Cognition-mediated coevolution – context-dependent evaluations and sensitivity of pollinators to variability in nectar rewards

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Abstract. In this paper we emphasize the role of pollinator perception and decision-making processes in mediating floral nectar distribution strategies. Since pollinator choice behavior is guided by how the pollinator perceives and evaluates floral rewards, we hypothesize that plants have evolved strategies that maximize their *perceived* profitability, through pollinator cognition-mediated coevolution. We focus on two classes of cognitive phenomena, context-dependent evaluations and risk-sensitivity. These phenomena are of interest to psychologists and biologists. Our paper is an attempt to show the value of cross-disciplinary exchange of theories and ideas. A review of the ecology literature suggests that pollinators evaluate variability in nectar volume in proportion to the mean, and thus choice behavior is guided by the coefficient of variation (standard deviation/mean) of the distribution. This functional relationship is predicted by Weber's law, which describes a wide range of psychophysical phenomena. Simulations show that this phenomenon also affects how pollinators perceive skewed nectar distributions. Cognition-mediated coevolution theory should be a fruitful approach to understanding the evolution of pollinator-plant interactions.

Key words: Pollinator, nectar volume, cognition, context-dependence, risk-sensitivity, skew, Weber's law.

Introduction

The long nectary of the Madagascar orchid *Angraecum sesqipedale* prompted Darwin to predict the existence of a moth with a proboscis 25 cm long, which was eventually discovered forty years later (Proctor et al. 1996). In addition to morphological adaptations, floral traits coevolve with pollinator behavior and sensory capabilities. Floral odors (Raguso 2001), colors (Chittka et al. 2001), and display patterns (Giurfa and Lehrer 2001), respectively, are adapted to some degree to the olfactory and visual perceptions and preferences of pollinators.

To predict the effect of floral traits on plant reproductive success it is necessary to know something about the choice behavior of pollinators. In many cases, however, we do not know the detailed floral visitation patterns of pollinators, and how different aspects of the nectar distributions affect their choices. As a general predictive tool, we employ optimal foraging theory. We assume a currency that a pollinator is likely to be maximizing, and predict the optimal plant strategy given that

the pollinator behaves according to optimal foraging theory (Stephens and Krebs 1986).

The evolutionary process, however, is complex, and there are several reasons for why we should not expect pollinators to have perfectly adapted perception and decision-making abilities. Chittka et al. (2001) discuss some of these in the context of color vision; the same arguments hold for other cognitive abilities, or any other trait. In particular, we find that some basic assumptions of optimality (and rationality) theory are not met (Real 1996). Just like humans, for example, alternatives are not assigned absolute values, but rather, choice is comparative, and hence context-dependent (Shafir 1994; Houston 1997; Wiegmann et al. 2000; Waite 2001a, 2001b; Bateson et al. 2002; Shafir et al. 2002; Weber 2003). It is also clear that animals do not always prefer higher mean rewards, but are also sensitive to other parameters affecting resource distribution, such as variability (Real 1981, Waddington et al. 1981, Kacelnik and Bateson 1996). We now better understand how pollinators perceive variability in nectar rewards (Shafir et al. 1999, Shafir 2000, Shapiro et al. 2001, Waddington 2001).

The greater emphasis on cognitive mechanisms has led to the development of cognitive ecology (Real 1993, Dukas 1998), and specifically in the context of pollination biology, to the cognitive ecology of pollination (Chittka and Thompson 2001). Some of the findings of animal cognition, such as context-dependence, complicate the more simple models that assumed absolute evaluations of alternatives. However, these findings also make this field of study more interesting. In particular, it suggests that we must incorporate more realistic pollinator cognition if we want to understand pollinator behavioral responses to plant nectar distributions, and the evolution of plant strategies through pollinator cognition-mediated coevolution.

Pollinator-cognition mediated coevolution

Figure 1 illustrates the selective forces involved in pollinator cognition-mediated coevolution.
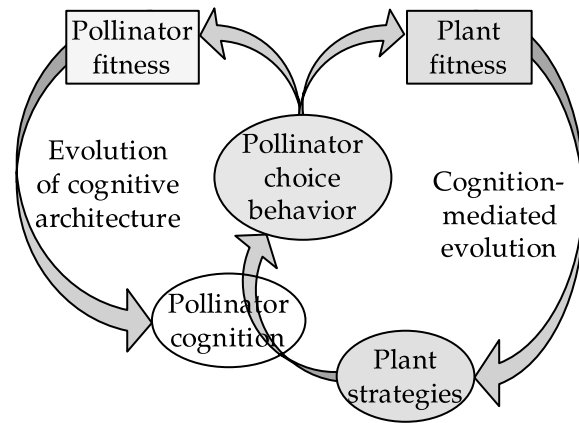

Fig. 1. Schematic representation of the processes involved in cognition-mediated coevolution

Floral choice behavior of pollinators affects the reproductive success of plants. Such pollinator-mediated effects have been envisioned by Darwin (1862), and modeled (Friedman and Shmida 1995) and demonstrated by various researchers since (Pyke et al. 1988, Mitchell and Waser 1992, Mitchell 1993, Mitchell et al. 1998, Manetas and Petropoulou 2000). Choice behavior is the outcome of pollinator cognition, how it perceives floral traits and its decision-making processes (Waddington 1983, 2001). As with other traits under selection, a cognitive architecture is expected to evolve that allows the pollinator to efficiently exploit floral rewards (Real 1991). Pollinator-mediated selection leads to the evolution of plant strategies that successfully attract pollinators and increase the reproductive success of the plant. Pollinator cognition is a subjective filter through which the objective reality of floral traits is processed in effecting choice; hence, plant traits are subject to pollinator cognition-mediated selection.

The study of pollinator-cognition mediated coevolution emphasizes the role of cognition in pollinator-plant interactions, just as cognitive ecology emphasizes the role of perception and decision-making in behavioral ecology (Dukas 1998, Chittka and Thompson 2001). This is not to say that cognitive issues have not been studied until the emergence of cognitive ecology, or that studies of pollinator-mediated evolution have not (at least implicitly)
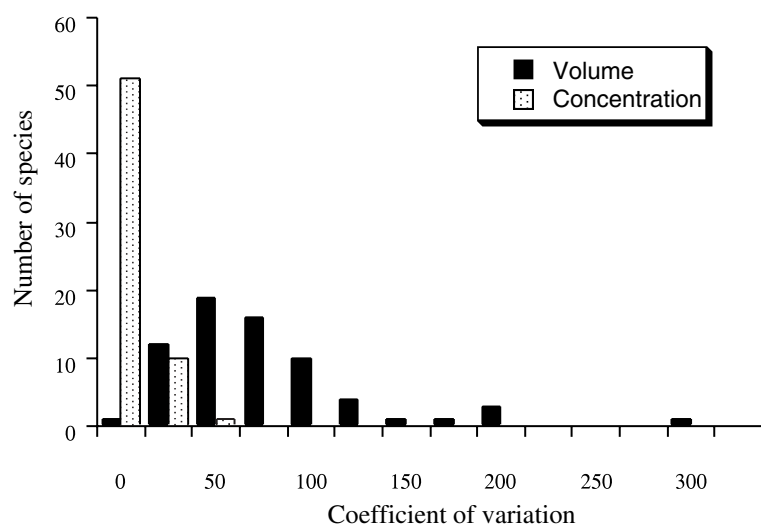
Fig. 2. The distribution of variability, measured by the coefficient of variation, of nectar volume and concentration of 68 plant species in a xeric Mediterranean ecosystem. Data from Petanidou and Smets (1995)

considered pollinator cognition. Pollinator-mediated evolution has been invoked, for example, in predicting the optimal nectar distribution along flowers of an inflorescence given the floral visitation behavior of bumble-bees of working an inflorescence from the bottom towards the top (Waddington and Heinrich 1979, Best and Bierzychudek 1982). The effect of nectar amount per flower on pollinator probing behavior, and the consequences for pollen transfer, have also been investigated (Mitchell and Waser 1992). A more explicitly cognitive perspective, however, introduces novel hypotheses, fuels alternative experiments, and contributes to a better understanding of animal behavior. It is especially exciting, when findings about animal perception and decision-making raise hypotheses about adaptive plant strategies that would not have been otherwise considered.

Nectar volume

The importance of pollination for plant reproduction suggests that natural selection will act on floral traits that influence reproductive success under conditions in which it is pollination limited (Feinsinger 1983, Cresswell 1999). Plants reward pollinators mainly by providing them with pollen and nectar (Proctor et al. 1996). Here we focus on nectar volume, which greatly influences pollinator

visits, has a significant genetic component, and is variable. These attributes make it a prime trait to be acted upon by natural selection through pollinator-mediated selection.

Nectar volume is often correlated with seed set, a measure of plant reproductive success (Real and Rathcke 1991, Holtkamp et al. 1992). Variability in nectar volume per flower between plants offers great potential for differential reproduction. The remarkably thorough study of Petanidou and Smets (1995) allows comparing patterns of variability in nectar production of plants from 68 different species in a Mediterranean shrubland (Fig. 2). Nectar volume per flower is more variable than nectar concentration, as is typical in many systems (Feinsinger 1978, Rathcke 1992), and is in fact the most variable floral characteristic (Cresswell 1998). Much of this variability has a genetic component as seen in the response of this characteristic to artificial selection in crop plants (Teuber and Barnes 1979, Teuber et al. 1983, Cane and Schiffhauer 1997). The heritability of nectar volume has also recently been shown for natural populations (Mitchell and Shaw 1993, Boose 1997, Klinkhamer and van der Veen-van Wijk 1999, Burke et al. 2000).

Context-dependent preferences

It is tempting to assume that animals evaluate options independently, such that the value

assigned to a particular option is not affected by the presence or absence of other options. Following the practice in psychology and economics (see Tversky and Simonson 1993), this assumption has also been adopted in behavioral ecology (Shafir 1994, Shafir et al. 2002). Testing this assumption in animals, however, revealed context-dependent preferences, in which alternatives are compared to each other, and hence choice behavior depends on the attributes of the alternatives being considered. Context-dependent preferences raise interesting hypotheses for the evolution of plant strategies through pollinator cognition-mediated coevolution. First, we briefly describe the findings supporting context-dependent evaluations.

When alternatives are assigned fixed values by the decision maker, there must be a rank order by which the alternatives can be arranged, which follows transitivity: if alternative A is preferred over B, and B over C, then it follows that A is preferred over C (Tversky 1969, Fishburn 1973). If alternatives are compared along their different attributes, however, then intransitive choice patterns may arise. Shafir (1994) tested the transitivity of preferences of honey bees using artificial flowers varying in corolla length and nectar volume. In pairwise comparisons between three sets of a short-corolla flower providing less nectar and a slightly longer-corolla flower providing a bit more nectar, bees tended to prefer the flower with the shorter corolla in each pair. However, in a fourth choice between the shortest flower providing the least amount of nectar and the longest flower providing the most amount of nectar, a few bees switched their preferences and chose the flower with the longer corolla, thus violating transitivity. Waite (2001b) found violations of transitive choice in a similar experiment with gray jays. These studies revealed that animals evaluate alternatives in a context-dependent manner.

Context effects in human choice behavior have also been studied by comparing subjects' preferences between two options when presented alone and when presented along with a third alternative (Huber et al. 1982, Huber and Puto 1983, Simonson 1989, Simonson and Tversky 1992, Shafir et al. 1993, Tversky and Simonson 1993, Doyle et al. 1999, Sedikides et al. 1999). In a particular construction of the three-option set, alternatives vary in two attributes, as in tests of transitive choice discussed above. One alternative is better than another in one attribute, but less good in another attribute. The third alternative acts as a decoy, which is asymmetrically dominated. An option that is clearly less attractive than an alternative is said to be dominated by it. In the asymmetric dominance construction (Huber et al. 1982), the decoy is dominated by one of the other alternatives (the target) but not by the other alternative (the competitor). The asymmetry may cause the target, which is more similar to the decoy than the competitor, to lose less than the competitor from the introduction of the decoy. The preference of the target relative to the competitor, therefore, increases when the decoy is introduced. This is in contradiction to the notion that the more similar alternatives should compete more strongly with each other, which prevails in economics (Tversky 1972, Huber et al. 1982), and in niche theory in ecology. The asymmetric dominance effect is a robust finding in human studies (Huber and Puto 1983, Shafir et al. 1993, Tversky and Simonson 1993, Doyle et al. 1999, Sedikides et al. 1999). Prompted by findings of context-dependent choice in animals, Shafir (cited in Real 1996) suggested that the asymmetric dominance effect may also occur in animals. The first to be tested were honey bees, using artificial flowers varying in corolla length and nectar volume (Shafir 1998, 1999; Shafir et al. 2002).

Individual foragers were first given a binary choice between an artificial flower with a short corolla that provided a small amount of nectar, and an alternative with a slightly longer corolla that provided a slightly greater amount of nectar. Over many choice trials, bees visited both flower types similarly. Then, a decoy alternative was added for trinary-choice trials. For one set of bees, the former (short) flower

was designated the target, and the asymmetrically dominated decoy provided a very small amount of nectar but had the same corolla length as the target. For another set of bees, the latter (long) flower was designated the target, and the asymmetrically dominated decoy had a much longer corolla but provided the same amount of nectar as the target. As predicted by the asymmetric-dominance effect, in the trinary-choice phase, the choices of the bees in the two groups diverged, with the targets gaining relative to the competitors. In conceptually similar experiments with gray jays, a decoy alternative dramatically increased the preference of the birds to the target alternative (Shafir et al. 2002).

Risk-sensitivity

Due to the great variability of nectar volume between plants of the same species, risk-sensitive foraging, the response of animals to variable resources, has received much attention by pollination ecologists; the review by Kacelnik and Bateson (1996) includes studies of nectarivorous invertebrates and vertebrates. When on a positive energy budget, animals are predicted to be risk-averse, to shy away from variable alternatives (Caraco 1980). When variability is in nectar volume (or concentration), animals are in fact risk-averse. The degree of risk-aversion, however, depends on the perception of variability. Animals are sensitive to the coefficient of variation (CV = standard deviation divided by the mean) of the resource distribution, which is a measure of relative variability (Shafir et al. 1999, Shafir 2000). In general, the higher the CV the stronger the risk-aversion, though other factors may also influence choice behavior (e.g. Hurly and Oseen 1999). We are gaining a better understanding of the cognitive mechanisms that lead to risk-sensitivity, and recent models are often able to predict risk-sensitive foraging behavior in choice experiments (Montague et al. 1995, Shapiro et al. 2001, Waddington 2001, Marsh and Kacelnik 2002). The consequences of existing perceptual regularities for cognition-mediated coevolution, however, have so far been less explored.

Consequences of sensitivity to the coefficient of variation for cognition-mediated coevolution

What should plants do to attract risk-averse pollinators that are sensitive to the CV of their nectar distribution? According to pollinator-cognition mediated coevolution, natural selection acts on plants to reduce the CV of their nectar distributions. Since the CV is a ratio, it can be decreased either by decreasing the standard deviation (numerator) or by increasing the mean (denominator). Plants whose standing crops are variable, can thus reduce perceived variability by increasing their mean nectar rewards. As a result, we may expect to see a correlation between the mean and the standard deviation. This pattern is expected both between plants of the same species, due to intraspecific competition, and between species, due to interspecific competition.

There is in fact a correlation between the mean and standard deviation of nectar volume of individual plants of the same species (Real and Rathcke 1988). These authors compared patterns of nectar production within individual shrubs of *Kalmia latifolia* (Ericaceae) in North America, and found strong correlations ($r^2 = 0.78$, and $r^2 = 0.77$, respectively) between the mean and standard deviation at each of two sites. In the study of Petanidou and Smets (1995), too, the standard deviation and mean nectar production were strongly correlated between plant species ($r^2 = 0.87$). Torres and Galetto (1998) found a correlation ($r^2 = 0.49$) in standing crop between the mean and variance (the correlation with the standard deviation is not reported) of flowers of *Mandevilla pentlandiana* in an inflorescence.

A strong linear correlation between standard deviation and mean implies that CV is not correlated to the mean. Indeed, the CV was not correlated with the mean ($r^2 = 0.01$, and $r^2 = 0.003$, respectively) for the individual shrubs at the two sites studied by Real and

Rathcke (1988). The CV was also not correlated with the mean ($r^2 = 0.05$) for the plant species studied by Petanidou and Smets (1995).

Real and Rathcke (1988) correctly note that the correlation between the standard deviation and the mean poses a problem for theoretical models of risk-sensitive foraging behavior that assume that nectar production mean and standard deviation act independently in shaping preferences. Fortunately, recent findings in animal cognition suggest that the standard deviation (or variance) does not independently shape preference; variability in outcome is perceived in relation to its average magnitude and, as a result, the index of variability that predicts risk sensitivity is the CV (Shafir et al. 1999, Shafir 2000).

The data of Petanidou and Smets (1995) reveal great variability in the CVs between plant species (Fig. 2). Such variability in nectar amount is quite common (Rathcke 1992, Cresswell 1998). Since pollinators seem to be sensitive to the CV in assessing floral rewards, we would expect that differences in CVs would affect visitation patterns between plants. While cognition-mediated coevolution should act to reduce variability between plants in their CVs, environmental factors and other floral attributes, of course, also affect nectar distribution patterns (Rathcke 1992).

Furthermore, flowers that are more attractive to pollinators do not necessarily increase plant reproductive success (Feinsinger 1978, Rathcke 1992). A pollinator that encounters some flowers that contain little or no reward will visit more flowers than a pollinator that can fill its crop after a few visits to highly rewarding flowers. The reduced attractivity of a plant that contains variably rewarding flowers results in pollinators moving greater distances between plants, increasing gene flow distance and reducing potential inbreeding depression (Waser and Price 1983).

The partial reinforcement effect is a robust finding in animal learning, including in honeybees (Ishida et al. 1992), in which animals that experience an alternative that is always rewarding abandon it quickly when they later fail to find reward compared to animals that had experienced the alternative with intermittent rewards. This greater perseverance (slower extinction of the learned association) may result in a pollinator probing an occasional non-rewarding flower intensely, thus achieving more efficient pollen transfer.

The optimal strategy for a plant also depends on the relative availability of flowers and pollinators. Floral nectar is expensive for plants to produce (Pyke 1991). If flowers are sparse relative to pollinators, then plants can afford to provide low and variable rewards. If flowers are abundant relative to pollinators, then pollinators can be more choosy, and competition between plants will favor those producing more attractive flowers (Feinsinger 1978).

Weber's law

Weber's law is a perceptual phenomenon that applies to a wide range of domains. It says that the perceived difference between stimuli is related to their mean magnitude. Jensen's inequality is often invoked to illustrate Weber's law in the context of risk-sensitive choice (Smallwood 1996). Jensen's inequality states that the mean value of a function of a variable need not equal the value of the function evaluated at the mean variable. Specifically, for a concave-down (increasing, but decelerating) function, the mean value of the function is less than the value of the function evaluated at the mean. For example, if the subjective perception of nectar volume follows a concave-down function, then the mean subjective perception of a variable distribution will be smaller than the subjective perception of a constant alternative with the same mean, leading to risk-aversion (Kacelnik and Bateson 1996, Perez and Waddington 1996, Marsh and Kacelnik 2002).

In honey bees, for example, evaluation of various parameters of nectar reward follow such a concave-down function, consistent with Weber's law (Waddington and Gottlieb 1990, Perez and Waddington 1996, Waddington 2001, Shafir and Menda, unpublished data).

Several patterns of risk-sensitivity follow from such concave-down utility curves, including risk-aversion to variability in nectar volume (Perez and Waddington 1996, Kacelnik and Brito e Abreu 1998), and risk-sensitivity that follows the CV rather than variance of outcomes (Shafir 2000, Weber et al. 2003). We illustrate these effects below, with simulations of how various nectar distributions are evaluated by pollinators with such concave-down utility curves. We also consider the effect of distribution skewness.

The effect of distribution skewness

In addition to mean and variance, distributions are characterized by skewness. As shown above for context-dependent choice, much insight can be gained from comparing studies of decision-making in humans and in animals. Below we discuss how the study of risk-sensitivity has gained from this process. We begin with a summary of how distribution skewness affects preference in human risky choice. We then illustrate schematically how distribution skewness is predicted to affect preference in animal risky choice, assuming concave-down functions of subjective perception.

Skewness preference in human risky choice

Preference for risky options with outcome distributions that are positively skewed (over distributions with equal mean and variance, but no skew or negative skew) is well-established in the human decision making literature. Positive skew was one of the strongest predictors of risk taking (controlling for other variables such as mean and variance) in a recent meta-analysis of 206 choice sets in which people chose between a two-outcome lottery and a sure option of equal mean (Weber et al. 2003). The effect occurs not just in lab studies, but has also been observed in the real-world betting preferences of gamblers at the horse track (Golec and Tamarkin 1998) or in state lotteries (Garrett and Sobel 1999). Preference for positive skewness seems to be so

strong and reliable to be the topic of lottery design recommendations made by economists (Walker and Young 2001).

These effects are consistent with prospect theory (Kahneman and Tversky 1979), a model proposed to provide a better fit to observed risky choice patterns than the expected utility model. One of the model features that allow prospect theory to do so is its nonlinear decision weight function. In both its original formulation and the recent model generalization (Tversky and Kahneman 1992), prospect theory assigns a decision weight to rare events that exceeds the weight they should receive based on their probability level. In other words, small probabilities are overweighted, which leads to the prediction that choice options become more attractive when the rare events have larger magnitude, as is the case for choice options that are positively skewed.

A plausible process level explanation for the overweighting of small probabilities and the accompanying underweighting of large probabilities results from the observation that probability levels are not always sufficiently attended (Brandstaetter and Kuehberger 2003). The result of such attentional neglect will be choice-inferred decision weights that look regressive, i.e., an overweighting of small probabilities and an underweighting of large ones. Greater attention to outcomes than to probabilities, in turn, can be explained by the fact that risky choice is driven as much or more by affective processes as it is by cognitive processes (Loewenstein et al. 2001). Described or experienced outcomes (especially when unusually large or small) usually evoke strong affective reactions, whereas described or experienced probability levels remain pallid statistics.

The last statement already alludes to a distinction that has recently generated some attention in the human risky choice literature, namely the distinction between decisions between alternatives that are described and decisions between alternatives that are personally experienced. Research on human risky choice has almost exclusively focused on

description-based choice, where people receive a complete account of all possible outcomes of each choice option and their probability levels, either in numeric form or by some visual representation (e.g. pie chart or relative frequency histogram). All of the 206 risky choice sets between two-outcome lotteries and a sure outcome identified by Weber et al. (2003), for example, involved description-based choice. Decisions by experience, on the other hand, are the only type of decisions that can be made by other animals, who do not have the ability to represent or process symbolic summary information about outcome magnitude and likelihood. The only way in which they can acquire information about the value and likelihood of choice options is to sample them repeatedly, keeping track of the outcome experienced each time. The distinction is important, because the two types of decision situations often result in very different choices. Weber et al. (2003) show that human risk preference is predicted very well by the coefficient of variation in decisions under experience, but not in description-based choice. Hertwig et al. (2003) show that rare events that are overweighted in description-based choice are, in fact, underweighted in decisions under experience.

Such underweighting of small probabilities results in preference for outcome distributions that are negatively skewed, all other things being equal, and especially when the number of samples drawn from each outcome distribution is very small. However, in the experiments that have documented such preference, it is only the outcome distribution that is learned from experience. The outcomes themselves were still presented numerically, making even small differences in value perfectly discriminable. When both outcome magnitude and frequency have to be ascertained by personal experience, limitations on the discriminability of outcome values that are close together would counteract the effect of the underweighting of small probabilities and may well result in risk preference that favors positively skewed lotteries.

Skewness preference in animal risky choice

The effect of outcome skewness has not been empirically tested in animal studies. Adding skewness (measured as the probability of the lower-valued outcome, $p(L)$) into Shafir's (2000) prediction equation of animal risk-preference instead of using only the coefficient of variation significantly improves the fit of the model (Weber et al. 2003). Both CV and skew were significant predictors of risk sensitivity ($F_{1,47} = 25.55$, $p < 0.0001$, for CV; $F_{1,47} = 9.43$, $p < 0.004$, for skew), with a significant increase in R^2 from 0.33 to 0.43. Increases in relative variability (CV) and greater negative skew (smaller $p(L)$) were associated with greater risk-aversion (i.e. negatively skewed distributions were disliked): probability of the constant alternative $= 0.76 + 0.0023$ CV -0.60 $p(L)$.

Simulating the effect of skewness

We can assess the qualitative effect of skewness in nectar distribution by calculating the subjective value of various distributions for a pollinator having a concave-down utility function, $u(x)$, for nectar-volume:

$$u(x) = a \cdot (1 - e^{-b \cdot x}), \qquad (1)$$

where $a = 100$ and $b = 0.3$ in our case (Figs. 3 and 4). We tested two families of nectar

Fig. 3. The effect of various shock-function distributions of nectar volume on their perceived profitability. The value below each figure is the perceived profitability of the distribution for the pollinator (see text). For all distributions, $\sigma = 2.5$, and $\mu = 7.5$ (**a–f**) or 12.5 (**g–l**). The left y-axis represents arbitrary units for the concave-down utility function shown. The right y-axis represents the probability of occurrence of reward values for various distributions: **a** and **g**, constant; **b** and **h**, symmetric; **c** and **i**, skew $= -0.25$; **d** and **j**, skew $= 0.25$; **e** and **k**, skew $= -0.40$; **f** and **l**, skew $= 0.40$. Skew is represented by the probability of the lower reward minus 0.5
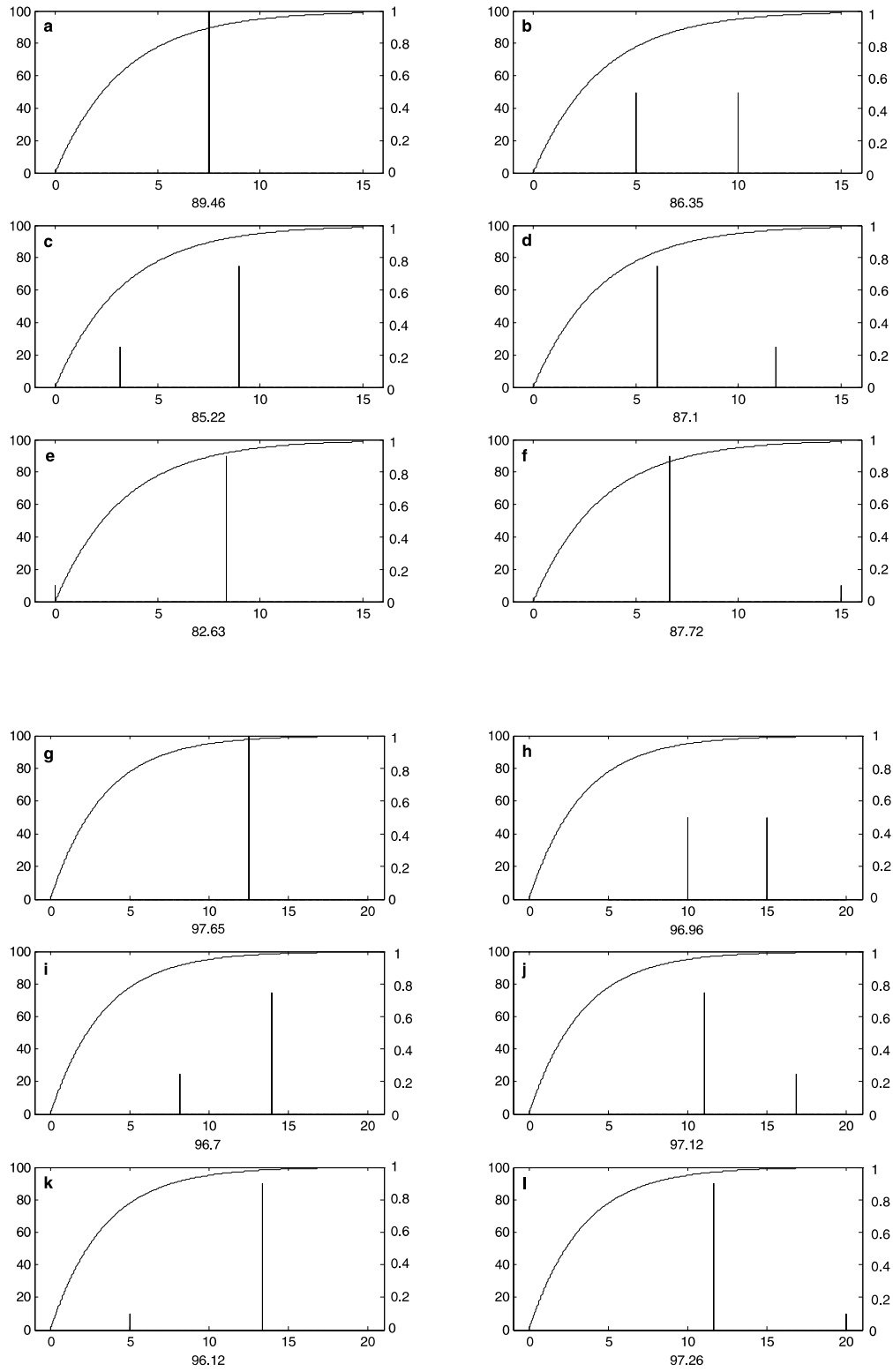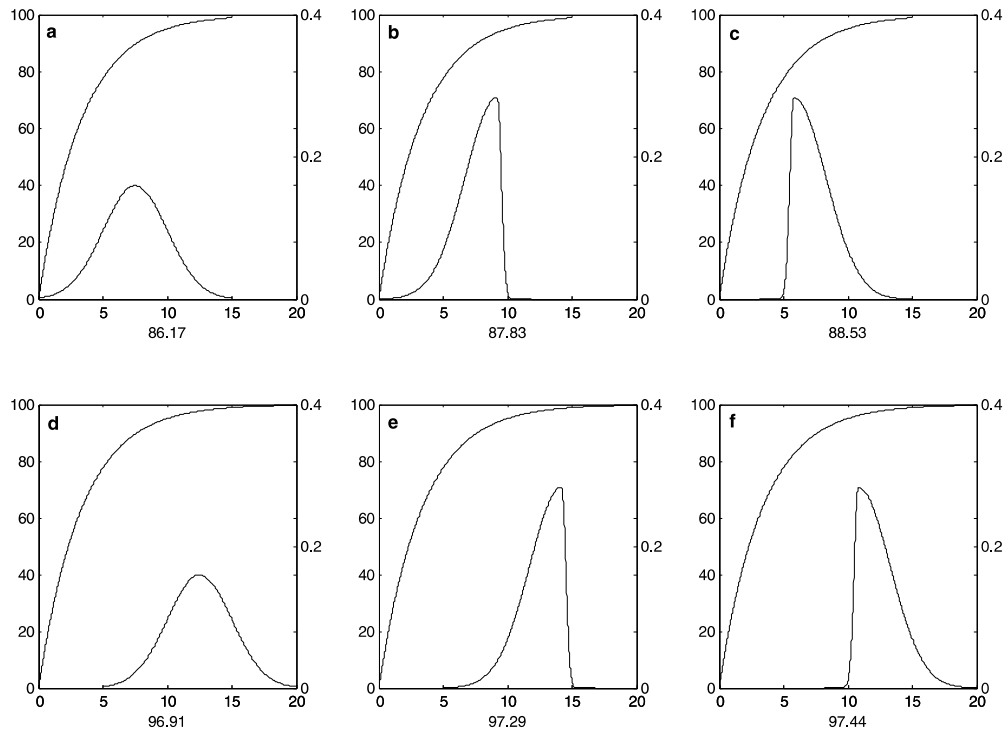
Fig. 4. The effect of various continuous (Gaussian) distributions of nectar volume on their perceived profitability. The value below each figure is the perceived profitability of the distribution for the pollinator (see text). For all distributions, $\sigma = 2.5$, and $\mu = 7.5$ (**a–c**) or 12.5 (**d–f**). The left y-axis represents arbitrary units for the concave-down utility function shown. The right y-axis represents the probability of occurrence of reward values for various distributions: **a** and **d**, symmetric; **b** and **e**, negatively skewed; **c** and **f**, positively skewed

distributions, shock and continuous functions. In shock functions, outcome values are discrete, occurring with specified probability. An example of a symmetric shock function is a 0.5 chance of receiving 5 µl and a 0.5 chance of receiving 10 µl (Fig. 3B). In continuous functions, the probability function is continuous over the whole range of values. An example of a symmetric continuous function is the Gaussian function with $\mu = 7.5$, and $\sigma = 2.5$ (Fig. 4A). Note that the mean and variance of this Gaussian function is identical to that of the shock function above. We compared several shock- and continuous functions, all with $\sigma = 2.5$, and with $\mu = 7.5$ or $\mu = 12.5$. In each case we also tested the effect of skewness.

Nectar distributions in nature are more likely to resemble continuous distributions than shock-functions. Our interest in studying

shock-functions is mostly methodological. The vast majority of risk-sensitivity studies employ such functions because it is easier to provide discrete values in choice experiments with variability in reward amount (an exception is Fulop and Menzel (2000), in which amount was estimated by time of access to reward, according to a continuous distribution). We therefore want to assess whether shock- and continuous functions having the same mean and variance would be perceived similarly or differently by pollinators.

In each case, we calculate the perceived value of the distribution for the pollinator, U_P, by multiplying the utility of each value, $u(x)$, by the probability of its occurrence, $p(x)$, and summing over all values. For a shock-function, it is the sum of the utility of each discrete value multiplied by its probability. For a continuous function, we integrate over all values:
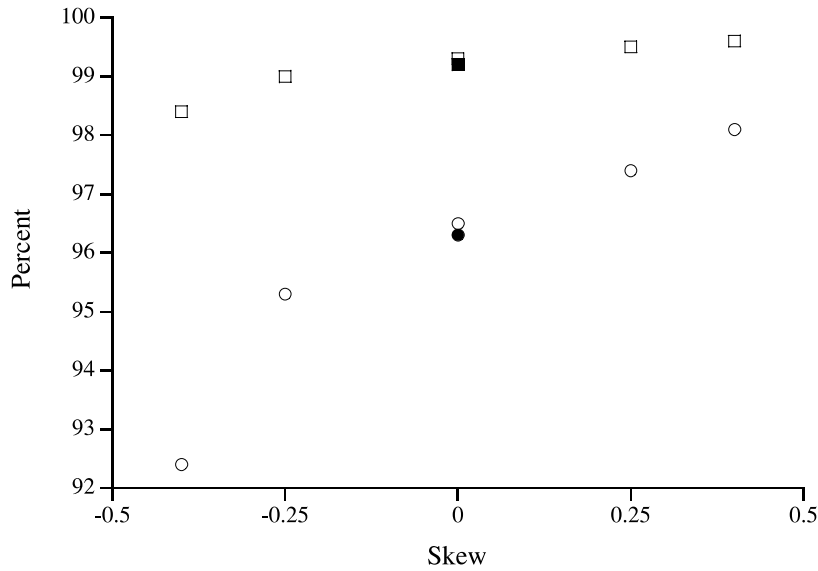
Fig. 5. The relative utility of various nectar distributions for a pollinator with a concave down utility function, expressed as percentage of the utility of the constant reward of equal mean. Means are 7.5 (circles) and 12.5 (squares), and $\sigma = 2.5$ in all cases. Lower percentages imply greater risk-aversion. For shock functions (empty symbols), skew is represented by the probability of the lower reward minus 0.5. For symmetric distributions skew = 0; the values for symmetric Gaussian distributions are also shown (full symbols)

$$U_p = \int p(x) \cdot u(x) \cdot dx. \qquad (2)$$

According to Eq. 1, the utility of 7.5 µl, $u(7.5)$, equals 89.46 (Fig. 3A). This corresponds to the perceived value of a constant reward of 7.5 µl. The utility of a variable reward distributed as a shock-function, with p(5 µl) = 0.5 and p(10 µl) = 0.5 ($\mu = 7.5$, $\sigma = 2.5$, skew = 0), is 86.35 (Fig. 3B). The relative utility (in percent) of each distribution to the utility of the constant reward of equal mean is shown in Fig. 5. The lower utility values of the variable-reward distribution imply risk-aversion.

The utility of the symmetric Gaussian function with the same mean and variance ($\mu = 7.5$, $\sigma = 2.5$) is 86.17 (Fig. 4A). This is less than the utility of the constant reward, and hence also implies risk-aversion (Fig. 5). Variability, therefore, reduces the utility of the distribution both for shock and continuous functions. However, the utility of the continuous distribution is a bit smaller than that of the shock-function. This suggests that risk-sensitivity in studies in which shock-functions were employed may have underestimated the degree of risk-aversion. Whether animals respond differently to shock and continuous functions remains to be tested.

Increasing the mean value of the distribution, while maintaining the same variance, reduces the difference between the utility of a constant and a variable distribution. Increasing the mean to 12.5, reduces the difference between the utility of a constant distribution, 97.65 (Fig. 3G), and that of the symmetric shock function ($\mu = 12.5$, $\sigma = 2.5$), 96.96 (Fig. 3H). This implies that increasing the mean reduces risk-aversion. Since increasing the mean, while maintaining the variance constant, reduces the coefficient of variation, these results are consistent with the CV-model (Shafir 2000). The utility of the shock-function is still greater than that of the Gaussian function ($\mu = 12.5$, $\sigma = 2.5$), 96.91 (Fig. 4D), though the difference is smaller than with a smaller mean (Fig. 5).

We next explore the effect of skewness. For both shock and continuous functions, the utility of positively skewed functions is greater than that of negatively skewed ones. For shock functions, positive skew increases, and negative skew decreases the utility relative to that of the symmetric function, and the effect increases with greater skewness (Fig. 5). For continuous distributions, both negative and positive skew increase the utility relative to the symmetric distribution. For $\mu = 7.5$, the utility of the symmetric distribution is 96.3% that of the constant value, and increases to 98.2% and 99.0% for negative and positive skew,

Table 1. Hypothesized adaptive plant strategies to increase pollinator attraction resulting from cognitive phenomena that affect pollinator choice behavior

Cognitive phenomenon	Effect on behavior	Plant adaptive strategy
Intermittent reward effect	Slower extinction, more floral visits	Produce blanks and bonanza flowers
Risk-aversion and the Weber effect	Preference for reward distributions with lower coefficients of variation	Reduce variance and/or increase mean reward
Risk-aversion and the Weber effect	Preference for positively skewed distributions	Produce many low- and few high-rewarding flowers
Asymmetric-dominance effect	Increased preference for the asymmetrically dominating alternative	Produce some unattractive, decoy flowers

respectively. For $\mu = 12.5$, the utility of the symmetric distribution is 99.2% that of the constant value, and increases to 99.6% and 99.8% for negative and positive skew, respectively.

We have shown above that Weber's law leads to risk-sensitive choice behavior, and in particular to encoding variability along the lines of the CV, and to sensitivity to distribution skew. The general effect of positive skew increasing the utility of the distribution is due to the concave down shape of the pollinator utility function. For the continuous distributions, the increased utility of also the negatively skewed functions can be explained by the characteristics of the skewed functions. Maintaining the same mean and standard deviation of the symmetric and skewed Gaussian distribution functions, decreased the range of nectar volume (x) and extended the probability values reached in the skewed functions relative to the symmetric Gaussian functions. The symmetric Gaussian distributions increase more rapidly in the low values range of the nectar-volume perception function, $u(x)$, and therefore the integration of the probability distribution and the nectar-volume perception function is lower in the symmetric distribution relative to the negatively skewed case.

Conclusion

Pollinators and flowering plants whose reproductive success depends on animal pollination, have coevolved floral visitation behavior and flowering strategies, respectively. Pollinator behavior is the outcome of perception and decision-making processes. We discussed several cognitive phenomena, their effect on choice behavior, and the plant strategies to attract pollinators that are expected to evolve through cognition-mediated coevolution (Table 1). We focused on two central themes that are of great interest in studies of cognition and that have important ecological consequences, context-dependence and risk-sensitivity. These phenomena may be themselves adaptive, or the manifestation of fundamental cognitive processes that are adaptive; presumably, several kinds of evolutionary constraints are involved. Regardless of the optimality debate (over which much ink has been shed, and we do not attempt to resolve here), the fact remains that these phenomena have now received much empirical support, and are undoubtedly real. The cognition-mediated coevolution perspective can generate interesting new hypotheses. Future studies explicitly aimed at testing these hypotheses will tell how productive this approach is at understanding pollinator-plant interactions and the evolution of pollinator cognition and of plant strategies.

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