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Cognition-mediated evolution of low-quality floral nectars

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REPORT

EVOLUTIONARY BIOLOGY

Cognition-mediated evolution of low-quality floral nectars

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Plants pollinated by hummingbirds or bats produce dilute nectars even though these animals prefer more concentrated sugar solutions. This mismatch is an unsolved evolutionary paradox. Here we show that lower quality, or more dilute, nectars evolve when the strength of preferring larger quantities or higher qualities of nectar diminishes as magnitudes of the physical stimuli increase. In a virtual evolution experiment conducted in the tropical rainforest, bats visited computer-automated flowers with simulated genomes that evolved relatively dilute nectars. Simulations replicated this evolution only when value functions, which relate the physical stimuli to subjective sensations, were nonlinear. Selection also depended on the supply/demand ratio; bats selected for more dilute nectar when competition for food was higher. We predict such a pattern to generally occur when decision-makers consider multiple value dimensions simultaneously, and increases of psychological value are not fully proportional to increases in physical magnitude.

When presented with a choice, hummingbirds and nectar-feeding bats prefer concentrated solutions of up to 60% sugar (1–3). Plants that are specialized for vertebrate pollination, however, generally offer relatively dilute nectars of 18 to 23% sugar (4, 5). Nectar value depends on both quality and quantity. Quality is primarily determined by sugar concentration, which is genetically controlled and relatively consistent for individual flowers (6–9). However, multiple foragers normally visit the same flowers, which causes nectar quantity

to be highly variable and dependent on the elapsed time since the previous visit. Consumer behavior thus determines availability, introducing a complex dynamic into the decision-making process. To study the factors contributing to the evolution of dilute nectars, we incorporated consumer behavior into a virtual evolution experiment by having free-range bats visit artificial flowers.

Field experiments were conducted with free-range adult *Glossophaga commissarisi* bats that had been outfitted with radio-frequency ID tags

in the rainforest at La Selva Biological Station, Costa Rica. We presented bats with a computer-controlled array of 23 artificial flowers (Fig. 1A). Each flower was equipped with an ID sensor and a photogate (a device that recorded the duration of a bat visit) and connected to a nectar-pump system capable of delivering nectar of defined sugar concentration and volume (10). The density of the array approximated the distribution of a local bat-pollinated bromeliad (*Werauhia gladioliflora*) that provides nectar with sugar concentrations between 14 and 16% (11). Visiting bats were rewarded with nectar, and the amount of nectar was determined by the secretion rate and the elapsed time since the previous bat visit.

We assumed individual plants in our population to have equal rates of photosynthesis and invest equal amounts of photosynthate, as sugar, into nectar (9). However, the sugar concentration of the nectar was determined by a flower's virtual genome, which consisted of a diploid set of four diallelic genes. The effect of the eight codominant alleles determined the water component of the nectar and thus its final sugar concentration. Some alleles coded for smaller water components and some alleles coded for larger water components, making the sugar concentration of nectar a multilocus trait (12).

Upon leaving a flower, a bat was assumed to transfer virtual pollen to the next flower and generate a virtual offspring seed there. Twenty-three such seeds, selected from a night's production by stochastic universal sampling, formed the next generation of virtual plants (Fig. 1B).

Fig. 1. Wild bats exert stabilizing selection on nectar concentration. (A) Artificial flower array. (B) Formation of plant generations. Starting population of plants (1); each plant has its own genome coding for water production rate in flower nectar. Bats visit flowers for nectar (2) and generate virtual seeds (3). The most common genotypes are most likely represented in the new generation of plants (4), which is then presented to bats. (C) Whether the initial mean sugar concentration [% weight of sugar/total weight of the solution (% w/w)] was low or high, bats selected for intermediate concentrations; solid lines indicate low (green) and high (blue) initial mean sugar concentrations. Phenotypic trajectories lie outside those expected under genetic drift; dashed lines indicate 95% prediction intervals. (D) Each dot represents a difference in mean sugar concentration between the offspring generation and the generation from the previous night, where green indicates low and blue indicates high initial mean sugar concentrations. Dashed lines show equilibrium concentration, and dotted lines show 95% confidence intervals. The orange line shows regression.

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Fig. 2. Psychophysical and population effects on decision making. (A and B) Probabilities of choosing an option compared to a reference (black circles) for nectar sugar concentration (A) or volume (B). The different line types (solid, dashed, or dotted) represent curves calculated from psychometric functions of intensity perception based on different references (black circles). Probabilities change more for decreased than increased values (2), and this asymmetry is stronger at low magnitudes (2), and this asymmetry is stronger at low magnitudes (2), and this asymmetry is stronger at low magnitudes (2).

Symbols with error bars labeled “3 bats” or “9 bats” are medians ($\pm$ interquartile ranges) of concentration (% w/w) or volume experienced during laboratory experiments over the complete runs; distributions differ primarily in volume. (A, inset) A psychometric function of intensity perception. Such functions were used to calculate choice probabilities in (A) and (B) for specific reference values (black circles). (C) An analytical example of reward value maximization when sugar energy is fixed but water content is variable, assuming logarithmic preference for alternatives. Consider a flower with a fixed rate of sugar production and an independent rate of water added to this sugar. When harvested by a single forager at regular time intervals (20, 60, and 120 min), the amount of sugar collected per visit decreases when collection intervals decrease. Iso-caloric lines connect combinations of volume and concentration with identical quantities of sugar in a portion resulting from the fixed revisit interval and constant secretion rate. Black dots show the nectar concentration at which perceived value is maximal. As the amount of sugar in a portion decreases, the optimal concentration also decreases (arrow).

Flowers that were visited more frequently were thus more likely to have their alleles represented in the next generation.

We tracked the evolution of two lineages of artificial flowers over multiple generations. The evolutionary outcome differed significantly from that expected under genetic drift (Fig. 1C). Bats made fewer visits to flowers with either very dilute or very concentrated nectar (fig. S1). As a result, sugar concentration of nectar in both lineages, which started from 17.8% for dilute nectar or 42.2% for concentrated nectar, evolved to about 36% [95% confidence interval (CI) 33 to 40%] within 10 to 12 generations, where one generation was produced per night (Fig. 1, C and D). This result was consistent with stabilizing selection converging on an equilibrium [Fig. 1D; linear regression: $P < 0.001$, adjusted coefficient of determination (R^2) = 0.48].

An optimal forager should choose among available alternatives based on the highest energy return. However, studies of the ability of bats to discriminate nectar volume (13) and concentration (2, 10) in binary choice designs have yielded psychometric curves consistent with Weber's law (Fig. 2, A and B). This law states that the ability to perceive a stimulus as different from another requires a minimum difference in intensity that is proportional to the intensity of the initial stimulus (2, 14). The proportional processing of volume and concentration may result from underlying subjective value (psychophysical) functions, in which value progressively increases with stimulus magnitude, but with a decreasing slope (10, 13–16).

With such concave-down value functions (e.g., logarithmic or power functions), if nectar quality changes by a specific amount, then a reduction in magnitude changes choice probabilities more strongly than a corresponding increase in magnitude. As seen in the psychometric function, the slope decreases with higher magnitudes (Fig. 2, A and B). This is relevant here, where nectar rewards are evaluated along two dimensions (volume and sugar concentration) and where there is a trade-off between a decrease in value along one dimension and an increase along the other dimension.

To explore potential effects of proportional processing on natural selection of nectar concentrations, we modeled the experimental flower array and tested the evolutionary consequences of virtual nectar-foraging bats. The virtual bats made choices by integrating information about nectar volume and concentration into a single representation of value (supplementary materials and methods). Our simulations contrasted logarithmic value functions (Fig. 2) with functions with a linear relationship between choice probability and caloric value. We also examined how the supply/demand ratio influences selection dynamics. At low supply, bats encountered smaller volumes of nectar, which made discriminating nectar quantity easier because smaller outcomes are represented internally more sharply than larger ones (14) (Fig. 2B).

Both psychophysics and pollinator density may thus affect nectar evolution. To elucidate their influences, we performed four simulations comparing linear versus nonlinear value functions in conditions of either high or low supply/

demand ratios. Only the simulations that incorporated nonlinear value functions (Fig. 3, A, B, E, and F) were congruent with the main result of our field experiments in that evolved concentrations converged to intermediate equilibrium values. In contrast, simulations incorporating linear value functions resulted in either directional selection to sugar concentrations greater than 43% or no selection (Fig. 3, C, D, G, and H). Because all simulations incorporated the designed dynamics of our flower array and the frequency and consistency of flower visits by bats in similar foraging situations, concave-down value functions appear essential to understanding our experimental results. Furthermore, we found that the simulations with a low supply/demand ratio (nine bats) resulted in lower equilibrium sugar concentration [Fig. 3F; $18.7 \pm 0.1\%$ (mean $\pm$ 95% CI); linear regression: $P < 0.001$, adjusted $R^2 = 0.34$] than simulations with a high supply/demand ratio (three bats) [Fig. 3E; $26.8 \pm 0.2\%$ (mean $\pm$ 95% CI); linear regression: $P < 0.001$, adjusted $R^2 = 0.12$]. This suggests that the evolutionary trajectory of the sugar concentration of nectar is influenced by the availability of nectar. We therefore tested our cognitive evolutionary model in the laboratory, which enabled independent control of the amount of sugar available and the number of bats.

Laboratory experiments were conducted using captive bats from our laboratory colony. We analyzed the evolution of an array of computer-controlled flowers in situations of high demand (nine bats foraging) versus situations of low demand (three bats foraging). There were between

Fig. 3. Selection for dilute nectar can be driven by nonlinear reward evaluation. Selection in a low-demand situation, where only three bats share available nectar (A, C, E, and G), and in a high-demand situation, where nine bats share available nectar (B, D, F, and H). Virtual bats encoded volume and sugar concentration either logarithmically (A, B, E, and F) or linearly (C, D, G, and H) with respect to caloric contents. Simulations had 100 generations, and n equals 100 replications. (A to D) Phenotypic trajectories; notation as in Fig. 1C, except here 95% prediction intervals indicated by dotted lines. (E to H) Responses to selection; notation as in Fig. 1D. Only a random selection of 10% of data points are shown.

Fig. 4. The mean sugar concentration at equilibrium depends on nectar demand. Selection exerted by nine bats (high demand) (A and D) caused slower convergence and a shift to a lower equilibrium sugar concentration than selection exerted by three bats (low demand) (B, C, E, and F). (A to C) Phenotypic trajectories; notation as in Fig. 1C. (D to F) Responses to selection; notation as in Fig. 1D. The supply was kept at the same constant rate for all experiments.

15 and 50 successive generations in each selective lineage. The flowers of the initial parental generations produced nectar with either high or low mean levels of sugar concentration. Data were collected automatically, and the results were analyzed using algorithms that were es-

entially identical to those used in the field study (supplementary materials).

These results replicated the fundamental finding from the field experiment: An intermediate equilibrium sugar concentration of nectar evolved (Fig. 4). The equilibrium concentration

was also shown to be affected by the supply/demand ratio; the concentration was lower under high competition [Fig. 4, A and D; $22 \pm 2\%$ (mean $\pm$ 95% CI); linear regression: $P < 0.001$, adjusted $R^2 = 0.35$] than under low competition [Fig. 4, B and E; $33 \pm 3\%$ (mean $\pm$ 95% CI); linear regression: $P < 0.001$, adjusted $R^2 = 0.33$; and Fig. 4, C and F; $29 \pm 2\%$; linear regression: $P < 0.001$, adjusted $R^2 = 0.29$]. The equilibrium from the high-competition treatment was also closer to the range of sugar concentrations found naturally in bat-pollinated flowers (Fig. 4, A and D). There was no significant difference in equilibrium sugar concentrations due to treatment order in the groups with three bats [Fig. 4, B, C, E, and F; lm in R (linear model function in R language), $t = 0.11$, $P = 0.92$; overall model $F_{3,82} = 13.28$, $P < 0.001$, adjusted $R^2 = 0.30$].

Our studies of the dynamic interactions of bats and flowers show that the evolution of nectars with lower sugar concentration can be driven by pollinators acting as economic decision-makers subject to the principles of psychophysics and reinforcement. If pollinators simply maximized energetic gains through linear-value encoding, they would not exert stabilizing selection pressure on the flowers, and an intermediate concentration would not be selected for (Fig. 3).

Our approach of combining field experiments, simulations, and confirmatory laboratory studies allowed us to elucidate an intricate evolutionary narrative. The dynamic interaction between nectar volume, sugar concentration, and psychophysics would have made predicting the direction

of selection from analyses based on only a single reward dimension impossible. The competition among bats that determines the supply/demand ratio provided an additional layer of causal complexity (figs. S2 and S3). These results demonstrate the power of iterating between simulation and experimentation and suggest a plausible account of the transition to producing nectars with low sugar concentrations in bat-pollinated plants as well as in other species that undergo evolutionary shifts between different pollinators (12, 17–20).

We replicated the natural situation most closely when we reduced the supply/demand ratio by increasing the number of consumers exploiting limited resources. The increase in demand reduced median food portions available at flowers from 60 to 6 μ L (Fig. 2B), but weakly affected sugar concentration (Fig. 2A, 30% versus 24%). When overall value is the product of multiple reward dimensions, proportional magnitudes attain importance. Since perceived differences are stronger at smaller physical magnitudes, discrimination along the volume dimension could take priority over the concentration dimension. Therefore, as predicted by our model (Fig. 2C), bats favored increases in volume instead of concentration, shifting the balance toward more dilute nectars. Similar processes are likely to affect the behavior of invertebrate pollinators, where the different shape of the psychometric function for concentration (2) and the preference for nectars with higher sugar concentrations even at the cost of profitability, (21) presumably cause selection for more concentrated nectars. For vertebrate and invertebrate pollinators,

body size correlates positively with nectar production rates and negatively with sugar concentration (5).

In contrast to some psychological models of economic choice that assume nonlinearity in utility (15), our approach is based directly on physiological processes underlying proportional (Fechnerian) reward evaluation. When multiple perceptual dimensions determine value, a trade-off (22) situation may arise as does between nectar volume (13) and sugar concentration (2, 10). These effects of proportional psychophysics on reward evaluation are of a general nature and should be applicable to other choice situations.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S6
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Supplementary Materials for

Cognition-mediated evolution of low-quality floral nectars

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Materials and Methods

FIELD EXPERIMENTS

Individual *G. commissarisi* ($n = 16$, nine males and seven females) were caught by mist-netting in the vicinity of feeders equipped with dimethyl disulfide odor attractants and were marked with unique radiofrequency identification (RFID) tags using silicon necklaces and heat-shrink tubing. After RFID-tagging, bats were released at the capture site. Non-marked bats were also attracted to the flowers, but since the identity of these visitors could not be determined, their visits (detected by photogates) were included in selection algorithm calculations as if they had been made by a single individual (see Genetic Algorithms below). Due to the automated nature of the analyses (see Genetic Algorithms), no blinding or random animal assignment to the experimental conditions was implemented. Animal experimental procedures were reviewed and permission for animal experimentation and RFID-tagging was granted by Sistema Nacional de Areas de Conservación (SINAC) at the Ministerio de Ambiente y Energía (MINAE), Costa Rica.

Artificial Flowers and Procedures

The experimental field consisted of 23 artificial flowers mounted under a steel frame canopy(10). Each flower was equipped with a photogate that was triggered when a bat inserted its snout and an RFID sensor that identified the individual. A tube connected each flower with two solenoid pinch valves to two gas-tight Hamilton glass syringes holding the nectar. Syringe pistons were advanced automatically with stepping motors. Differential activation of each syringe during reward delivery allowed the regulation of reward amount and concentration. The data collected consisted of the time stamp, the identity of the bat (unknown if the bat was not tagged), the duration of the visit (from photogate signal), and the reward amount and sugar concentration.

The smallest reward volume that could be delivered was about 4.5 μL . Nectar consisted of one part sucrose and two parts fructose diluted in water, similar in its mono- to disaccharide ratio to natural nectars of glossophagine-pollinated plants(23). The two pumping systems contained nectars with different sugar concentrations, 10% and 50% by weight. The sugar concentrations delivered to each flower were regulated by adjusting the ratio of the volumes of the two concentrations that were delivered. The mixing algorithm allowed for 21 different concentrations from 10% to 50%, in 2% unit increments. The accuracy of the mixing process had a SD of $\pm 3.5\%$ units, estimated from experimentally delivered volumes using a hand refractometer.

To mimic the variation in nectar volume that bats experience in nature, we assigned a virtual “nectar account” to each flower. The current account balance determined the amount of nectar a bat could receive as a reward upon making a visit. During the nightly experiments, the amount in this account increased continually at a constant production rate. The maximum reward a flower could deliver to a bat was 54 μL . If the account balance was smaller than the maximum value, the bat received the full balance remaining in the account. Flowers delivered no rewards until the minimum reward amount of 4.5 μL had accumulated. Thus, flowers could deliver different discrete reward volumes, ranging from 0 to the maximum reward (54 μL) in increments of 4.5 μL .

Bats were allowed to forage on the array of flowers from 17:30 until 05:30. One to six tagged bats were detected making visits each night (median: 4; including estimates

for untagged bats, range: 4-17, median: 10). Virtual nectar secretion was initiated at 16:30, so that at the beginning of each evening's foraging session, all flowers had accumulated some nectar in their accounts.

Relationship between Volume, Concentration, Secretion Rate and Standing Crop

The secretion rate determines the volume of nectar that a flower produces in a given time interval. If sugar concentration is constant then concentration multiplied by volume gives the amount of sugar that a plant offers to pollinators, and that originally comes from photosynthesis. Pollinators will always want more sugar but both a plant's rate of photosynthesis and life history will cap the amount of photosynthate channeled into nectar. Now, when the amount of sugar is fixed a plant can still vary its nectar sugar concentration by varying the amount of water added to the sugar resulting in nectar. Thus, when the amount of sugar is constant then secretion rate will strictly correlate with nectar sugar concentration. Plants that keep concentration low will offer larger volumes and vice versa. Empirical data confirm that nectar secretion rate correlates negatively with nectar sugar concentration(9). In different species of the plant tribe *Sinningieae*(9), nectar volume and dilution were found to increase by a similar factor, so that total sugar production was comparable between plant species with different pollinators. All the same, on a visit to visit basis a pollinator is confronted with a flower's standing crop(24). That is the amount of nectar actually available during a specific visit(24). The major factor that causes variability in standing crop, however, is not the plants' secretion rates but the pollinators' visitation activity(25). Therefore, pollinators are confronted with a variability in nectar availability in a flower that is less dependent on floral nectar secretion and more dependent on the supply/demand ratio caused by competition through other flower visitors. Our experimental set-up mimicked natural conditions, in which the nectar standing crop is determined by both nectar secretion rate and bat activity.

Genetic Algorithms

The artificial flowers remained unchanged from night to night, except for their nectar properties, which were specified in virtual genomes. These genome parameters were uploaded to the experimental control computer and used so that the syringe pumps mixed the correct sugar concentration for each flower during each night. The diploid genome of the flowers was set so that four diallelic genes simultaneously determined the nectar production rate and concentration. Sugar production rates were fixed and equal among flowers at 41.7 mg h^{-1} but water production rates were encoded by the genome, resulting in a trade-off between sugar concentration and nectar production rate(9). For the sake of simplicity we refer to phenotypes only by their sugar concentrations, not their corresponding nectar production rates. Genetic variation was additive and the individual contributions of the different codominant alleles to the concentration phenotype were $A = B = C = 7.5\%$ sugar concentration units, $a = b = c = 1.5\%$ units, $D = 2.5\%$ units, and $d = 0.5\%$ units. This genome structure yielded a total of 21 different phenotypes (from 10% to 50% concentration, in 2% unit increments) encoded by 81 different genotypes. The redundancy in the genome allowed for fine control over sugar concentration, while maintaining genetic variance in the population even after many rounds of selection.

Reproduction entailed the transfer of virtual pollen among flowers, which was simulated by running a genetic algorithm on the bat visitation data collected after each foraging night. Every flower visit was interpreted as the removal of a single pollen grain

from that flower. During meiosis the four genes assorted independently without mutation. Prior to pollen removal, a bat that already carried pollen would deposit its cargo for fertilization, generating a virtual seed, the product of a standard tetrahybrid cross between the parental pair of flowers. For the sake of simplicity the virtual plants were treated as self-incompatible and did not generate seeds when selfing. The different genotypes present in the pool of potential offspring generated by the visits of all bats during the foraging session (range: 357-2729, median: 1264) were ranked based on their frequencies. This ranking was then taken as the fitness measure for a Stochastic Universal Sampling(SUS, 26, 27) used to select the genotypes for the following generation. If necessary, allele fixation was prevented by replacing a single copy of the fixed allele in a random individual with the extinct allele, reintroducing it to the population. Allele fixation needed to be prevented only infrequently, and in over 90% of these cases, the extinct allele coded for the higher concentration. Finally, the newly generated genotypes were randomly assigned to the 23 positions on the flower array.

The High run (parental generation with mean sugar concentration of 42.2%) was conducted first and lasted for 11 days; the Low run (17.8%) lasted for 14 days. Bats were presented with a parental population of flowers under non-evolving, control conditions for six nights before the High run and for three nights before the Low run. During the control presentations, the populations always had the same overall allelic frequencies within the same experimental condition, but the alleles were randomly combined across individuals and distributed at different locations in the flower array. Genetic algorithms were implemented in VBA, and subsequent analyses were performed with R (version 3.3.0).

Analytical Measures

The main dependent variables analyzed were the mean sugar concentration and the response to selection in every generation. Response to selection was calculated as the mean concentration of the pool of potential offspring generated by the bats minus the mean concentration of the population of flowers presented to the bats. For every experimental condition the mean concentration at equilibrium is the concentration for which the response to selection is zero. Selection towards higher concentrations is indicated by a positive response to selection. Selection towards lower concentrations is indicated by a negative response to selection. The mean concentration at equilibrium was estimated by performing a linear regression with response to selection as the dependent variable and mean concentration as the independent variable.

In order to compare the observed phenotypic trajectories to the expected trajectories in the absence of selection, we conducted a randomization selection test by shuffling the genotypes in the parental generation. We then used the real visitation and fertilization sequences in order to produce the following generation, using the same algorithm as in the actual selection experiments. The resulting offspring were assigned random array positions and the visitation sequences from the following day were taken to generate the next step in this genetic drift simulation, until the desired number of generations was produced.

SIMULATIONS

Flower Array

The simulated environment consisted of 24 virtual flowers with properties similar to those of the array we deployed in the field experiment. The sugar production rate of all flowers was 26.1 mg h^{-1} . Nectar secretion and pollen production and dispersal occurred according to the algorithms we used previously. Reward volumes were real values in the range of 0-60 microliters, 60 being the maximum amount a virtual bat could imbibe in one visit. Nectar secretion was initiated at time 0 and a virtual foraging session lasted for 12 hours. The selection algorithm was the same as previously described, except for a control on the occasional extreme effects of stochastic universal sampling. In general, candidate offspring were only chosen if they differed by no more than 0.3% units from the mean concentration of the complete pool of potential offspring. In rare cases, however, this criterion could not be met. To avoid infinite loops, if no suitable offspring population was found after 1000 attempts, the difference threshold was increased by 0.1% units and sampling was repeated until the new criterion was satisfied. All simulations were implemented in C# .NET and analyzed with R.

Virtual Bats

The time intervals (in seconds) between two successive flower visits were drawn from two lognormal distributions, approximating the time intervals observed in groups of three bats in the laboratory. With probability $(1 - \varepsilon)$ a sample was drawn from a distribution generating shorter intervals ($\mu = \exp(3.2)$, $\sigma = \exp(1.8)$), representing the intervals for visits within a bout; otherwise the sample was drawn from a distribution generating longer intervals ($\mu = \exp(5)$, $\sigma = \exp(2)$), representing the intervals between different bouts. The range of time intervals was restricted to between 1 and 8000 seconds and the value of ε was set at 0.3. All parameters were chosen to approximate the interval distributions of real bats from previous laboratory studies. When a choice was being generated, the time interval was drawn first and then the bat's memory was consulted to select the next flower to fly to. The interval distribution resulted in bats making 175 ± 71 (mean $\pm$ 95% CI) visits per 12 hours, comparable to the visits made by bats in our field study (mean: 164, 95% CI: 1-725). Bats could fly from any flower to any other flower in one second and inter-flower distance in our field array simulating the crown of a small tree did not affect bat decisions. This is realistic considering flight speeds between 3-6 m/second (28). The memory of a virtual bat consisted of a vector of remembered values $[V_{R1}, V_{R2}, \dots, V_{Rn}]$ that were real numbers from the unit interval $[0,1]$, one for each flower ($n = 24$). Remembered values were initialized at 0, so that the first visit was random.

Each individual reward obtained by a bat at flower i was evaluated as V_{li} , the instantaneous reward value, also a real number from the unit interval $[0,1]$ (see Instantaneous Value Calculation below). The remembered value V_{Ri} at time t_n for a flower i was calculated as the mean of the instantaneous values experienced at that flower from the time of the first visit t_0 :

$$V_{Ri}(t_n) = \frac{V_{li}(t_0) + \dots + V_{li}(t_n)}{n(t_n)}, \quad (1)$$

where $n(t_n)$ is the total number of visits at flower i up to t_n .

In order to avoid immediate revisits to flowers that have just been emptied, each remembered value was transformed to a time-dependent remembered value (V_{Ri}^*) with the following revisit avoidance function:

$$V_{Ri}^* = (1 - e^{-0.02\Delta t}) \times V_{Ri}, \quad (2)$$

where Δt is the time elapsed since the last visit at that flower. Finally, the next flower to be visited was chosen with Softmax action selection(29) as follows:

$$P_i = \frac{e^{V_{Ri}^* / \tau}}{\sum_{k=1}^n e^{V_{Rk}^* / \tau}}, \quad (3)$$

where P_i is the probability to select flower i , $n = 24$ is the total number of flowers, and τ determines how strongly the choice relies on the vector of remembered values (fig. S4). In all simulations the value of τ was set at 0.15, in order to allow for sufficient exploratory behavior, so that in groups of three, bats visited on average 14 ± 4 (mean $\pm$ 95%CI) flowers per generation, and in groups of nine they visited 18 ± 4 flowers per generation, both of which are comparable to the results of the lab experiments. As we wanted to understand the consequences of different reward evaluation mechanisms, we did not implement direct interactions between bats and only allowed for exploitation competition.

Instantaneous Value Calculation

We used two different instantaneous value methods and compared their corresponding phenotypic trajectories and responses to selection over 100 simulation replicates with 100 generations per replicate. With **linear value encoding**, the reward obtained at a flower i was evaluated as:

$$V_{Ri} = 1.7 \times (15.96 \times 10^{-6} v \times (0.05298c^2 + 9.56955c + 3.32727)), \quad (4)$$

where 1.7 is a scaling constant that sets the value of a reward of 60 μ L and 50% concentration to one, 15.96 KJ/g is the specific energy of the sugar mixture used in the real bat experiments, v is the volume of the reward in microliters, and c is the concentration of the reward, the quadratic term of which converts concentration into grams of sugar per liter of solution (regression based on data from ref.(30)). Thus, reward evaluation was linear with respect to the energetic content of a reward.

With **non-linear value encoding** instantaneous value was assumed to be the product of independent evaluations of volume and concentration. In accordance with Fechner's hypothesis, the subjective perception of nectar volumes and concentrations can be modelled as an increasing but decelerating function(16):

$$V_{Ri} = (1 - e^{-0.06v}) \times (1 - e^{-0.06c}), \quad (5)$$

where V_{Ri} is the instantaneous value, v is the volume of the reward, and c is the concentration of the reward. The exponents were chosen for consistent scaling in the linear and non-linear evaluation functions. We selected a logarithmic, rather than a power function(31), following previous analyses of animal choice(16, 32).

An alternative to non-linear value encoding is scalar linear encoding, where the representations of the stimulus magnitudes are lognormally distributed with a constant coefficient of variation(14). This approach also generates value functions consistent with

Weber's law(14). We implemented it in our simulations and obtained results similar to the simulations using Eq. 5 (fig. S5). Underlying this conceptual issue is the following chain of information processing: physical quantity → perception → representation → retrieval → decision → behavior (14). When representation is a logarithmic function of physical quantity, and the decision-producing behavior is antilogarithmic, then behavior is linear with respect to physical quantity. With scalar encoding(14), there is again a logarithmic encoding of physical quantity, but the error associated with it is proportional to the logarithmic value. When later the antilogarithmic function is taken, the larger quantities are associated with larger errors, and information is lost in the linear scale. This approach takes into account that the data that can be observed and measured are behaviors and not sensations.

SUPPLY VS DEMAND EXPERIMENTS

Subjects

We worked with adult Pallas's long-tongued bats (*Glossophaga soricina*). All subjects were females, save for one male in the group of nine. During the experiment, the bats received most of their food as nectar from the artificial flowers. However, each day this was supplemented with 6 ml of water mixed with 1.2 g nectar concentrate for hummingbirds (Nekton, Nektar Plus) and 1.8 g human infant follow-on formula (Alete Folgemilch 2), as well as three teaspoons of dry pollen. In the group of nine bats, pre-training was done with 12 bats, 3 of which were removed before the selection experiment began, because they did not consistently visit the feeders. This was done to minimize the training time until achieving the target number of nine bats. Also in the group of nine bats, one bat had to be replaced on the 22nd night of the low run, and a different bat had to be replaced on the 39th night of the high run, due to weakened condition. Treatment of the experimental animals complied with German regulations on animal care and experimentation, under the supervision of Veterinäramt Bielefeld.

Procedures

The 24 artificial flowers(33, 4 rows × 6 columns) were mounted pointing downwards on a horizontal rectangular frame suspended 180 cm above and parallel to the floor. The distance between flower "corollas" was 40 cm within and between rows, as in the field experiment. In addition to the experimental flowers, two flowers providing ad libitum 10% sugar solution were available about one meter away from the experimental array (fig. S6). These provided a constant food supply for any bats that may have received insufficient food from the main flower array. Visits to the supplemental flowers were not analyzed. The room was maintained at 22°C and approximately 60% humidity. Light conditions were LD 12:12 and all experiments were conducted during the dark phase. Nectar secretion was initiated two hours before the onset of an experiment and continued throughout the foraging session, so that at the beginning of the session every flower had accumulated some nectar in its virtual account.

We followed the same basic procedure as in the field, except for the modifications listed here. The smallest reward volume that could be delivered was about 1 µL and the maximum reward volume was 60 µL. Nectar consisted of equal parts of sucrose, glucose and fructose dissolved in water. Visits with duration under 200 ms were never rewarded

to exclude inspection flights and were also not analyzed. The sugar production rate of all flowers was 52.1 mg h^{-1} . The selection algorithm was identical to the one used in the simulations.

The starting mean nectar concentrations were 36.7% in the High runs and 14.2% in the Low runs. The duration of the runs was 50 generations (nights) in the group of nine bats, and between 15 and 22 generations in the groups of three bats. The cut-off criterion for the selection runs with three bats was based on the response to selection. There was a minimum of 15 generations per run. After that, a run was ended when the six-day mean response to selection switched signs from its previous direction.

The first group of three bats started the experiment with the High run and the second group of three bats and the group of nine bats started the experiment with the Low run. We reversed the order of treatment presentation to control for sequence effects. Before each selection experiment bats were presented with a parental population of flowers under non-evolving conditions for three nights. Occasionally (one to two times per run in the groups of three bats and four to five times per run in the group of nine bats), due to tubing leaks or software glitches, the experiment was interrupted, usually for only one day. The failed condition was then repeated, with newly randomized feeder positions.

Fig. S1

The average proportion of nightly visits in the field experiment was highest for flowers with intermediate nectar concentrations. Dashed line gives the chance probability (0.042). Even after controlling for the effect of day and flower position within the array, a quadratic polynomial regression (MCMCglmm in R, $P < 0.001$, $DIC = 4206$) fits the data better than a simple linear regression (MCMCglmm in R, $P = 0.046$, $DIC = 4209$).

Fig. S2

A simultaneous decrease of the supply and the demand by a third. Selection exerted by nine bats at the regular supply (A,C) caused convergence to a similar equilibrium concentration as selection exerted by three bats when the supply was decreased by a third (B,D). Same notation as in fig. 3.

Fig. S3

A simultaneous tripling of the supply and the demand. Selection exerted by three bats at the regular supply (A,C) caused convergence to a similar equilibrium concentration as selection exerted by nine bats when the supply was tripled (B,D). Same notation as in fig. 3.

Fig. S4

Remembered value predicts the outcome of selection in the simulations. (A) Mean remembered values (Eq. 1) for the different concentrations in the first generation, averaged over the High and Low conditions, with 100 replicates for each condition. On average the remembered value was higher for all concentrations in the group of three bats, than in the group of nine bats. In both groups the highest average remembered values were close to the equilibria established after selection (dashed and dotted lines). (B) Over time the average remembered value increased in the groups of three and in the groups of nine bats. Data for each group of bats are averaged from 5 replicates of 100 generations over two run types, High and Low.

Fig. S5

Noisy linear encoding also causes stabilizing selection. Selection exerted by three (A,C) or nine (B,D) bats lead to results comparable to non-linear value encoding (fig. 3). The simulations only differed in the formula used for instantaneous value calculation. Instead of using Eq. 5, we used:

$$V_{li} = 2.79 \times 10^{-4} (e^{N(\log(v), 0.2 \log(v))}) \times (e^{N(\log(c), 0.2 \log(c))}), \quad (6)$$

where 2.79×10^{-4} is a scaling constant that sets the value of a reward of 60 μL and 60% concentration to one, $N(\mu, \sigma)$ is a sample from a normal distribution with mean μ and standard deviation σ , and 0.2 is the constant coefficient of variation. Same notation as in fig. 3.

Fig. S6

Bats only visit the ad libitum 10% flowers if they have to. The proportion of nightly visits to the two feeders that always delivered a reward with 10% sugar concentration (but were excluded from the selection algorithms) was around 40% in the group of nine bats (low supply/demand ratio) and around 0% in the two groups of three bats (high supply/demand ratio). Similar proportions of visits were observed in the High and Low runs.

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Proportional perception by the nectar-feeding bat *Glossophaga commissarisi* can explain why the flowers they feed on evolve to have intermediate sugar concentrations.

EVOLUTION

Perception drives the evolution of observable traits

Bats choose flowers on the basis of nectar volume and concentration, affecting how the flowers evolve

By **Hamilton Farris**

The phrase “perception is reality” is used in many contexts but is often not true. For example, human inability to perceive ultraviolet light does not negate its reality. Nevertheless, perception can cause reality to evolve. **This is the insight of the study by Nachev *et al.* on page 75 of this issue (1).** The authors integrated field and laboratory experiments with computer simulations to explain how perceptual mechanisms in a pollinator—a bat—can cause the evolution of counterintuitive traits in flowers.

The appearance, sound, taste, and smell of an organism are determined by the perceptual abilities of the observer. This means that the perceptual abilities of observers are likely to have played a role in the evolution of countless traits across species. For example,

morphological traits such as those used in the visual camouflage of prey species are under selection from predators with particular visual abilities, resulting in the evolution of traits that the predators perceive to be less distinguishable from the inedible background (2). Thus, understanding perceptual abilities, including the ability to notice differences in stimuli, is critical to understanding the evolution of observable traits.

Are there general perceptual rules that could be used to explain and predict selection on such traits? It has been known since the 1800s that for a constant or linear change in the physical magnitude of a stimulus, humans do not experience an equivalent change in perception (3). For example, if the number of bulbs lighting a room is increased from one to two, an observer is likely to notice the difference in brightness. If, however, the increase is from 50 to 51 bulbs, many observers will struggle to notice the change, even though the absolute change is the same in both cases. In fact, to be noticeable, the difference between two stimuli must be not constant but rather proportional to its physical

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magnitude (4), which is historically called the Weber fraction (3). In the example above, an increase in bulbs in the second condition that would be proportional to the first is from 50 to 100 bulbs.

Thus, as a stimulus increases in physical magnitude, the just-noticeable difference also gets larger. In other words, using proportions to compare ever larger stimuli makes it more difficult to perceive stimulus changes; as a large stimulus increases, perception of its size or value appears to remain the same.

The use of proportional perception is not limited to humans. In other animals—including insects, birds, amphibians, and nonhuman mammals—perception of visual, acoustic, chemical, magnetic, tactile, and electrical stimuli is also proportional (5). As evidence for the universality of proportional perceptions accumulates, we must determine how it drives the evolution of observable traits. This is important because one possible limit on the evolution of ever more exaggerated traits (such as sexual signals included in plumage and song) is the diminishing return on increasing the size of already large traits; observers will be unable to perceive differences unless the change is proportional to their large magnitude (6). Such a check on directional selection has been inferred from data showing proportional perception (7). Furthermore, when a trait is so large that it becomes too difficult to produce a perceivable change, the observer may evaluate a different trait that is still within its distinguishable range.

Proportional perception may limit trait evolution in many ecological contexts. In their study, Nachev *et al.* (1) investigate how perception that is based on proportions affects the evolution of traits in flowers that attract pollinators. They designed field experiments to determine how flowers evolve dilute nectar, even though pollinator bats prefer higher concentrations of sugar. The authors allowed bats to visit computer-controlled artificial flowers with virtual genomes that varied in their nectar production. Thus, although the bats were real pollinators, they were selecting for new generations of virtual “seeds” with different genomic profiles for nectar production. The resulting artificial flowers evolved intermediate nectar concentrations rather than an ever more syrupy juice.

There are at least two stimuli that the bats could be evaluating: the sugar concentration and the overall nectar volume. The magnitudes of both concentration and volume can, however, change as a result of consumption by bats. These changes can affect which stimulus is more easily distinguished. Nachev *et al.* used computer simulations and laboratory experiments to understand how these stimuli and their changes

contribute to the evolution of intermediate nectar concentrations. They show that the field results can only be confirmed if bats judge the stimuli according to proportions. The reason is that differences in high nectar concentrations and larger volumes are more difficult to discriminate than are the same absolute differences in low nectar concentrations and small volumes.

Decisions based on the two stimuli are not necessarily coupled, however. The authors show that when proportional perception makes it difficult to distinguish one stimulus dimension because its magnitude is too high, bats may choose flowers according to the other stimulus dimension. That is, when distinguishing high concentrations is too difficult, the bats may choose flowers on the basis of nectar volume, leading to the evolution of diluted nectar.

Nachev *et al.*'s study successfully integrates psychophysics (measuring the psychological experience of a physical stimulus) and evolutionary biology. This integration is long overdue; Darwin wrote in 1872 that inherited variation in certain traits depends “on the powers of perception, taste, and will” of observers (8). Models of trait evolution that are driven by the ability of individuals to choose or distinguish characters (9) would benefit from definitive measurements of perceptual systems. Such data would improve our understanding of how perception influences trait evolution.

In concert, a comparative approach in psychophysics could determine which perceptual mechanisms are universal and which have evolved specializations to mediate particular decisions in particular species (10). For example, even though proportional perception has been studied for more than a hundred years, it is still unknown how selection alters those proportions in different species and whether the underlying neural mechanisms are shared. The study by Nachev *et al.* should serve as a model for how such interdisciplinary work can lead to novel and more complete explanations of trait evolution. ■

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