environmental conditions.

Parameterization of the model

Where possible, we parameterized the model using primary literature sources for the hematophagous endophilic anthropophilic mosquito species *Anopheles gambiae*. *Anopheles gambiae* is arguably the most important disease-vectoring mosquito because of its role in the transmission of *Plasmodium falciparum*, a parasite that causes malaria in humans. Furthermore, this species is of particular interest to our research group as we maintain and perform empirical studies using this species.

A typical environment for *A. gambiae* has blood hosts and oviposition sites spatially segregated. Blood hosts are predominately found in and around domiciles (which we refer to as ‘inside’) (Gillies, 1954), whereas oviposition sites are predominately found away from houses (which we refer to as ‘outside’) and near more dense vegetation and thereby a source of sugar hosts. Thus, for our baseline parameter set, we use values of $\lambda_{ovip,out} = 1$, $\lambda_{ovip,in} = 0$, $\lambda_{blo,in} = 1$, and $\lambda_{blo,out} = 0$. All other $\lambda_{k,m}$ values are set to 1 for simplicity but $\lambda_{blo,in}$, $\lambda_{sug,out}$ and $\lambda_{sug,in}$ are varied during our sensitivity analysis.

We set all metabolic costs ($\alpha_{i,j}$) as linear functions of time, where resting and unsuccessful decisions have $\alpha_{i,j} = 1$, and the metabolic energy required for successful actions has a 1 : 1 relationship with the time spent for each decision ($\tau_{i,j}$). We break the day into 10-min steps, where unsuccessful decisions are associated with a $\tau_{i,0} = 1$ and successful decisions have $\tau_{i,1} = 2$, except for the decision to leave, which we assume takes one hour (i.e. $\tau_{leave,1} = 6$).

The maximum volume of blood in the midgut (B_{0max}) and sugar in the crop (S_{0max}) for *A. gambiae* are estimated at 4 μl and 1 μl respectively (Briegel, 1990), which also yields a relative size ratio of midgut to crop of $\lambda = 4$ and a maximum proportion of midgut size with a full crop of $v = 0.8$. Without access to energy resources, a female mosquito will die within a few days due to starvation (Briegel, 1990); thus we use $R_{max} = 64$, which means that mosquitoes that do not feed (or conversely, rest the entire time) will die within a few days. This also allows for sufficient resolution for energy lost to metabolism from activity as well as for differences between the conversion of blood and sugar to reserves.

Blood must be broken down by proteolytic enzymes and therefore is absorbed more slowly than sugar; Van Handel (1965) estimated that reserve accumulation of sugar is ten times faster than it is for blood. Nayar and Van Handel (1971) determined that *Aedes taeniorhynchus* and *Aedes sollicitans* mosquitoes flown to exhaustion could fly almost immediately after a sugar meal but required 4–6 h to fly after imbibing a blood meal and could only do so for short periods. To capture this difference, we use a conversion rate of blood to reserves (β_r) of 1 and a conversion rate of sugar to reserves (σ) of 10. We also

include a conversion rate of blood to egg production (β_e) set to unity. The conversion efficiency of blood to reserves (c_b) is considered to be lower than the conversion efficiency of sugar to reserves (c_s) because of the additional processes necessary for digesting a blood meal. An unmetabolized sugar meal supplies over 10 times the flight range of blood meals (Nayar and Van Handel, 1971), and thus we use $c_b = 1$ and $c_s = 10$ for our analysis.

The conversion of the egg reserve state to eggs for *A. gambiae* taking a complete blood meal yields an eggload of 90–120 eggs (Briegel, 1990; Fernandes and Briegel, 2005; Roitberg and Gordon, 2005). We discretize the egg state into ten units ($E_{\max} = 10$) and assume that the conversion of egg state into eggs is $c_e = 10$; thus a female with a full egg state can produce 100 eggs. Briegel (1990) determined that no eggs matured when the energy invested in egg development was less than 1.3 calories for *A. gambiae*, which as a ratio of the total calories from a blood meal, corresponds to a threshold egg reserve state of $E_{\text{crit}} = 4$.

For *A. gambiae*, the daily mortality rate estimated from a mark–recapture study is 0.22 (Takken *et al.*, 1998a), which, given our 10-min time steps and assuming that mortality is independent of time, translates to a 0.005 hourly mortality rate. We use this as our baseline mortality rate ($\mu_{\min,i}$) for all decisions except resting, which we assume is very safe and does not change with weight ($\mu_{\text{rest}} = 0.001$). Accurate measures of mortality rates for each decision are difficult, and thus we can only make qualitative assumptions about the relative risk of death for each decision a mosquito makes. As weight increases, we assume that a mosquito is five times as likely to die, yielding a mortality rate at full weight of $\mu_{\max,i} = 0.025$. We assume that there is no difference in the mortality rate functions for the search for a sugar host, blood host or oviposition site because we have no data that suggest otherwise. Additional mortality associated with blood-host defensive behaviour is assumed to be $\mu'_{\min} = 0.05$ and $\mu'_{\max} = 0.25$. For simplicity, we also assume that the mortality rate function for leaving is the same as for the other decisions.

METHODS

We develop the decision-making policy of a female mosquito for the DSV model coded using the programming language C (source code available upon request). We focus our analysis on the availability of resources in the environment, with most of our attention given to the availability of sugar indoors ($\lambda_{\text{sug,in}}$), outdoors ($\lambda_{\text{sug,out}}$), and the availability of blood hosts indoors ($\lambda_{\text{blo,in}}$). We also explore the model's robustness by performing a sensitivity analysis on survivorship, where we vary the steepness of the mortality curve with respect to weight, and we vary the risk of host defensive behaviour while blood feeding. We also examine the robustness of our results to changes in the time ($\tau_{\text{leave},1}$) and costliness ($\alpha_{\text{leave},1}$) of leaving. Our interpretation of the results is divided into what a mosquito decides indoors and outdoors, and we focus on the decisions to blood- and sugar-feed, since for the most part the trends for where the other two decisions (oviposition and resting) occur remain qualitatively similar. The methodology and corresponding results are divided into two major sections: the DSV deterministic model and the Monte Carlo simulations.

DSV model

Because of the complex nature of state space (i.e. excluding time as a state, we have five states over which decisions can vary), we first divide the analysis into indoor and outdoor components. We summarize the proportion of the total state space where making each of

the five possible decisions maximizes lifetime reproductive success for a given parameter set. However, this does not tell us everything about the physiological conditions under which a mosquito should blood- or sugar-feed. Thus, we also take two-dimensional slices of state space, where two states vary and two states are fixed. We concentrate on three scenarios that we think are the most biologically interesting: (1) blood (B) and reserve (R) states vary (and sugar (S) and egg (E) states are fixed at 0); (2) S and R vary (and $B = E = 0$); and (3) E and R vary (and $B = S = 0$).

Monte Carlo simulations

We also simulate a female's lifetime using a Monte Carlo simulation that uses the time-independent solution to the DSV model. We assume that mosquitoes have evolved in a world where blood hosts are spatially separated from oviposition sites. Sugar is readily available outside near oviposition sites but is in limited supply near the blood host habitat.

We simulate mosquitoes in several novel environments, using 5000 individuals per run. Individuals begin relatively malnourished (Beier, 1996), where their initial energy reserve state is drawn from a normal distribution with a mean of $\sim 10\%$ of the maximum energy (i.e. $R = 5 \pm 0.5$; mean \pm standard error) (Walker, 2008). The quantity of blood or sugar taken on a given feeding event is randomly drawn from a binomial distribution where the proportion of large meal sizes is high – that is, most mosquitoes feed to near repletion ($n = 10$, $P = 0.7$).

We incrementally increase and decrease the availability of blood (inside) and sugar (inside and outside) and track several key outcomes of the simulations. We track the frequency of each decision made over the lifetime of the mosquito; this is analogous to the proportion of the total state space results from the DSV component but gives us a better idea of the state space that is most commonly experienced by an individual. Because the decisions an individual makes will likely affect its survivorship and fecundity, we also track mean values for longevity (i.e. life expectancy from birth), number of gonotrophic cycles per individual, number of blood and sugar meals per gonotrophic cycle, and egg production.

RESULTS

DSV model

Several general patterns emerge from the results of the DSV model. We first examine the entire decision space across the blood, sugar, reserve, and egg states, keeping in mind that much of the decision space included in these summary statistics may not be readily attained by the mosquito. Then, from the examination of the two-dimensional plots of state space, we gain a better understanding of what the best decisions are under different state combinations.

The decisions made around the houses (inside) and around the vegetation (outside) are very different. In the habitat 'inside', most of the decision space is dominated by resting (97%). Of the remaining decision space, 48% is to leave the inside, 22% is to search for a blood meal, and 30% is to search for a sugar meal. In the habitat 'outside', the decision to rest is the best for 89% of the decision space. Of the remaining decision space, the most frequent decision is to oviposit (93%), whereas searching for a sugar meal is 5% and the decision to leave is 2%.

Generally, a female mosquito will begin its life outside with low energy reserves and an empty abdomen. Under these conditions, the best decision is to search for a sugar meal (Fig. 1a, b). If an individual successfully imbibes a sugar meal, and that sugar meal is large, it will rest and allow for the sugar meal to be processed (Fig. 1 b). However, if the individual is unsuccessful at finding a sugar meal or the sugar meal is small, it will attempt to take a sugar meal again. Once an individual has successfully imbibed and processed a sugar meal, its reserve state will increase and therefore the best decision is to move inside.

In the inside habitat (Fig. 1d, e), an individual with very low energy reserves and no blood or sugar in the abdomen will search for a sugar meal. Conversely, with higher energy reserves, an individual will take a blood meal. With a small amount of sugar in the crop, at low energy reserves a mosquito will blood-feed, and with high energy reserves it will decide to rest (Fig. 1e). Conversely, with blood in the midgut, at low energy reserves a mosquito will search for a sugar meal, and with higher energy reserves it will rest (Fig. 1d). When egg reserves have accumulated to a sufficient level, which is greater than the critical egg state for egg production to occur, mosquitoes leave the inside provided that they have sufficient energy reserves to make the trip to the outside. If an individual has insufficient energy to make the trip, it will take a sugar meal to supplement its energy reserves (Fig. 1f).

Once outside with high egg reserves, an individual will oviposit (Fig. 1c). Then, if her energy reserves are low, she will take a sugar meal and then rest until her sugar meal is processed; if her energy reserves are high, she will immediately return indoors.

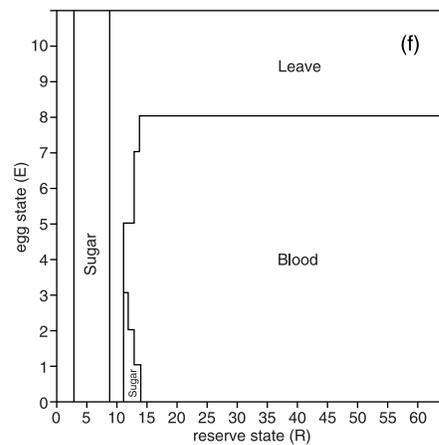
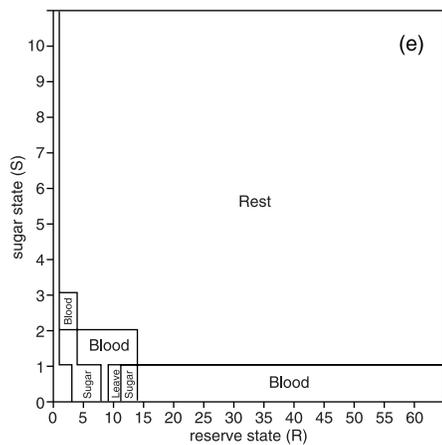
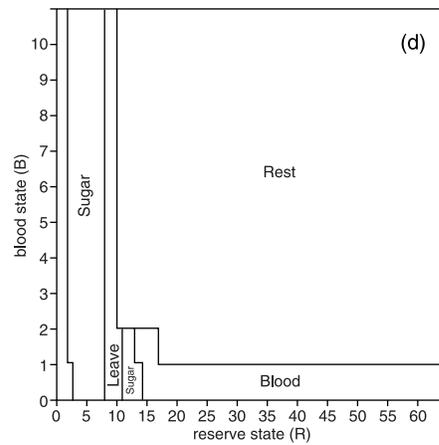
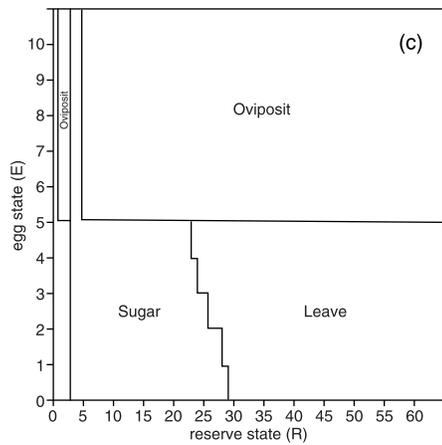
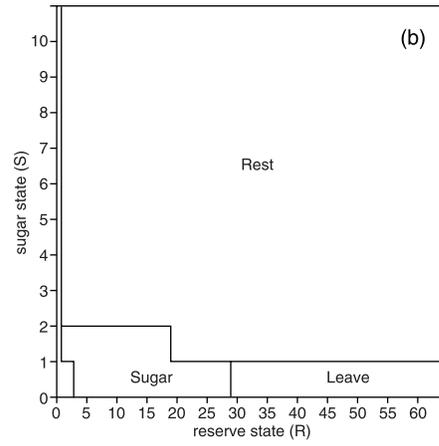
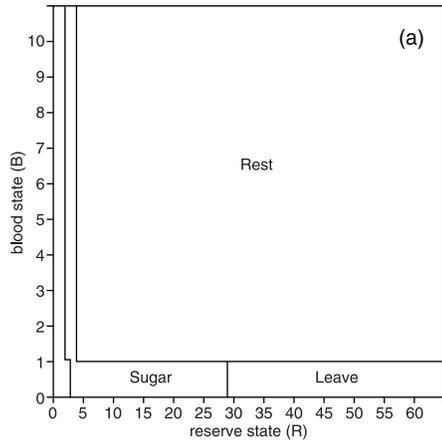
Although we have only presented a single parameter set with fixed probabilities of finding resources, the results from the DSV with different probabilities of finding resources follow similar qualitative trends: the changes in the (historical) probability of finding sugar inside does not dramatically change the frequency of each decision. The decisions to blood-feed and sugar-feed inside are particularly invariable to changes in resources.

Monte Carlo simulations

The frequency of blood feeding declines only when blood becomes very difficult to find (Fig. 2). The increase in frequency of blood feeding from low blood availability ($\lambda_{blo,in} = 0.1$) to high blood availability ($\lambda_{blo,in} = 1.0$) is ~10%. Conversely, the frequency of blood feeding is highly invariable to changes in sugar availability ($\lambda_{sug,in}$). Note that we do not consider the case where $\lambda_{blo,in} = 0$, because if no blood is available in the environment, individuals cannot develop eggs and therefore do not contribute to the next generation.

The frequency of sugar feeding inside increases asymptotically with increasing sugar availability inside ($\lambda_{sug,in}$), but is relatively invariable to changes in sugar available outside ($\lambda_{sug,out}$) (Fig. 3). However, this relationship only exists when blood availability is low ($\lambda_{blo,in} = 0.1$). As blood availability increases (i.e. when $\lambda_{blo,in} = 0.4-0.5$), sugar feeding inside becomes negligible, and stops entirely at values of $\lambda_{blo,in} > 0.5$. Furthermore, the frequency of sugar feeding inside, even at its highest value (when $\lambda_{sug,in} = 0.7$; $\lambda_{sug,out} = 0.1$; $\lambda_{blo,in} = 0.1$), is ~20 times less frequent than the decision to blood-feed.

The frequency of sugar feeding outside increases when blood is scarce (i.e. when $\lambda_{blo,in}$ is low), but does not change with changes in sugar availability inside ($\lambda_{sug,in}$) or outside ($\lambda_{sug,out}$) except when sugar outside is absent (Fig. 4). Because the availability of sugar inside ($\lambda_{sug,in}$) also has very little effect on the frequency of sugar feeding outside, we only show a single example of $\lambda_{sug,in} = 1.0$ (Fig. 4). The percent increase in the frequency of sugar feeding outside is at most ~50% from high blood availability to low blood availability.



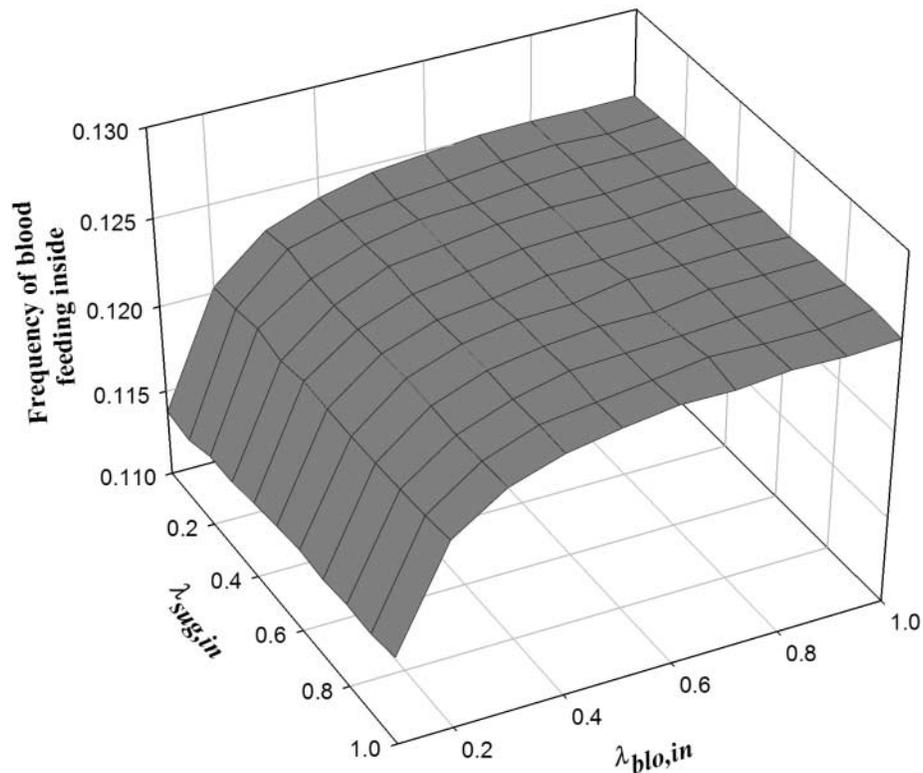


Fig. 2. The frequency of blood feeding by a mosquito in the inside habitat as a function of the availability of sugar ($\lambda_{sug,in}$) and blood in the inside habitat ($\lambda_{blo,in}$). The results presented are for the probability of finding sugar outside ($\lambda_{sug,out}$) of 1.0. This figure is representative of the same relationship for values of $\lambda_{sug,out}$ from 0.1 to 1.0.

The mean longevity of an individual is largely unaffected by the availability of sugar inside ($\lambda_{sug,in}$). However, increasing availability of sugar outside ($\lambda_{sug,out}$) increased longevity in an accelerating manner, and increasing blood availability inside ($\lambda_{blo,in}$) increased longevity asymptotically (Fig. 5). Overall, the effect of increasing $\lambda_{sug,out}$ had a greater effect on longevity than did increasing $\lambda_{blo,in}$. The most frequent cause of death was starvation, except when resources were abundant (i.e. $\lambda_{sug,out}$ and $\lambda_{blo,in}$ are high), where death resulted from either background mortality while searching for blood hosts, or host defensive behaviour.

Fig. 1. The best decision for a mosquito under different physiological state combinations based on the DSV results where two states vary and the other two states are fixed. The spaces where each decision is best are labelled on each figure: ‘Blood’ is the decision to search for a blood host; ‘Sugar’ is the decision to search for a sugar host; ‘Rest’ is the decision to rest; ‘Oviposit’ is the decision to search for an oviposition site; ‘Leave’ is the decision to leave the current habitat. Panels (a–c) represent decision space ‘outside’; panels (d–f) represent decision space ‘inside’. In panels (a) and (d), sugar state (S) = egg state (E) = 0; in panels (b) and (e), blood state (B) = egg state (E) = 0; in panels (c) and (f), blood state (B) = sugar state (S) = 0.

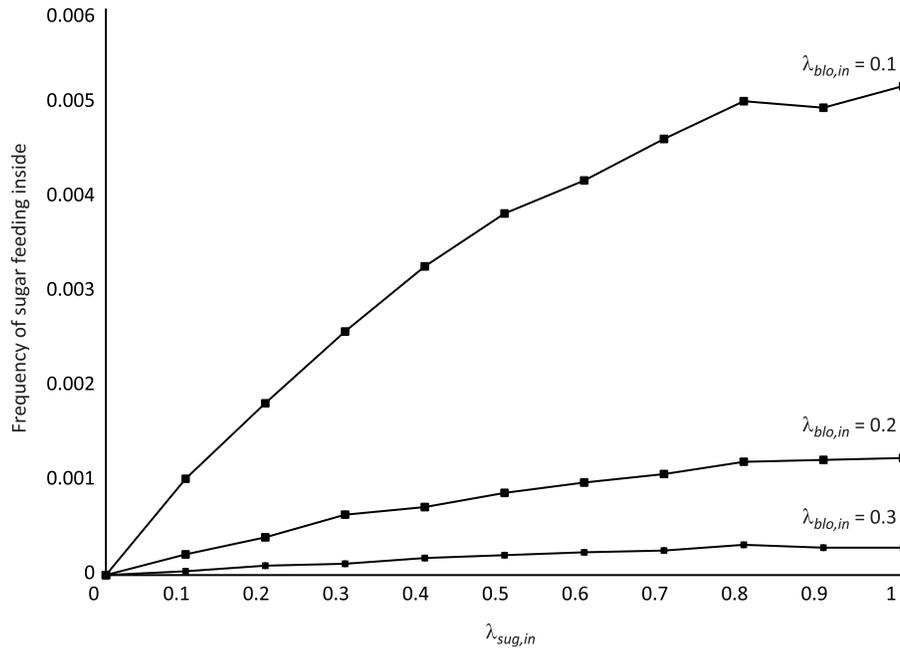


Fig. 3. The frequency of sugar feeding by a mosquito in the inside habitat as a function of sugar availability inside ($\lambda_{sug,in}$). The sugar availability outside ($\lambda_{sug,out}$) is 1.0. This figure is representative of the same relationship for values of $\lambda_{sug,in}$ from 0.0 to 1.0.

Mean fecundity was only affected by the availability of blood hosts inside ($\lambda_{blo,in}$) and sugar hosts outside ($\lambda_{sug,out}$) (Fig. 6a). The effect of the availability of sugar hosts inside ($\lambda_{sug,in}$) was negligible. Overall, the effect of increasing $\lambda_{sug,out}$ had a larger effect on fecundity than did increasing $\lambda_{blo,in}$. The increases in fecundity are likely attributable to a combination of an increase in the mean number of gonotrophic cycles (Fig. 6b) and, to a lesser degree, an increase in the mean number of eggs per gonotrophic cycle with increasing $\lambda_{sug,out}$ (Fig. 6c). Additionally, the mean length of the gonotrophic cycle increases with an increase in $\lambda_{sug,out}$, decreases with an increase in $\lambda_{blo,in}$, and is relatively insensitive to changes in $\lambda_{sug,in}$. Even though the gonotrophic cycle is longest when $\lambda_{blo,in}$ is low and $\lambda_{sug,out}$ is high, the overall effect is that there are a greater number of gonotrophic cycles at high $\lambda_{blo,in}$ levels.

DISCUSSION

We present a model of blood-feeding female mosquito foraging decisions that explicitly considers the trade-offs between blood feeding, sugar feeding, and oviposition. The model predicts that both blood and sugar are utilized throughout the mosquito's lifetime, but that the conditions under which each is taken are very different. Although at any given time the acquisition of blood is in direct conflict with the acquisition of sugar, our results suggest that a female blood-feeding mosquito solves the trade-off between blood and sugar feeding sequentially across the blood host and oviposition microhabitats. The search for blood hosts occurs in the blood host microhabitat. However, in this microhabitat, sugar is largely ignored except when individuals are starved. The search for sugar, on the other hand,

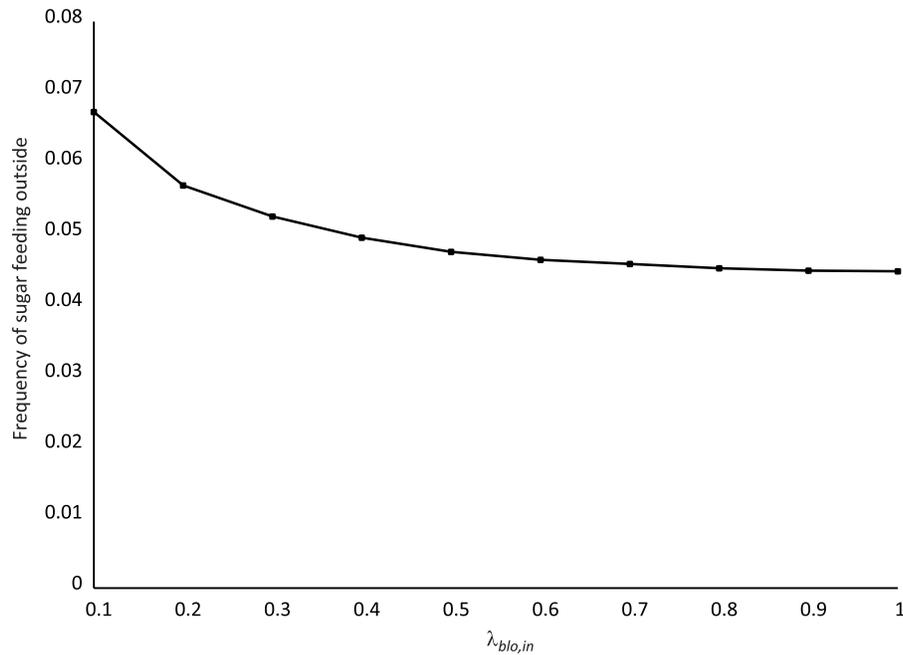


Fig. 4. The frequency of sugar feeding by a mosquito in the outside habitat as a function of blood availability ($\lambda_{blo,in}$) at a sugar availability inside ($\lambda_{sug,in}$) of 1.0. This figure is representative of the same relationship for values of $\lambda_{sug,in}$ from 0.0 to 1.0.

generally occurs when mosquitoes are low on energy and away from the blood host microhabitat (and near oviposition sites).

The availability of different resources has implications for different feeding frequencies, survivorship, and fecundity. Our results suggest that a decrease in the availability of blood hosts does not have a marked effect on fecundity and little effect on longevity. An increase in blood availability increases fecundity but only marginally increases longevity, even though we explicitly allow mosquitoes to allocate energy from a blood meal towards energy reserves. The frequency of blood feeding is not affected by sugar availability in the blood host habitat, which suggests that within the microhabitat near blood hosts, female mosquitoes prioritize egg production (i.e., direct fitness payoff) in lieu of future fitness. To mitigate the effects of lower host availability, female mosquitoes likely become more persistent in their search for a blood host and sugar-feed to avoid starvation. Sugar near oviposition sites is heavily relied upon, such that when sugar availability increases, there is a sharp increase in longevity coupled with an increase in fecundity. However, sugar available near blood hosts will only be used when blood is difficult to acquire, and even then only when reserves are very low regardless of the availability.

Our results suggest that sugar is an important component of a female mosquito's life history, even in species that are closely associated with humans and capable of allocating energy derived from blood to fuel activity. Mosquitoes are more likely to search for a sugar source when they are low on energy reserves; this energy-deprived condition is especially prevalent at emergence (Walker, 2008) where individuals emerge outside (i.e. at oviposition sites and away from blood hosts). During this initial period, the risk of starvation is very high but

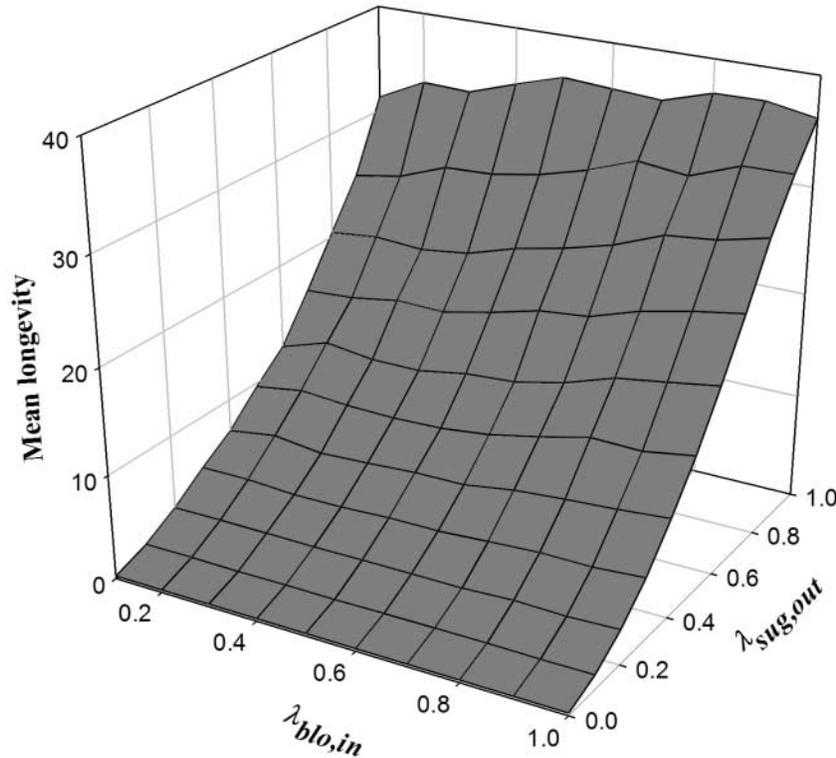


Fig. 5. Mean longevity of a mosquito as a function of blood availability inside ($\lambda_{blo,in}$) and sugar availability outside ($\lambda_{sug,out}$) based on the Monte Carlo simulation results at $\lambda_{sug,in} = 1.0$. This figure is representative of the same relationship for values of $\lambda_{sug,in}$ from 0.0 to 1.0.

can be ameliorated through feeding on sugar (Foster and Takken, 2004). When energy reserves are sufficient, our theory states that sugar should be ignored and the mosquito should leave the emergence habitat in search of a blood meal.

The importance of sugar to blood-feeding female mosquitoes has often been overlooked (Foster and Takken, 2004), especially for anthropophilic and endophilic mosquitoes such as *Anopheles gambiae* and *Aedes aegypti* (Briegel, 1990). Many studies have demonstrated that sugar intake increases the lifespan of mosquitoes (Nayar and Sauerman, 1975; Andersson, 1992; Straif and Beier, 1996; Okech *et al.*, 2003; Gary and Foster, 2004), yet sugar feeding in anthropophilic endophilic mosquitoes is often thought to be infrequent and incidental (Edman *et al.*, 1992; Foster, 1995; Beier, 1996). For instance, in a census study, a very low proportion of sugar-positive *A. gambiae* female mosquitoes was found around blood host microhabitats (Beier, 1996). The reason for the under-representation of sugar feeding may be due to the location of sugar feeding. The reliance on sugar away from blood host microhabitats predicted by the model suggests that census data for sugar-positive females captured near blood host microhabitats (e.g. Beier, 1996) will grossly under-represent the frequency of sugar feeding by mosquitoes throughout their lifetime.

The resource acquisition dilemma faced by mosquitoes is similar to the dilemma faced by some host-feeding parasitoids. Like mosquitoes, these parasitoids use sugar sources to fuel

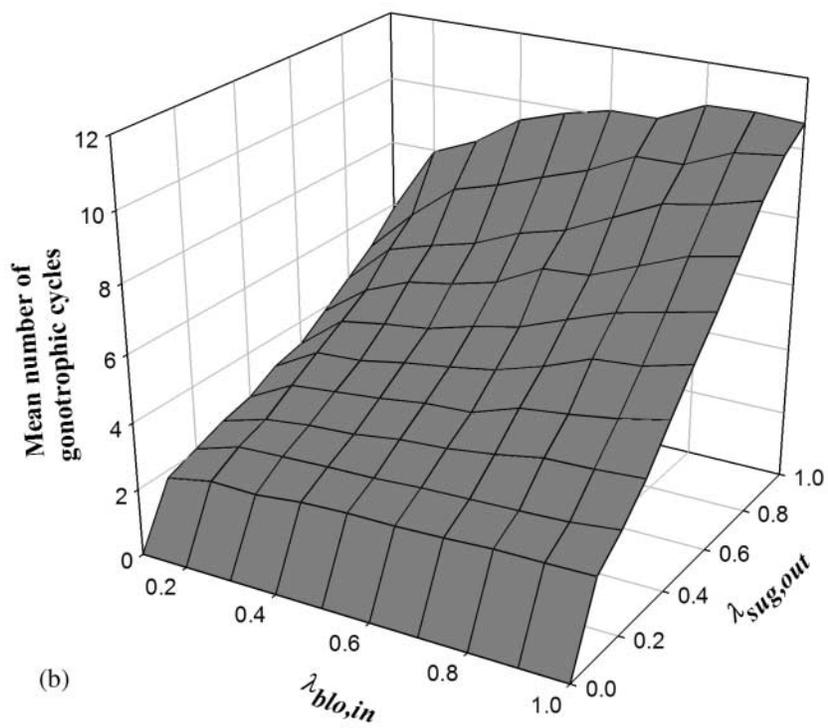
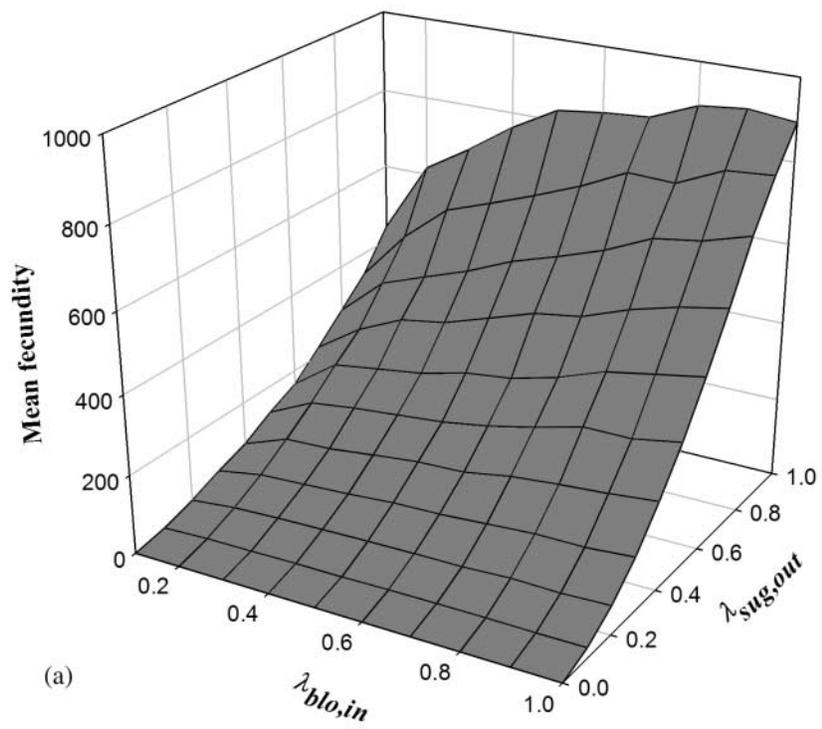
maintenance (Jervis and Kidd, 1986, 1999), and also use their hosts as a source of nutrients required for egg maturation (Heimpel and Collier, 1996). Empirical evidence suggests that in host-feeding parasitoids, host-feeding occurs when energy reserves are low, and oviposition occurs when energy reserves are higher (Heimpel and Collier, 1996). Furthermore, studies have shown that sugar is required by some host-feeding parasitoids to experience the benefit of host-feeding (Heimpel *et al.*, 1997). Unlike the mosquito system, egg-laying in the host and the potential source of egg-laying nutrients (i.e. the host) are within the same microhabitat, and potential sources of sugar such as floral nectaries are spatially separate (Bernstein and Jervis, 2008). For female mosquitoes, the microhabitat in which the direct fitness payoff of oviposition is linked with sugar sources, and the microhabitat linked with the resource required to oviposit (i.e. blood), are spatially separate. There have been numerous models of the trade-off between host-feeding and oviposition (reviewed in Jervis and Kidd, 1986, 1999; Heimpel and Collier, 1996), and at least one model of the trade-off between sugar feeding and oviposition in non-host-feeding parasitoids (Clark and Mangel, 2000; Bernstein and Jervis, 2008), but we know of no models that explicitly consider the interaction between sugar feeding, host-feeding, and oviposition behaviour.

The model presented in this paper complements and expands on existing models of mosquito decision making (e.g. Roitberg and Friend, 1992). Previous models have considered limited decisions over a single gonotrophic cycle, whereas the model introduced here presents a mosquito with an entire suite of decisions over her entire lifetime. We explicitly track the egg state of a female mosquito, which is important because of the direct fitness benefit that oviposition entails. We also allow for the possibility of multiple blood or sugar meals within a single gonotrophic cycle, as well as carryover of nutritional reserves from one gonotrophic cycle to the next. This latter characteristic can lead to different decisions being made with each gonotrophic cycle, which becomes especially important in light of the fact that the decisions made during the first gonotrophic cycle are sometimes different from those in subsequent gonotrophic cycles (Takken *et al.*, 1998b). Furthermore, considering more than one gonotrophic cycle is important because parasites such as *Plasmodium* spp. have an incubation period that is greater in duration than a gonotrophic cycle.

Our model could be expanded in several ways. Physiological states we did not consider that may affect feeding decisions include age (Xue *et al.*, 1995; Anderson and Roitberg, 1999), body size (Takken *et al.*, 1998b), and the presence of parasites (Koella, 1998; Anderson and Roitberg, 1999). Our analysis could be expanded to include the availability of oviposition habitat; we recognize that reduction in oviposition sites reduces the ability of the mosquitoes to transmit malaria (Gu *et al.*, 2006). Finally, we caution against extrapolating our model predictions to situations where blood hosts and oviposition sites are not spatially segregated. We only consider a resource distribution scenario that is representative of anthropophilic endophilic mosquitoes such as *A. gambiae*.

Implications for mosquito and vector-borne disease control

The results from our model have implications for mosquito and vector-borne disease control. Our results suggest that controlling the availability of sugar near oviposition sites would be the best way of controlling mosquito populations, as even a small decline in the availability of this resource has a noticeable effect on female mosquito fecundity and survivorship. Conversely, there has to be a significant reduction in blood host availability to reduce the survivorship and fecundity of the mosquitoes. In practice, bed nets have been used to limit a mosquito's access to blood hosts (i.e. reduce blood host availability).



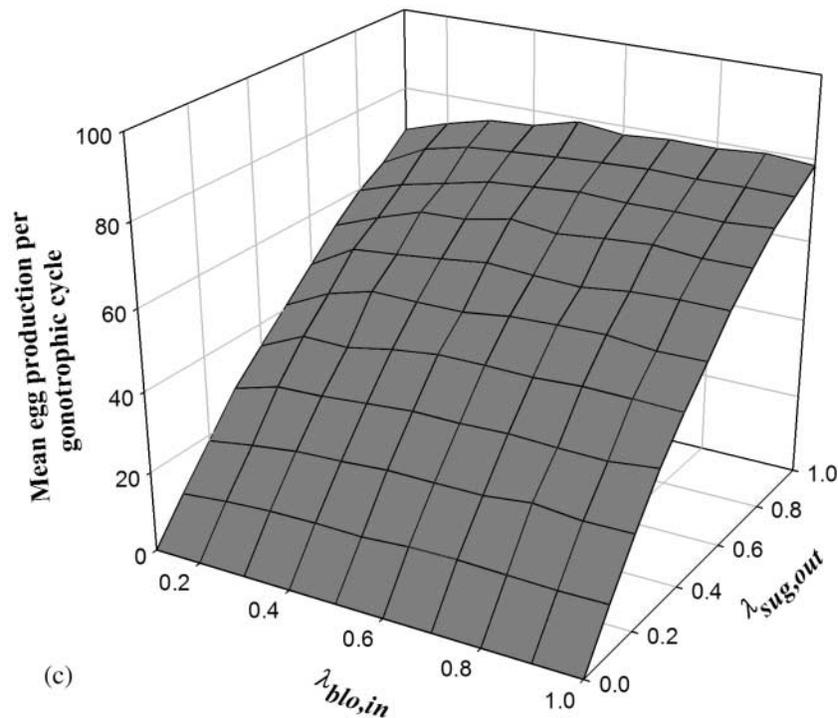


Fig. 6. Reproductive capacity of individuals as a function of blood availability inside ($\lambda_{blo,in}$) and sugar availability outside ($\lambda_{sug,out}$) based on Monte Carlo simulation results at $\lambda_{sug,in} = 1.0$. These results are representative of the same relationship for values of $\lambda_{sug,in}$ from 0.0 to 1.0. Panel (a) shows the mean fecundity, panel (b) shows the mean number of gonotrophic cycles, and panel (c) shows the mean egg production per gonotrophic cycle of an individual over her lifetime.

However, our results suggest that a very large proportion (~50%) of individuals would have to be covered by bed nets for there to be a significant reduction in mosquito survivorship and fecundity.

For vector-borne disease control, mosquito control is further complicated because the biting rate of the mosquito must be considered. In the case of *A. gambiae* transmitting *Plasmodium falciparum*, the parasite that causes malaria in humans, the parasite can be transmitted to and from the mosquito even from an unsuccessful blood feed (i.e. when the mosquito has not taken a complete blood meal or has only been allowed to probe). Furthermore, once inside the mosquito, *P. falciparum* requires approximately 10 days to reach the infectious stage. Therefore, the increased persistence of individuals when blood meals are difficult to acquire may in fact mitigate the effect of lower availability. However, both unsuccessful blood meals and multiple blood meals within a gonotrophic cycle can increase the likelihood of transmitting the disease (Briegel and Horler, 1993). We do not explicitly consider disease transmission in our model, but the predictions from other studies are conflicting. Some have suggested that reduced sugar feeding can drastically reduce the chances of transmitting the disease (Impoinvil *et al.*, 2004), while others have suggested that blood feeding in lieu of a sugar meal can lead to a higher transmission rate (Gary and Foster, 2001).

Given these advances in our understanding of the link between physiological state of the mosquito and feeding decisions, we need to reconsider the assumption of constant biting rates prevalent in most disease–vector models. Incorporating more complex vector behaviour into analytical models of mosquito–host dynamics may give us a better understanding of how to control vector-borne diseases because it will more accurately account for how environmental and physiological factors influence the resulting dynamics. The trade-offs in the acquisition and allocation of resources result in non-linear functions relating to resource availability and feeding decisions that may have important implications for disease epidemiology.

Summary

We designed a state-dependent model of mosquito behaviour based on first principles using the problems that a female mosquito faces. Specifically, given the trade-offs and constraints associated with blood, sugar, and egg acquisition, when should a blood-feeding female mosquito sugar feed, blood feed or oviposit? Our results emphasize the intimate link between survivorship and fecundity in female mosquitoes and demonstrate the importance of sugar feeding in a female mosquito's life history. With more sugar available, mosquitoes live longer and therefore take more blood meals and complete more gonotrophic cycles. Even with this simple model, the behaviour of the mosquitoes is consistent with our understanding of mosquito behaviour in nature.

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