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Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions

JAMES G. BURNS
Department of Zoology, University of Toronto, Canada

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One of the major challenges in conducting experiments in evolutionary ecology is selecting the currency that most closely parallels individual fitness (e.g. Crone 2001). The fitness surrogate measured must represent a currency that directly impacts individual survival or reproduction, and must not trade off with another relevant fitness currency. The fitness of a foraging nectivore should be closely linked to its rate of resource collection. Presumably, resource collection rate is higher in nectivores that can learn the difference between rewarding and unrewarding flowers, and therefore make more accurate foraging decisions. Based on this line of reasoning, accuracy (the proportion of choices that are correct) is frequently used as the variable of interest in tests of learning rate (e.g. bees: Menzel 1967; Dukas & Real 1991; Dukas & Waser 1994; Wittstock & Menzel 1994; Dukas 1995; Kunze & Gumbert 2001; Ney-Nifle et al. 2001; Cnaani et al. 2003; Paldi et al. 2003; hummingbirds: Brown & Gass 1993; Sutherland & Gass 1995; lepidopterans: Stanton 1984; Kelber 1996). Accuracy is a reasonable measure in many experimental contexts, but a danger is present when accuracy is used as a surrogate for fitness in studies of function and evolution. Although accuracy is a logical surrogate for nectar collection rate when mistakes have large time costs, it is not clear whether the time cost involved in making an accurate choice is always outweighed by the time cost of mistakes.

Here I provide an example that illustrates how, when we focus on accuracy, we might be in particular danger of misconstruing the optimal behavioural strategy. Chittka et al. (2003) observed a trade-off between foraging speed and accuracy in 10 bumblebees, *Bombus terrestris*, discriminating between similarly, but not identically, coloured rewarding and nonrewarding artificial flowers in two experiments. Speed–accuracy trade-offs in discrimination tasks have been observed largely in humans (e.g. Phillips & Rabbitt 1995; Rival et al. 2003), but rarely in an ecological or evolutionary context (but see Franks et al. 2003; Dyer & Chittka 2004). In the first experiment, 10 bees were tested for their accuracy in choosing between flowers containing sucrose solution versus flowers containing only water. The amount of time taken between flower choices (called 'response time' by Chittka et al. (2003), referred to here as 'interflower interval') was also observed. Bees that took longer between flower visits, presumably to make judgements on the next flower to choose, made more accurate choices (interflower interval to accuracy correlation: $r = 0.963$, $P = 0.00007$). In a second experiment, the same 10 bees were tested for accuracy and interflower interval while foraging on rewarding flowers that contained sucrose solution and unrewarding flowers that contained a quinine hemisulphate salt solution that is aversive to bees. With this punishment for incorrect choices added, the bees increased their interflower interval and made more accurate choices (interflower interval to accuracy correlation: $r = 0.723$, $P = 0.018$). Of particular salience to this discussion, there was a tendency for each individual bee to be loyal to a strategy that was either fast and inaccurate or slow and accurate across the two experiments (correlation within bees between experiments 1 and 2, accuracy: $r = 0.951$, $P = 0.00023$, interflower interval: $r = 0.699$, $P = 0.024$). Here I expand upon their analysis to show that when performance is measured as nectar collection rate, the fast, inaccurate bees performed better than the slow, accurate bees. I also discuss other issues, including how consistent behavioural variation between individual bees across situations (behavioural syndromes; Sih et al. 2004a) may complicate behavioural experiments and also be selectively advantageous for social insects in natural settings. In the end, it may be that our focus on accuracy is ecologically inappropriate, because it is only an unambiguously good currency if all else (e.g. speed of making choices) is held equal. After all, an accurate but slothful bee can starve to death.

Methods

With data kindly provided by Chittka et al. (2003), I used accuracy and time between flower choices (interflower interval) to calculate the nectar collection rate

Correspondence: J. G. Burns, Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada (email: jgburns@zoo.utoronto.ca).

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(μl nectar collected per second) for each bee in both experiments 1 and 2:

$$\text{Nectar collection rate} = \frac{c \times v}{c(r+i+h)+(1-c)(r+h)}$$

where c is the percentage of correct choices, v is the nectar volume per flower, r is the interflower interval, i is ingestion time and h is handling time.

Because handling and ingestion times were not available, I estimated them as follows. I estimated handling time as 1 s per flower, which reflects typical handling time on simple Plexiglas flowers and simple natural flowers (Inouye 1980, personal observation). I also estimated that bees took 13.3 s to ingest 10 μl of 2 M sucrose at each rewarding flower, based on established functional relationships, which account for nectar concentration and volume, for bumblebees from Harder (1986). I performed sensitivity analyses in which I varied handling time and ingestion time over a realistic range of values to assess the effect of my estimates of handling time and ingestion time on the results (nectar volume was not included in the sensitivity analysis because varying it did not affect the correlation between nectar collection rate and either accuracy or interflower interval). I included handling times (which in this context only include entrance into and exit from a flower, not the time taken to ingest the nectar) up to 10 s as a reasonable range expected of an experienced bumblebee in nature (Inouye 1980; R. Gegear, personal communication). Ingestion time was varied between 1 and 20 s.

Results

Chittka et al. (2003) reported that accuracy increased with interflower interval. However, my analysis shows that nectar collection rate decreased with interflower interval in both experiments (linear regression: experiment 1: $F_{1,8} = 7.8$, $r^2 = 0.49$, $P = 0.023$; experiment 2: $F_{1,8} = 14.4$, $r^2 = 0.64$, $P = 0.005$; Fig. 1b). Interestingly, accuracy was not significantly correlated with nectar collection rate (experiment 1: $F_{1,8} = 0.95$, $r^2 = 0.11$, $P = 0.36$; experiment 2: $F_{1,8} = 0.45$, $r^2 = 0.05$, $P = 0.52$; Fig. 1a). These two results together indicate that accuracy is not an appropriate surrogate for nectar collection rate and therefore is probably not associated with fitness in this discrimination task.

Results of the sensitivity analysis show that visits to unrewarding flowers become more costly as handling time increases (Fig. 2). The negative correlation between nectar collection rate and interflower interval weakened with increased handling time, but was still significant for handling times less than 1.8 s in experiment 1 and for handling times less than 5.5 s in experiment 2. Note that at 6.8 s there was a switch in experiment 1 from a negative correlation to a positive correlation between interflower interval and nectar collection rate. Thus, with longer handling times, slow, accurate bees would perform better than fast, inaccurate bees in Chittka et al.'s experimental context. Ingestion time had only a minimal effect on the relationship between nectar collection rate and interflower interval (e.g. for handling times between 1 and 10 s, varying ingestion time between 1 and 20 s changed the value of r-squared between interflower interval and nectar collection rate by a maximum of 0.024 and thus only marginally affected P values).

Discussion

Chittka et al.'s (2003) study demonstrates a trade-off between a standard fitness surrogate used in foraging studies, foraging accuracy, and another plausible fitness currency, foraging speed (interflower interval). This raises the question of which of the two possible fitness currencies is the better surrogate. I demonstrate that those bees that make more mistakes but make decisions more quickly (fast, inaccurate), probably collected nectar at a higher rate than more careful bees (slow, accurate). Thus, under the conditions of Chittka et al.'s (2003) experiment, foraging speed would be a better fitness surrogate than the more commonly used foraging accuracy.

The consistent propensity of individual bees across the two tests to be fast and inaccurate or slow and accurate suggests a new facet for the emerging study of stable interindividual differences in animals, called either 'behavioural syndromes' (Sih et al. 2004b) or 'personality' (Dall et al. 2004). A behavioural syndrome is a correlation between behaviours within a population across observations or contexts, such as a positive relationship between hunting aggression and sexual cannibalism in female fishing spiders (Johnson 2001), with each individual in that population having a behavioural type (e.g. more or less aggressive). This field has focused on such topics as the adaptive value of differences in individual levels of boldness (Wilson et al. 1994; Wilson 1998). For instance, bold individuals in a population might benefit from greater access to mates because of social dominance and greater access to resources because of their greater willingness to forage when predators are nearby, but would also suffer a greater risk of capture and death. Similarly, there may also be individual differences in the propensity to use a foraging strategy that is fast and inaccurate or slow and accurate. This idea has not yet received attention from behavioural ecologists. In human personality research, the fast and inaccurate versus slow and accurate phenomenon is referred to as 'impulsivity', with 'impulsives' responding quickly with a low certainty of being correct and 'reflectives' responding more slowly with a greater certainty of being correct (Kagan 1965; Phillips & Rabbitt 1995; Schweizer 2002).

Mechanisms for the maintenance of multiple behavioural types in the same population (which are related to those for maintenance of genetic variation) include negative frequency-dependent selection, local adaptation with migration between locales, and fluctuating selection in which there are trade-offs among traits related to fitness (Stamps 2003). Here I suggest possible explanations for the existence of behavioural types in the context of social insect colonies, a topic that has received little, if any, attention. A social insect colony could benefit from having workers with different behavioural types in the same

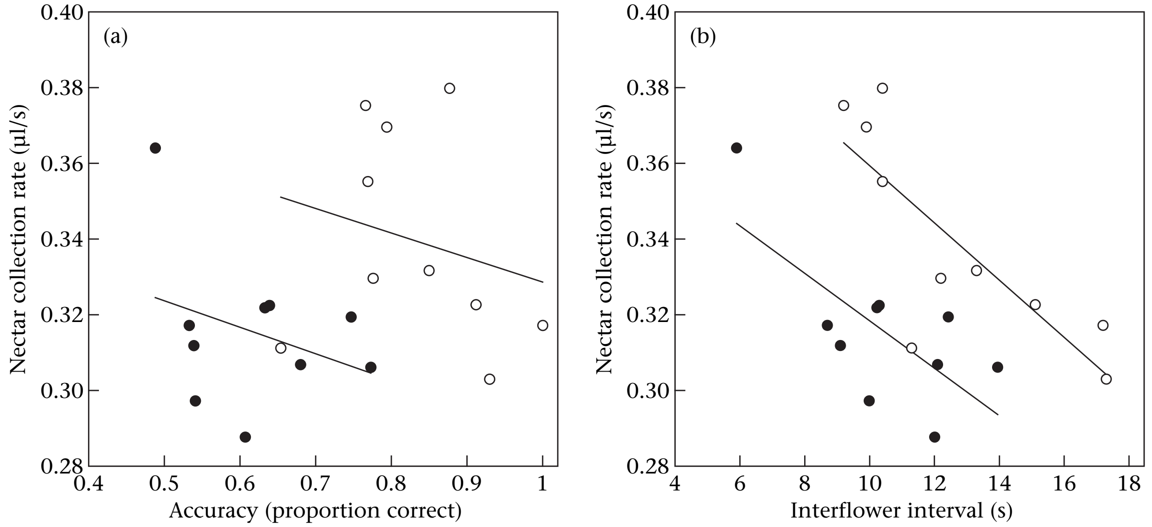

Figure 1. Relation between nectar collection rate and (a) accuracy and (b) interflower interval in experiment 1 (●) and experiment 2 (○).

way they benefit from classic labour castes (e.g. nurse, guard, forager). That is, through the efficiencies afforded by task allocation. Task allocation adjustments have been most thoroughly studied in ants, where workers will switch tasks if, for example, food availability changes or colony maintenance is required after a disturbance (Gordon 1996). Many models of the mechanisms underlying task allocation in social insect colonies assume that individual workers vary in their thresholds to stimuli that determine whether they will engage in an activity (Gordon 1996; Beshers & Fewell 2001). There is evidence for both genetic and environmental effects on such thresholds. In honeybees, *Apis mellifera*, for example, the propensity of foragers to collect pollen or nectar is highly correlated with their sucrose response threshold (the concentration of sucrose solution to which they reflexively respond in a classic conditioning paradigm called the 'proboscis extension reflex'; Bitterman et al. 1983). Sucrose response threshold is dependent upon genotype, but also several environmental factors including colony pheromone levels and the concentration of nectar being brought back to the colony (Pankiw et al. 2002, 2004; Pankiw & Page 2003). Behavioural types do not necessarily correspond to such thresholds, but could be another example of individual variation within a colony that allows optimal task allocation.

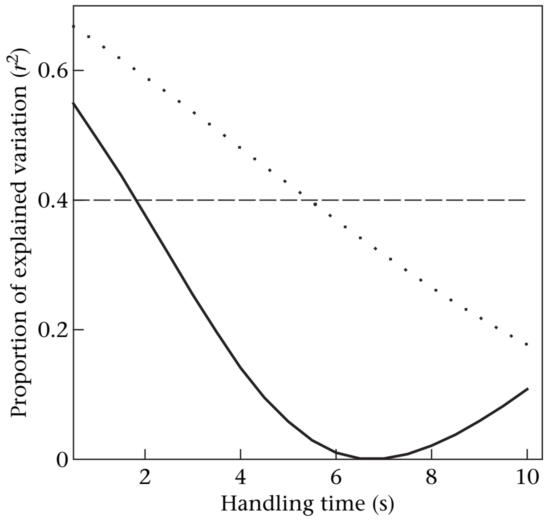

Figure 2. Relation between the proportion of variation explained by the correlation (r^2) between nectar collection rate and interflower interval (*Y* axis) and handling time (*X* axis). The horizontal dashed line denotes the point above which $P < 0.05$ for the same relationship. Solid line: experiment 1; dotted line: experiment 2.

In the present case, based on their optimal behaviours according to the sensitivity analysis on handling time (see Results), fast, inaccurate bees would forage on flowers of simple design with short handling times, but slow, accurate bees would forage on more complex flowers with longer handling times. This scenario is favourable for the maintenance of multiple behaviour types through environmental heterogeneity. That is, a variable environment with different kinds of flowers varying in handling time could maintain variation in foraging styles if the different styles are equally successful in the long run. In the short term, if there is an abundance of one of these flower types in the colony's range, adjustments in the forager force could potentially be made. Also, overstocking of a colony with one behavioural type (or one end of a gradient of a syndrome) might reduce the resources they specialize in, leaving the other resources less well harvested and thus favouring the opposite syndrome.

In Chittka et al.'s (2003) simple scenario with bees discriminating between two flower types with no predators, the best solution was met by impulsive foragers and not by reflective ones. However, predation risk from crab spiders, *Misumena vatia*, hiding on flowers could be important in nature (Dukas 2001; Dukas & Morse 2003). High densities of predatory crab spiders, however, could favour bees that carefully select which flowers to visit and shift the balance towards a reflective strategy. Keep in mind that all of these suggestions are untested and I do not imply they are always at work or are isolated from other factors. For instance, variation in bumblebee worker size (Knee & Medler 1965; Spaethe & Weidenmuller 2002) could interact with, or replace, some behavioural types.

In regards to future research, behavioural syndromes should be considered when planning experimental designs because they can affect the accuracy of choices in discrimination tasks. When accuracy is used as the response variable in sensory acuity tests (e.g. honeybees: Gould 1986; Lehrer 1999; bumblebees: Church et al. 2001; Macuda et al. 2001), syndrome-based differences between individuals will add noise to the observations (presuming the animals are assigned to treatments randomly). This may obscure real differences caused by the treatment (a type II error), but should not systematically bias the results. When differences in learning ability between individuals or between treatment groups are being studied, however, the problem is potentially more serious. In this case it is not whether accuracy is the best measure of fitness, but that foraging speed (e.g. interflower interval) must also be considered as a response variable. For instance, if accuracy and foraging speed are correlated, it could be difficult to distinguish what factor a treatment is directly affecting if only accuracy is measured. This concept is, of course, a problem for any manipulative experiment in behavioural biology, but in this case is particularly pertinent because there is evidence that accuracy and foraging speed are correlated.

Ultimately, the benefit of saving time in measuring only one fitness currency (such as speed or accuracy in flower choice) may not be worth the loss in reliability of the estimate of fitness. Furthermore, when net rate of energy gain can be determined easily, as is the case for nectivores, more distant surrogates of fitness such as foraging accuracy and speed should probably be avoided. In the present case, if we were to follow tradition in equating accuracy to intelligence, natural selection would be expected to favour less intelligent behaviour.

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