TECHNICAL COMMENT

EVOLUTIONARY BIOLOGY

Comment on "Cognition-mediated evolution of low-quality floral nectars"

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Nachev *et al*. (Reports, 6 January 2017, p. 75) present dilute nectar in bat-pollinated plants as "paradoxical" because bats prefer concentrated nectar, but paradox disappears with realistic assumptions about nectar evolution. We argue that they make unrealistic assumptions about the cognitive abilities of bat pollinators, invoke Weber's law inappropriately, and cannot predict observed nectar concentrations of bat flowers or negative correlations between pollinator body size and average concentration.

Nachev *et al*. (*1*) suggest that production of dilute nectar in plants pollinated by bats and hummingbirds represents an unsolved evolutionary paradox because these animals prefer more concentrated nectar. They argue that such dilute nectar is explicable on the basis of nonlinear responses to nectar volume and concentration, consistent with Weber's law.

To investigate their proposition, Nachev *et al*. recorded nighttime foraging by bats at fixed arrays of artificial nectar feeders, set up in both the field (23 feeders) and the laboratory (24 feeders) and maintained for 10 to 12 nights per experiment. Each feeder produced sugar at the same constant rate, but varying volumes of water were added so that nectar concentration varied across feeders, decreasing directly with volume production rate. Multiple bats shared these foraging arenas, so nectar standing crops depended on rates of volume production and times since feeders were last visited. Bats removed available nectar from a feeder and visited multiple feeders during foraging bouts. Nectar concentrations changed between successive nights; otherwise, conditions remained constant.

Bats preferred feeders with intermediate nectar concentration over feeders with more concentrated or dilute nectar (*1*). Consequently, when nectar concentrations across feeders were allowed to "evolve" over successive nights, in accordance with visitation frequencies, average nectar concentrations tended toward intermediate levels. Nachev *et al*. obtained similar "evolution" of intermediate nectar concentration from a simulation model, with bats choosing which feeder to visit next as increasing, but nonlinear, functions of nectar volume and concentration. They conclude that this evolutionary process is a general phenomenon that explains relatively dilute nectar in bat-pollinated plants.

However, dilute floral nectar is not necessarily paradoxical, as evolution should result in nectar concentrations beneficial to individual plants rather than to pollinators (*2*–*5*). Nachev *et al*.'s assumption of a constant rate of sugar production across all feeders is unrealistic because there will be trade-offs between allocation of photosynthate to nectar and allocation to other plant activities, such as seed production (*6*). This assumption is also unrealistic in allowing "evolution" only of nectar concentration, and not of total sugar production or volume production independent of concentration. These authors justify identical sugar production across feeders on the basis of one study that reported similar average amounts of accumulated nectar per flower across plant species, when grouped by pollination syndrome (*7*), but did not provide accurate measures of sugar production per flower, gave no information regarding sugar production per plant, and indicated high variability in nectar attributes among flowers and plants, as generally occurs.

We believe the study by Nachev *et al*. fails to provide a satisfactory explanation for evolution of dilute nectar for the following additional reasons.

1) The foraging arena is unrealistic, as are assumptions regarding bat cognitive abilities and behavior. The array of feeders mimics plants having just one flower each, with individual plants attracting visits on the basis of nectar they provide; however, plants generally have more than one flower, and they manipulate rather than attract their pollinators (*4*). It is also difficult to believe that bats can remember the identity and location of each visited feeder, the volumes and concentrations of nectar obtained during each visit to a feeder, and the times when these visits occurred over each 12-hour foraging period, especially as each bat made approximately 175 visits to feeders during these periods (*1*).

2) Assumptions concerning how bats make foraging decisions are also unrealistic. A bat, given the memory capabilities assumed by Nachev *et al*., should choose its next feeder not solely according to energy yields from previously visited feeders, but also on the basis of the volumes and concentrations of nectar obtained from these feeders as well as times since each feeder was previously visited, because expected energy yields at potential feeders will depend on all these factors in combination, and not only (or not simply) on energy obtained from each feeder. Such a bat should also be influenced by its expected times to move to and collect nectar from potential feeders, as these times will determine rates of energy yield and expenditure. Furthermore, a bat is likely to choose its next feeder on the basis of its direction of travel and distance (*8*, *9*), rather than randomly with different probabilities for each possible feeder.

3) Nachev *et al*.'s adoption of Weber's law is inappropriate, as this law relates to an animal's ability to differentiate among levels of stimuli (in this case, varying nectar attributes) and to store and retrieve this information (*10*), and not to how an animal chooses to respond to perceived stimuli. An observed nonlinear response to a stimulus does not demonstrate a similarly nonlinear ability to discriminate stimuli. Furthermore, these authors struggle to justify how their assumed nonlinear responses by bats to nectar volume and concentration are consistent with Weber's law, relying on their observation that "evolution" of intermediate nectar concentration occurs in their simulations only with this particular nonlinear response, and not when responses are assumed to be linear (*1*).

4) The approach taken by Nachev *et al*. fails to accurately predict observed nectar concentrations or to explain the observed negative correlation, across plant species, between pollinator body size and average nectar concentration (*2*). Average nectar concentration across feeders "evolved" toward about 35% (w/w) [figure 1C of (*1*)], approximately double the observed nectar concentrations for the plant species (*Werauhia gladioliflora*) that the foraging arena aimed to mimic and for other bat-pollinated plants (*2*, *11*, *12*). Animals are unlikely to differ in their responses to these nectar attributes simply on the basis of body size, as they exhibit no apparent size-related differences in their abilities to differentiate among nectar attributes and, regardless of body size, prefer high volumes and concentrations of nectar (*4*).

An alternative approach could remedy the problems. Determining how bats observed by Nachev *et al*., if foraging optimally (*13*), should respond to nectar volume and concentration, along with other variables, could explain their results. Incorporating such an optimal foraging approach more generally into models of plant-pollinator coevolution that simultaneously consider the interests of both plants and pollinators (*14*) could provide explanations for observed pollination syndromes involving nectar (*3*).

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