Response to Comment on “Cognition-mediated evolution of low-quality floral nectars”

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Pyke and Waser claim that our virtual pollination ecology model makes unrealistic assumptions and fails to predict observed nectar concentrations of bat flowers and negative correlations between pollinator body size and sugar concentration. In their comment, crucial model features are misrepresented, misunderstood, or ignored. Sensitivity to the supply/demand ratio explains both the equilibrium concentrations and the selection for lower concentrations by larger pollinators.

We agree with Pyke and Waser (1) that pollinator-mediated evolution should result in concentrations beneficial for the plants. The crucial question is how bats can prefer sweeter nectars but select for lower concentrations at the same time.

We proposed and tested the hypothesis that diluting the nectar with more water offers a selective advantage to plants, even without additional nectar production costs. Therefore we assumed that the rate of sugar secretion was equal between plants, as has been proposed for plants pollinated by birds (2, 3). Researchers suggest that dilute nectars are a consequence of increased expression of the enzyme invertase, which hydrolyzes sucrose to glucose and fructose, thereby increasing osmolality that draws in water from the nectar (3). There is at least partial support for this hypothesis for bat-pollinated plants (4, 5).

We modeled our artificial plants on the bromeliad *Werauhia gladioliflora* (6), because it usually has one flower per plant open each night, which made the selection experiment more tractable. The natural situation is without a doubt more complex than the model, but evidence needs to be provided for the assumption that two fundamentally different processes have led to the same evolutionary outcome: one in plants with multiple flowers, and another in plants with single flowers.

Glossophaga bats have demonstrated a remarkable capacity for remembering individual locations (7, 8). However, contrary to the claim by Pyke and Waser, bats need not have remembered “volumes and concentrations of nectar obtained during each visit to a feeder, and the times when these visits occurred.” Our virtual bats integrated volume and concentration into a single remembered value (only one for each flower), updated upon each visit. Moreover, the full vector of available flowers in the memory of the virtual bats was only a bookkeeping method, in which unvisited as well as “forgotten” flowers had remembered values near zero and were unlikely to be visited. Furthermore, in the foraging session, real as well as virtual bats focused on a smaller subset of the available flowers. The revisit avoidance observed in real bats at a 64-flower array (7) demonstrates their capacity to remember recently visited locations, and we implemented this in Eq. 2 of the model. But this does not require remembering each time a flower was visited.

Because the virtual bats did not remember the full set of all spatiotemporal events, as was criticized by Pyke and Waser themselves as difficult to believe, we see no reason to defend them as factors influencing choice. We will only mention two points: (i) When several bats are foraging and competing for nectar, the time elapsed between two visits at the same flower by any of them is an unreliable predictor of the standing crop; (ii) a group of omniscient bats foraging in the same selection experiment yields the same pattern as the one with linear value encoding.

In the field and in the lab, the flight distances between flowers and their corresponding durations were negligibly small; therefore, they were not modeled in the current simulations. When the distribution of flowers on the array is random, as it was in our experiment, then a visit to a flower because of its physical position is random with respect to its nectar properties and can be modeled as probabilistic decision-making (9).

We are not the first authors to apply Weber’s law—or, more precisely, Fechner’s hypothesis (10)—to value-based decision-making (11, 12) or predicting the behavior of pollinators (13). The crucial feature is a sharper sensory resolution for smaller magnitudes, and this can be achieved by postulating a decelerating utility (value) function, a common feature of models of economic decision-making ([11] and references therein). In essence, the objective magnitude is transformed nonlinearly to form a neural representation, the subjective value. As we have shown elsewhere (14), pollinators prefer both larger volumes and sweeter nectars, but the resolution of discrimination diminishes with the magnitude of the stimuli.

Pyke and Waser correctly point out that the equilibrium concentration achieved in the field study was higher than naturally observed nectar concentrations. However, they fail to mention that this can be explained by the sensitivity of the system to the supply/demand ratio (figures 2, 3, and 4 in 15). Put simply, when there is hardly any perceived variation in nectar volume, bats prefer the flowers with the sweeter nectars. This occurs when the standing crops are high, especially when these exceed the maximum removal capacity of the pollinators. In the field study, the supply/demand ratio was higher than in the lab study, and a higher supply/demand ratio results in a higher concentration at equilibrium.

Similarly, a plant transitioning from a smaller to a larger pollinator also experiences an increase in demand, which lowers the supply/demand ratio and shifts the equilibrium toward higher volumes and lower concentrations. Contrary to the claim of Pyke and Waser, the effect of pollinator size is a feature predicted by our model. If we simply reduce the maximum amount a bat is able to consume in one visit from 60 μl to 20 μl, the equilibrium concentrations are shifted upward (from 27% to 37% for three virtual bats, and from 19% to 24% for nine bats). This result is observed without any changes to the value functions, demonstrating that body size need not correlate with discrimination ability to explain the negative correlation between pollinator size and nectar concentration. However, the equilibrium concentrations can be affected by differences in discrimination abilities. Data suggest that vertebrate pollinators are worse than bees at discriminating sugar concentrations (14) and that bumble bees may ignore the volume dimension completely when flower nectars vary simultaneously and incongruously in volume and concentration (16). Thus, bees, as opposed to bats, are expected to select for lower volumes and higher concentrations.

The optimality approach needs to be properly bounded by the constraints of pollinator cognition (15). We emphasize that pollinators do not directly experience the calories contents of nectar rewards but perceive them through the dimensions of volume and concentration. These dimensions are most likely integrated to form a subjective value for the available options— a process that causes specific deviations from optimality (7, 16) and may also result in counterintuitive selection pressures (15).

**REFERENCES**

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