Blacklegged tick (*I. scapularis*) host-seeking behavior: a dynamic state variable model

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INTRODUCTION

The nymph of the blacklegged tick (*Ixodes scapularis*) must attach to a host by the end of its questing season in order to molt into an adult. Properly timing this behavior is critical both for the tick's survival and for perpetuating the transmission of tick-borne pathogens.

Questing requires nymphs to climb from relatively sheltered leaf litter into the surrounding air, depleting limited energy reserves and risking desiccation [1]. Given the likely intense selection pressure exerted on questing behavior and the tradeoff between costs and rewards that underlies it, this foraging behavior and its environmental influences are classically tractable by dynamic programming methods.

OBJECTIVES

-Design dynamic state variable model of nymphal questing.

-Identify effect of leaf litter and air microclimate on questing strategy.

-Compare questing strategies in island and mainland climates, in light of *I. scapularis*' spread inland from coastal areas.

METHODS

Dynamic programming equation

In the model, a tick is characterized by three state variables:

-Life stage (**λ**): either **N** (off-host) or **A** (on-host) (after [2])
-Energy reserves (**x**)
-Water reserves (**w**)

and allocates a percentage of each day (**p_u**) to two behaviors (**u**):

-Resting in the leaf litter (denoted by subscript **r**)
-Questing for a host (denoted by subscript **q**)

Each behavior is associated with:

-Energy expenditure **c_u** (in μg water/day)
-Net change in water state **β_u** (in μg lipid/day)
-Probability of finding a host **h_u**

Fig. 1
I. scapularis *nymph*
(from TickEncounter Resource Center).

The payoff (**H**) for decision p_u is

$$H(x,w,t:p_q) = (1-(h_r p_r + h_q p_q))V(N, max[(x - c_r p_r - c_q p_q), x_{min}], max[(w + \beta_r p_r + \beta_q p_q, w_{min}], t+1) + (h_r p_r + h_q p_q)V(A, ...)$$

Given p_q, probability host not found before t+1 — *Fitness if nymph at t+1* — *Change in energy state between t and t+1* — *Fitness if adult at t+1* — *Payoff for choice p_q given time t, state x, w* — *Change in water state between t and t+1* — *Given p_q, probability host found before t+1*

where the nymph will maximize its fitness (**V**) on each day (**t**).

Changes in state variables were drawn from normal distributions. We assumed constant environmental conditions and host population densities over a brief 20-day season. Equations were solved in Igor Pro.

METHODS (cont.)

Water state

Water gain was modeled as passive sorption [3]:

$$\beta_G(av,T) = a_v T a + b$$

T is temperature, **a_v** is water activity (relative humidity/100), **a** and **b** are constants that take on different values over different ranges of a_v.

Water loss was modeled as a single-compartment transpiration process [3]:

$$\beta_T(a_v,T) = k_T T^2 ln(\frac{a_w}{a_v})$$

k_T is a constant, **a_W** is the tick's body water activity. Function proportional to T^2 to account for temperature effects on cuticle permeability.

Significant physiologic thresholds included in the model are:

-Critical equilibrium activity (**CEA**)=0.88, below which ticks are unable to maintain water balance [4]

-Pump threshold (**PT**)=0.75, below which ticks are unable to take up water.

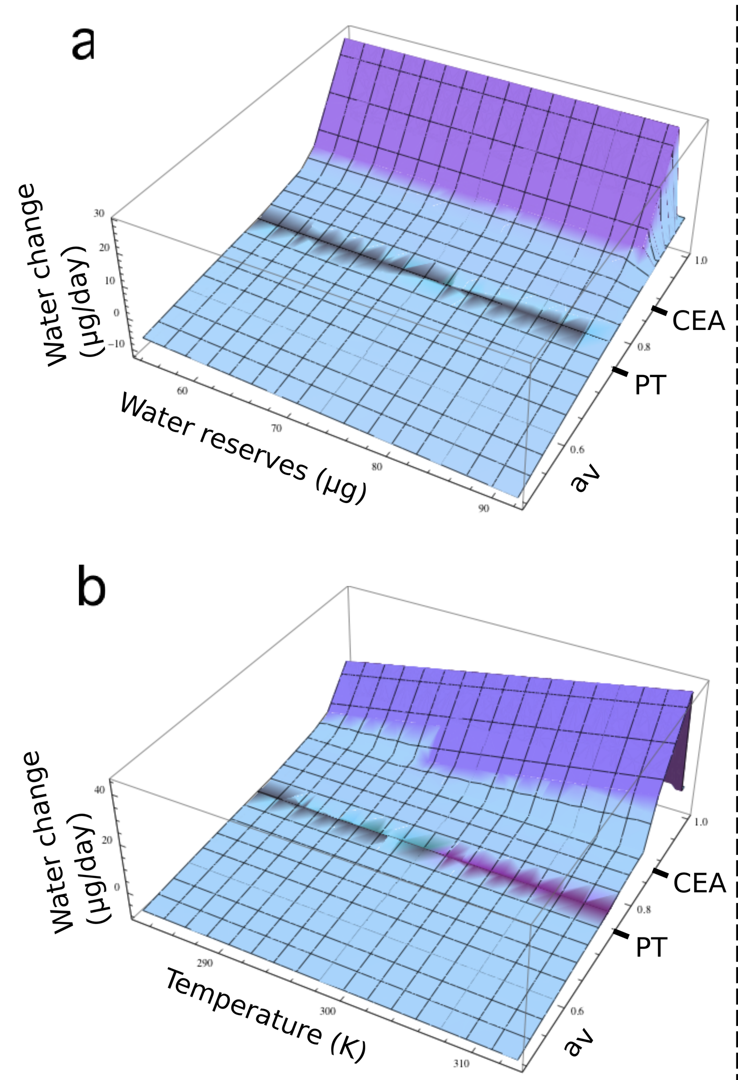

Fig. 2 ***Daily water change* a)** *as a function of water activity and tick water state at constant temperature (23C), and* **b)** *as a function of water activity and temperature at constant water state (72.5 μg).*

RESULTS

Theoretical findings

General results:

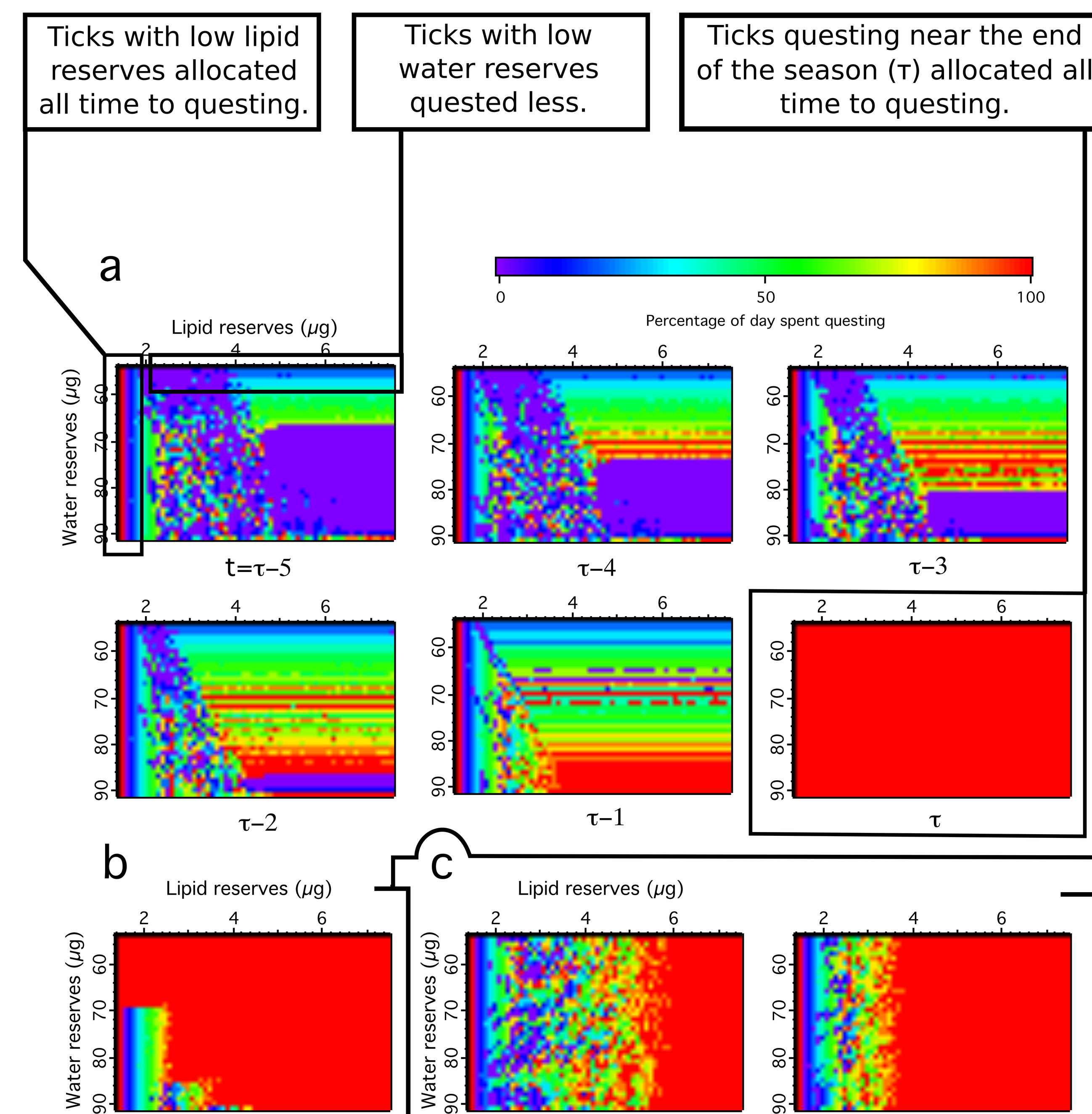

Fig. 3 ***Sample heatmaps of model output for three climate categories.*** *Each grid is a matrix of all possible lipid-water state combinations on a given day (where τ is the final day of the season). Each cell's color shows the percentage of the day a tick with that combination of lipid and water reserves should allocate to questing (warmer colors corresponding to higher percentages). Outputs generated from a single stochastic run.* **a)** *Change in strategies over time for category a.* **b)** *Strategy for category b - constant for all days except τ.* **c)** *Change in strategies over time for category c.*

Qualitatively different questing strategies emerged under three microclimate categories:

a) Air av<CEA<litter av (in which the tick loses water while questing and may replenish water stores by resting):

-Behavior was dependent on both lipid and water state and changed over the season (Fig. 3a).

-Higher air water activity led to increasing questing by lower-water-state ticks. Higher temperature decreased questing at low water activities (Fig. 4a).

b) Litter av<CEA (in which the tick is unable to replenish water stores by resting):

-The array of optimal strategies was the same for all t<τ, and resulted in 100% questing for ticks in nearly all states (Fig. 3b).

-Air water activity and temperature had little effect on strategy except in very dry air conditions (Fig. 4b)

c) Air av>CEA (in which the tick does not lose water while questing):

-Water state did not affect optimal strategy (Fig. 3c).

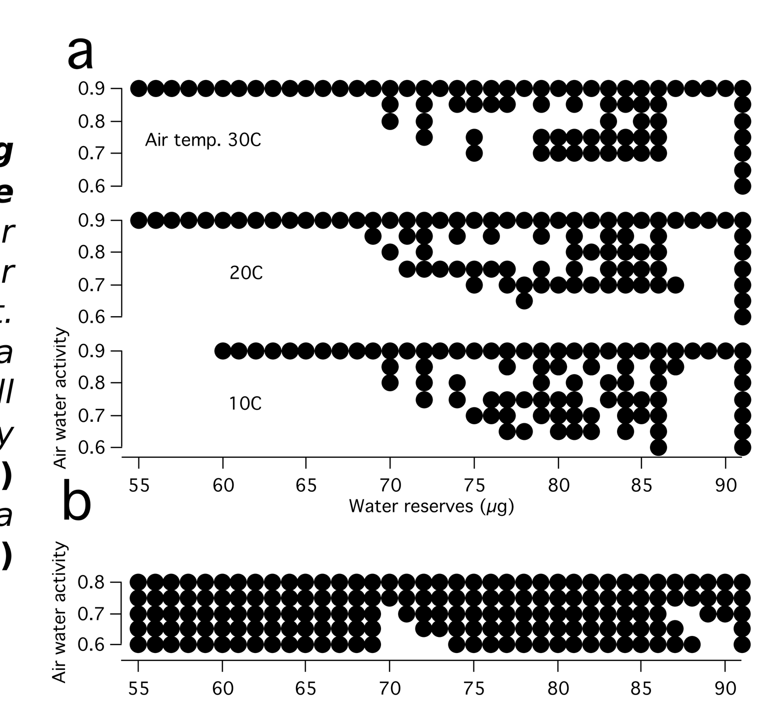

Fig. 4 ***Sensitivity of questing behavior to air microclimate and water state.*** *Air water activity was varied, leaf litter conditions were held constant. For each a_V, a dot represents a water state at which a tick will quest 100% of the day on day τ-5, given full lipid reserves.* **a)** *Questing in scenario a over a range of air temperatures.* **b)** *Questing in scenario b.*

Island vs. Mainland

We compared optimal questing strategies in "Island" and "Mainland" scenarios derived from field data (Fig. 5). "Island" air humidity was above the CEA, "Mainland" questing conditions fell below .

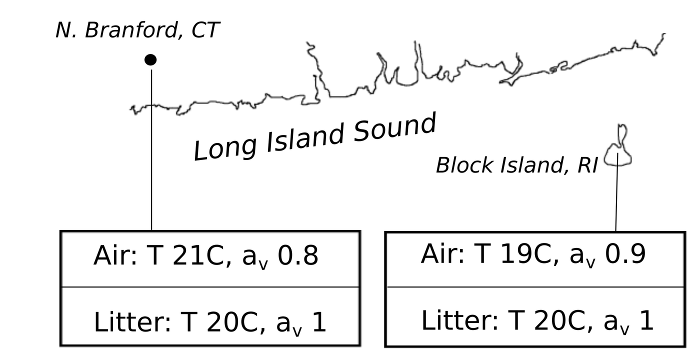

Fig. 5 ***"Island"/"Mainland" comparison schematic.*** *Scenarios were derived from climate measurements taken at field sites on Block Island, RI and North Branford, CT, respectively. Air measurements were made with HOBO weather stations, litter measurements were made with iButton loggers. Data from June to September 2014 were edited for outliers and averaged.*

Fitness (i.e., probability of encountering a host before the end of the season) remained higher overall in the Island scenario than in the Mainland scenario (Fig. 6a), corresponding to slightly increased questing late in the season (Fig. 6b).

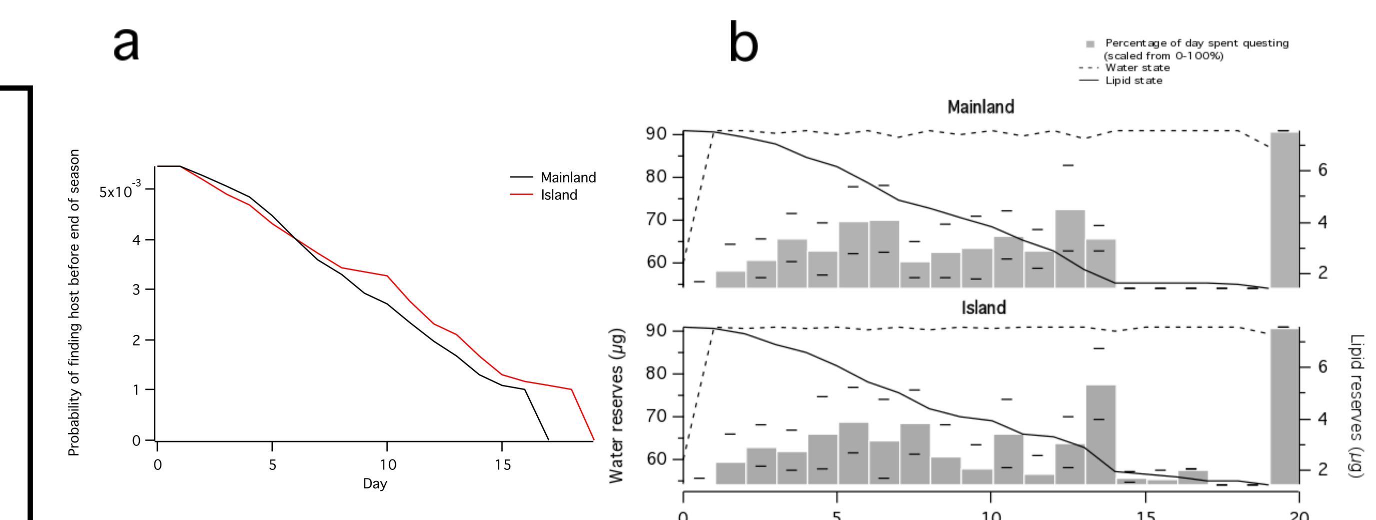

Fig. 6 ***Comparison of "Island" and "Mainland" climate scenarios.*** *Dynamic programming equation was run stochastically ten times and averaged. Plots represent a Monte Carlo simulation along this averaged result, with deterministic energy and water state equations.* **a)** *Plot of fitness scores over season (starting parameters x=7.6, w=91). 95% CI too small to include.* **b)** *Host questing strategies (bars) and energy (solid lines) and water reserves (dashed lines) over time for a tick in each scenario (starting parameters x=7.6, w=65). Error bars are 95% CI.*

DISCUSSION

-Questing increases at the end of the season and when lipid levels are low. Otherwise, climate affects the optimal timing of questing.

-Questing strategy may change nonlinearly as climate conditions cross physiologic thresholds.

-Optimally questing ticks living in relatively cool, humid coastal climates likely enjoy a fitness advantage relative to optimally questing ticks in dryer, warmer environments farther inland, secondary to increased questing time.

REFERENCES

[1] A.D. Lees, Parasitology 37(1-2):1-20 (1946)
[2] A. Fenton and S.A. Rands, Int J Parasitol 34(7):813-821 (2004)
[3] G. Wharton and A. Richards, Ann Rev Entomol 23(1):309-328 (1978)
[4] J.A. Yoder and A. Spielman, J Insect Physio 38(11):863-869 (1992)

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