ARTICLES

Colour learning in two behavioural contexts: how much can a butterfly keep in mind?

MARTHA R. WEISS*† & DANIEL R. PAPAJ‡

*Center for Insect Science, Tucson
†Georgetown University
‡Department of Ecology and Evolutionary Biology, University of Arizona, Tucson

Here we examine the ability of butterflies to learn colour cues in two different behavioural contexts, nectar foraging and oviposition, more or less simultaneously. We first trained female *Battus philenor* (Papilionidae) butterflies to associate a given colour with the presence of host plant leaf extract and assayed their colour preference; we then trained a subset of these butterflies to associate a second colour with the presence of sucrose solution and assayed colour preference once more. When offered an array of four unscented and unrewarding coloured models, 'single-trained' butterflies consistently alighted most frequently on their oviposition training colour. Green-trained butterflies landed on nontrained colours only about 4% of the time, while butterflies trained to red, yellow or blue made about 23% of their landings on nontrained colours; of those nontrained landings, most were on green. The majority of 'dual-trained' butterflies made the greatest number of visits to both training colours in the appropriate behavioural context; that is, they probed the models of their sucrose-associated colour and alighted on the models of their oviposition-associated colour. Landings or probes on nontrained colours in one context were consistently biased towards what was learned in the alternative context, suggesting an information–processing constraint in the butterflies. This paper provides a clear demonstration that butterflies can learn in two behavioural contexts within a short span of time. A capacity for such dual conditioning presumably permits female butterflies to forage effectively for egg-laying sites and nectar resources even when those activities are intermingled in time.

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Learning plays an important role in the location and utilization of food and oviposition sites for a broad range of insects, including nectar feeders, herbivores and parasitoids (Papaj & Prokopy 1989; Papaj & Lewis 1993). Although several studies have examined concurrent associative learning of more than one stimulus, most have done so within one behavioural context (e.g. colour and odour in the context of nectar foraging: Couvillion & Bitterman 1988; Villa & Weiss 1990; Funayama et al. 1995). In nature, however, insects will often encounter relevant stimuli in a given sensory modality (e.g. vision, olfaction, etc.) in more than one behavioural context

Correspondence: M. R. Weiss, Biology Department, Georgetown University, 406 Reiss Building, Washington, D.C. 20057-1229, U.S.A. (email: weissm@georgetown.edu). D. R. Papaj is at the Department of Ecology and Evolutionary Biology, Biological Sciences West 310, University of Arizona, Tucson, AZ 85721, U.S.A.

within a very short time span. This is particularly true for individual nonsocial insects, which do not have a division of labour and so must perform a range of tasks. A female butterfly or moth, for example, may use a particular cue, such as colour or shape, when foraging for nectar and when searching for a larval host plant (Rausher 1978; Papaj 1986; Bernard & Remington 1991; Goulson & Cory 1993; Weiss 1995; Allard & Papaj 1996; Kelber 1999). Similarly, a parasitoid wasp commonly uses odour cues in locating both oviposition hosts and food (Takasu & Lewis 1993; Wackers 1994). Thus, we might expect that such insects would have the capacity to learn a given type of stimulus in two different behavioural contexts at once and therefore to show motivational state-dependent expression of learning.

Such 'dual conditioning' has been demonstrated in the parasitic wasp *Microplitis croceipes* (Braconidae), the

females of which generally feed on floral nectars and lay their eggs in lepidopteran larvae (Lewis & Takasu 1990; Takasu & Lewis 1993). Female wasps previously trained to associate two novel odours with separate food and host resources were able to make an accurate choice between the two odours on the basis of their relative needs, such that hungry wasps chose the odour associated with food and sated wasps chose the odour associated with oviposition (Lewis & Takasu 1990; Takasu & Lewis 1993). In a less biologically realistic, but none the less compelling example, bumblebees, *Bombus terrestris* (Apidae) can be trained to choose one of a pair of visual patterns at a feeder and the alternate member of the pair at the nest entrance (Colborn et al. 1999). Here we use butterflies to investigate the capacity for visual dual conditioning in two different behavioural contexts in which learning is known to take place: nectar foraging and oviposition on host plants.

With respect to foraging, butterflies can learn to manipulate flowers to reach nectar (Lewis 1986; Lewis & Lipani 1989), to associate colour with the presence of a sugar reward in artificial or real flowers (Goulson & Cory 1993; Weiss 1995; Kandori & Ohsaki 1996; Weiss 1997; Kinoshita et al. 1999) and to follow a regular daily pattern of visits to flowers, suggestive of an ability to learn spatial locations (Gilbert 1980). With respect to oviposition on host plants, butterflies have been shown to associate leaf shape and colour with successful egg laying, an association mediated by contact with phytostimulants (Traynier 1984, 1986; Papaj 1986; Papaj & Rausher 1987; Allard & Papaj 1996). Such learning appears to permit butterflies to find host plants more efficiently in the field (Rausher 1978; Stanton 1984).

In many butterfly species, females intermingle short bouts of nectar gathering with short oviposition bouts (Stanton 1984; May 1988; Lewis & Lipani 1989). Such situations may require females to learn and use a cue such as colour in two different behavioural contexts. Can butterflies learn two cues more or less at once?

In this study we examine learning of a single type of visual stimulus, colour, in two behavioural contexts. We use *Battus philenor* (Papilionidae), the pipevine swallowtail butterfly, as our study organism. We ask whether *B. philenor* butterflies can first learn a given colour in the presence of an oviposition stimulant (single training) and, having learned to do so, whether they can additionally learn a second colour in the presence of a sugar water reward (dual training). We then examine the behavioural responses of the dual-trained butterflies in an array of four unrewarding colours, two trained and two novel. In conducting this work, we took advantage of the fact that our butterflies display distinct behavioural patterns in the context of oviposition search and nectar foraging, such that we could determine what a butterfly was foraging for independent of her colour choices. We examine the distribution of visits to both trained and untrained colours, as both kinds of choices provide information about the learning process. We also discuss innate colour preferences with respect to behavioural context.

METHODS

Butterfly Collection and Rearing

Battus philenor larvae feed only on plants in the genus *Aristolochia* (Aristolochiaceae). Adult females caught in the field in southern Arizona readily laid eggs on fresh leaves of *A. fimbriata*, an ornamental species cultivated on the University of Arizona campus. Two subsequent generations were reared in the laboratory; field-caught females were added to the colony each generation. Larvae were fed either fresh leaves of *A. fimbriata* or an artificial diet containing freeze-dried *A. californica* leaves. Adult female butterflies used in the study mated naturally or were hand-paired, and were at least 3 days old.

Basic Butterfly Behaviour in the Field and Laboratory

In nature, *B. philenor* butterflies intermingle bouts of nectar foraging and oviposition search (unpublished observations). During nectar foraging, a hungry butterfly approaches a flower and either alights on it with her proboscis already extended, or extends her proboscis immediately upon alighting. She then inserts the proboscis directly into the corolla, or probes repeatedly until the corolla is located. During oviposition search, by contrast, the proboscis is never extended. A gravid female alights on a leaf briefly, sometimes drumming its surface with its foretarsi. The foretarsi bear contact chemoreceptors that are used to 'taste' chemicals on the leaf surface (Bernays & Chapman 1994). If the plant is a member of a suitable species within the genus *Aristolochia*, the female may curl her abdomen until its tip contacts the stem or the underside of a leaf. The female may or may not lay a small clutch of eggs before resuming host search. Host search also differs from nectar foraging in terms of flight behaviour, with the female fluttering close to the array, flying slowly and making tight turns. In short, oviposition and nectar search consist of distinctly different patterns of behaviour.

Design of Leaf/Flower Models

We designed paper models (5 cm in diameter) for oviposition and nectar training to appear intermediate in shape between leaves and flowers. They consisted of five rays projecting out from an inverted plastic pipette tip. Five centimetres in diameter, the models were constructed of Canson brand papers in red, yellow, green and blue. Papers of different colours were not equivalent in brightness; yellow was the most reflective, blue the least (Fig. 1). However, we have previously established that *B. philenor* foragers spontaneously prefer yellow and blue paper colours in the context of nectar foraging, irrespective of the colours' relative intensities (Weiss 1997). Moreover, recent studies of learning in papilionid butterflies demonstrate that these insects show true colour vision, responding to wavelength, rather than intensity (Kelber & Pfaff 1999; Kinoshita et al. 1999). Finally, although it is likely that these butterflies also respond to
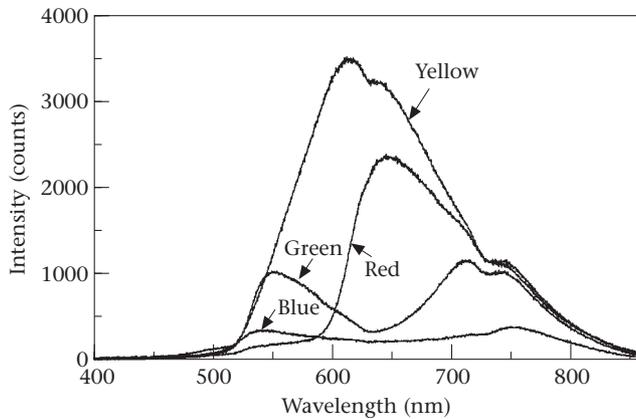
Figure 1. Reflectance spectra of coloured papers used for construction of leaf/flower models.

wavelength rather than intensity, the distinction is not a central focus of the present study.

Training Protocol

Single-trained butterflies

To train butterflies to associate oviposition stimulus with colour, we made a methanol-based extract of fresh *A. fimbriata* leaves at a concentration of 1 g/ml (see Papaj 1986 for methods). *Battus philenor* females respond to the presence of D-pinitol and aristolochic acid in the extract (Papaj et al. 1992; Sachdev-Gupta et al. 1993). A mated adult female butterfly, which had no prior exposure to *Aristolochia* or its extract, was placed on a red, yellow, blue or green paper model freshly sprayed with extract. After one to six exposures over the course of 1–3 days, most butterflies readily laid clusters of eggs on the extract-soaked models. Only those that did so were included in the study. Insects were not exposed to other coloured models during this training period. We trained 27 females to associate an oviposition stimulus with colour; eight were trained to red, six to blue, six to yellow and seven to green. Single-training for a given butterfly was always to the same colour; since a butterfly may not have laid eggs during a given presentation of the stimulus, both the timing and overall frequency of oviposition rewards varied haphazardly among individuals.

Dual-trained butterflies

Of 27 butterflies that were trained to associate the oviposition stimulus with a colour, 17 were additionally trained to associate a different colour with a sugar water reward. (The 10 butterflies that were not dual-trained either were injured, died, or failed to respond to a nectar test colour after nectar training). Following 1–2 days of testing and reinforcement in association with oviposition stimulant, we placed an individual butterfly on a model of a colour that differed from her oviposition training colour and unrolled her proboscis with an insect pin into a 20% sugar water solution placed over agar in the well of the model. After one to seven exposures over the course of 1–3 days, butterflies generally probed the models on their own. Training to sugar water reward was always to

the same colour for a given individual; both the timing and frequency of sugar water rewards varied haphazardly among individuals.

Testing Protocol

The test array consisted of 40 paper models (10 of each colour) identical to those used in training, except that they bore no reward (i.e. they were neither sprayed with extract, nor filled with sugar water). The models were regularly arranged at points on a Cartesian grid on a masonite pegboard (1.25 × 1.25 m); adjacent models were 4 cm from one another in a line and 5 cm apart on the diagonal. Models of different colours were alternated systematically throughout the array. The test array was placed within a mesh field cage (2 × 2 × 2 m), which was situated outdoors on the University of Arizona campus. Tests were conducted between approximately 0900 and 1400 hours.

During testing, which lasted approximately 30 min, we first gently placed a butterfly on her assigned oviposition training model and then allowed her to depart the training model and fly over the test array. We recorded the colours of any models visited and how the butterfly behaved during the visit. Thus, when a butterfly landed on a model and inserted her proboscis near or into its centre well, we scored the visit as a 'nectar probe' or, simply, 'probe'. When she landed briefly on a model without extending her proboscis, we scored the visit as a 'host landing' or, simply, 'landing'. In rare cases, alighting butterflies drummed their forelegs on the model and occasionally even curled their abdomens towards the model surface, as they did when laying eggs. These more involved sequences were also scored as landings. In our test array, as in observations in nature (unpublished observations), there were virtually no visits that could not be categorized as either a landing or a probe.

Under single training, the test butterfly was periodically re-exposed to the extract-soaked training model, up to seven times during the course of the test. Dual-trained butterflies were tested in a similar fashion, except that they were intermittently reinforced during the course of the testing episode with exposure to each of their training models (oviposition stimulant or sugar water).

Analysis

Results were analysed with SYSTAT or JMP statistical software (SAS Institute). Proportions data were arcsine transformed.

RESULTS

Single Training

Individual butterflies consistently made more landings on their oviposition training colour than on any of the other three colours (Fig. 2). In the absence of any prior quantitative knowledge of innate preferences for oviposition colours, we expected that the mean percentage
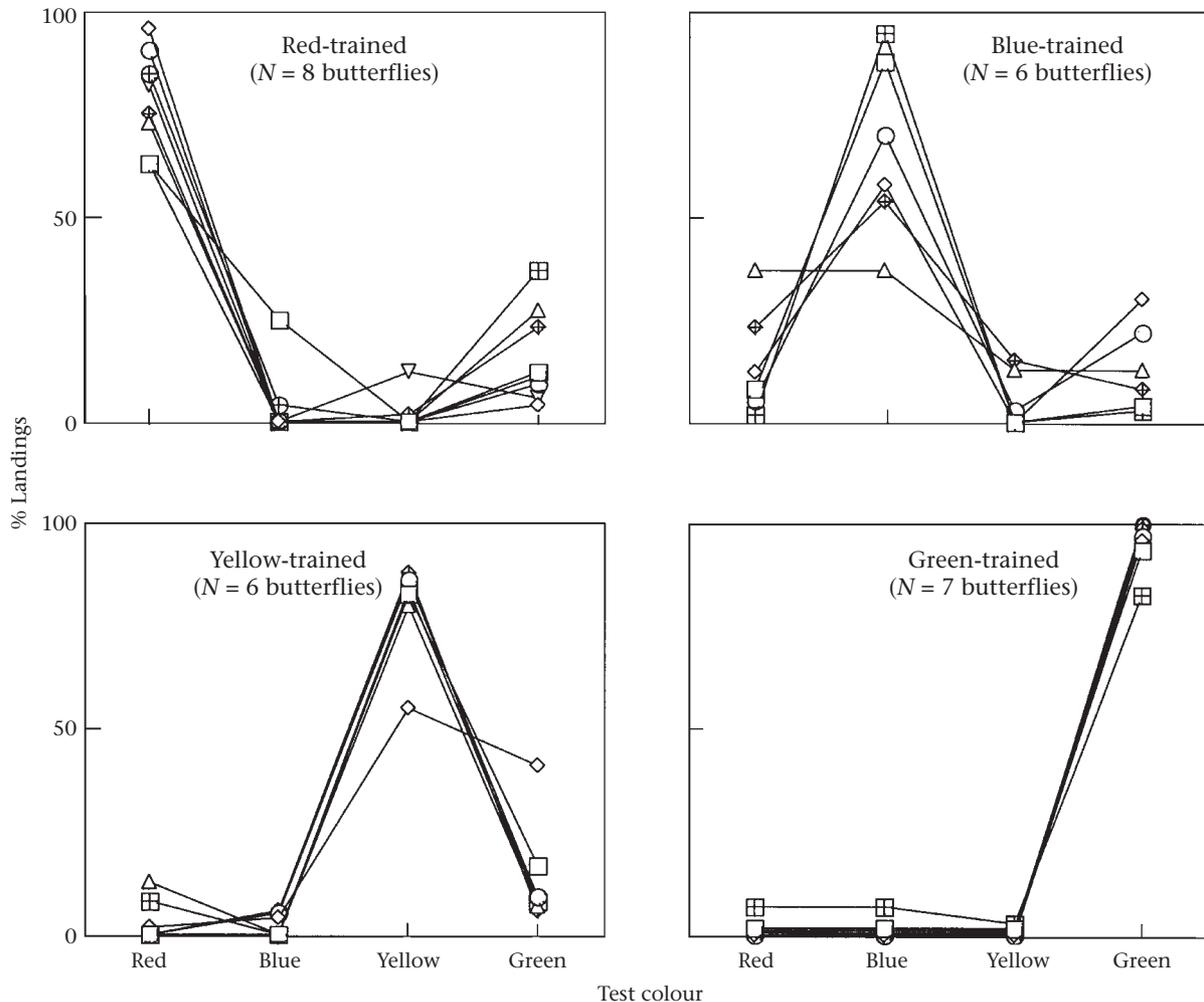
Figure 2. Oviposition colour learning in single-trained butterflies. Each line represents an individual butterfly. Red-trained, N=196 total visits; blue-trained, N=218 total visits; yellow-trained, N=95 total visits; green-trained, N=187 total visits.

of landings on each colour should have been 25%. For each training colour treatment, the mean training colour preference was significantly greater than 25% (t test of sample mean against the presumed parametric mean of 0.25: blue: t_5=4.75, P<0.01; red: t_7=12.16, P<0.001, yellow: t_5=10.92, P<0.001; green: t_6=29.88, P<0.0001).

The distribution of landings on nontraining colours depended on training colour and differed in two ways between butterflies trained to green and those trained to other colours. First, individuals trained to oviposit on green made only 4.3% of their landings on colours other than green (Fig. 3). Individuals trained to red, blue or yellow, in contrast, made approximately 23% of their landings on nontrained colours (Fig. 3). An analysis of variance indicated a highly significant effect of training colour on level of accuracy (ANOVA on arcsine-transformed data: $F_{3,23}$=8.92, P<0.0005, R^2=53.8%). Training colour preference for green-trained butterflies was significantly higher than training colour preference for butterflies trained to the other colours (ANOVA contrast, green versus other colours: $F_{1,23}$=25.53, P<0.00005).

Second, whereas the few landings made by butterflies

trained to green were distributed more or less evenly over the other three colours, the majority of nontraining-colour landings by butterflies trained to red, blue or yellow ($\bar{X} \pm$ SE=63.7 $\pm$ 9.2%) were on green (Fig. 3). Collapsing across colour treatments for all single-trained butterflies that had not been trained to green (N=20), the trained oviposition colour received the highest mean percentage of landings ($\bar{X} \pm$ SE=75.1 $\pm$ 3.5%), the colour green received the next highest mean percentage of landings (16.3 $\pm$ 2.6%) and the two remaining colours together received only 5.2 $\pm$ 1.9% of the landings.

To test the apparent propensity of butterflies not trained to green to alight on green models, we conducted a repeated measures ANOVA on the distribution of landings for butterflies trained to any colour but green. We specifically compared the number of green landings for these butterflies against the pooled number of landings on their other two nontraining colours. Since landings on green were compared against the sum of landings on two other colours, our analysis constituted a conservative test of the hypothesis that nontrained green landings were more common than expected by chance alone. The
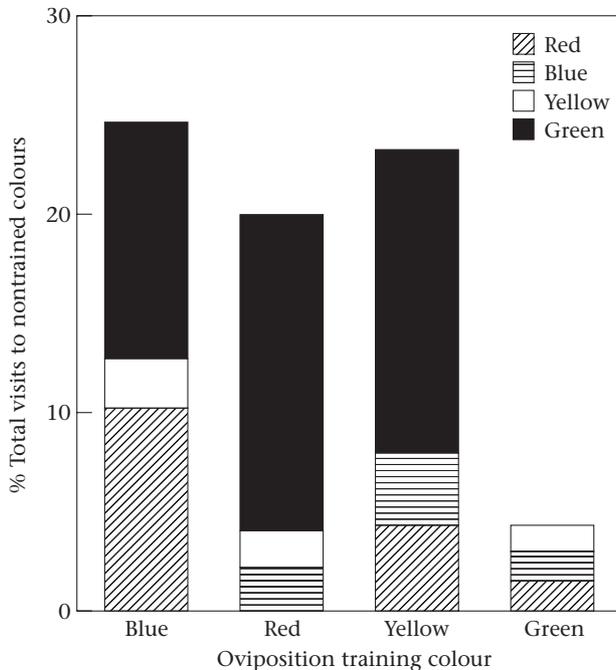
Figure 3. Mean percentage of landings on nontrained colours for single-trained butterflies. Blue-trained, $N=54$ landings on non-trained colours (24.8% of total visits); red-trained, $N=39$ landings on nontrained colours (19.9% of total visits); yellow-trained, $N=22$ landings on nontrained colours (23.2% of total visits); green-trained, $N=8$ landings on nontrained colours (4.3% of total visits).

number of green landings was nevertheless significantly greater than the pooled number of landings on the other two nontraining colours (repeated measures ANOVA: $F_{1,17}=4.65$, $P<0.05$).

Dual Training

Only those butterflies that made a minimum of eight probes and/or alights during the testing period were included in the analysis, so as to achieve a greater degree of reliability in our estimates of colour preference ($\bar{X} \pm SE = 63.3 \pm 11.8$ probes and alights, $N=17$ butterflies). Our decision to set the minimum at eight is somewhat arbitrary, eight being equivalent to one visit per colour per context. Using these criteria, 17 dual-trained butterflies made landings on models during testing; 13 of the 17 also probed models (Table 1).

Although we attempted to train butterflies to each of the 12 possible colour combinations, some combinations were better represented than others and certain combinations were not represented at all. Six individuals were trained to probe for nectar on yellow (Yn) and oviposit on blue (Bo) and one was trained to the opposite combination (Bn/Yo); three were trained to probe on red and oviposit on blue (Rn/Bo) and one was trained to the opposite combination (Bn/Ro); three were trained to probe on red and oviposit on yellow (Rn/Yo) and one was trained to the opposite combination (Yn/Ro); one was trained to probe on yellow and oviposit on green (Yn/Go); and one was trained to probe on red and oviposit on green (Rn/Go). Our failure to collect data on other colour combinations may reflect intrinsic predispositions on the part of the butterflies to learn certain colours in certain contexts (for example, it seemed to be difficult to train butterflies to forage for green in the context of nectar rewards). However, given the relatively small sample sizes involved, the biases in colour combinations could also reflect stochastic variation in the longevity of the butterflies.

Table 1. Total number of probes and landings for dual-trained butterflies upon models of four colours (Y: yellow; B: blue; G: green; R: red) in two behavioural contexts (n: nectar probing; o: oviposition landings)

Butterfly ID and training colours	Probes				Landings			
	Y	B	G	R	Y	B	G	R
76 Yn/Bo	**2′**	0	0	0	9	**26′**	8	5
75 Yn/Bo	**22′**	0	0	0	**9**	8′	1	0
114 Yn/Bo	**16′**	0	0	0	**13**	2′	2	3
104 Yn/Bo	**10′**	0	0	0	**19**	18′	2	4
84 Yn/Bo	**73′**	7	1	0	21	**65′**	15	13
86 Yn/Bo	**8′**	0	0	0	8	**19′**	2	6
57 Rn/Bo	0	0	0	0′	5	**32′**	15	9
81 Rn/Bo	0	5	1	**36′**	1	7′	7	**16**
67 Rn/Bo	0	0	0	**11′**	0	1′	0	0
77 Rn/Yo	3	1	0	**15′**	15′	0	**10**	0
99 Rn/Yo	0	0	0	0′	**7′**	1	0	1
110 Rn/Yo	12	0	0	**72′**	**30′**	0	5	3
116 Bn/Yo	6	**39′**	0	4	**54′**	14	3	3
111 Yn/Ro	1′	0	0	3	1	0	1	**9′**
109 Bn/Ro	0	**12′**	0	3	0	13	7	**66′**
95 Yn/Go	0′	0	0	0	5	0	**72′**	2
88 Rn/Go	0	0	0	0′	2	0	**27′**	5

Bold type indicates the colour most frequently visited; an apostrophe indicates each butterfly's trained colour.

Sequence of Visits

Because testing sessions for dual-trained individuals involved intermittent reinforcement with both oviposition stimulant and nectar, it was necessary to assess whether landings alone directly followed oviposition experience and probes alone directly followed nectar reinforcement. In fact, butterflies almost always intermingled landings and probes in relation to rewards; that is, not all landings followed oviposition reinforcement and not all probes followed feeding reinforcement. As an example, butterfly 110, trained to probe for nectar on red and oviposit on yellow, probed on red and landed on yellow and green following exposure to the red nectar model; she landed on yellow and probed on yellow and red following exposure to the yellow oviposition model.

Visits to Trained Colours

For either context, the training colour preference was significantly greater than 25%, the value expected if butterflies visited training colours according to their frequency in the test array. Collapsing across nectar training colours, the mean ($\pm$ SE) percentage of probes on the trained nectar colour was 86.55 ($\pm$ 5.62%), which was significantly greater than 25% (t test of sample mean against the presumed parametric mean of 0.25: $t_{12}=10.83$, $P<0.001$). Collapsing across oviposition training colours for butterflies that both probed and alighted during testing, the mean percentage of landings on the trained oviposition colour was somewhat less, $62.8 \pm 5.76\%$, but still significantly greater than 25% ($t_{12}=4.93$, $P<0.001$). Preference for the training colour in the nectar foraging mode was not correlated with preference for the training colour in the oviposition mode (Pearson correlation: r_{11}, NS).

For the majority of dual-trained butterflies, the greatest number of visits in each context was made to the training colour. Eight of the 13 butterflies visited both colours appropriately in accordance with the particular task; that is, they made the highest number of probes on models of their trained nectar colour and the highest number of landings on their trained oviposition colour (Table 1). Examining landing and probing separately, 13 of the 17 dual-trained butterflies made the greatest number of landings on their trained oviposition colour (Table 1). Of 13 butterflies that both probed and alighted on models, all but one made the greatest number of probes on their trained nectar colour. Six of the 13 butterflies probed only their trained nectar colour.

Visits to Nontrained Colours

Given the pattern of visits described above for single-trained butterflies, we were especially interested in analysing visits to nontrained colours with reference to the colour green. We additionally noted nontrained visits made in one context to the colour trained in the alternative context. We collapsed data across colour combinations, including all dual-trained individuals except the
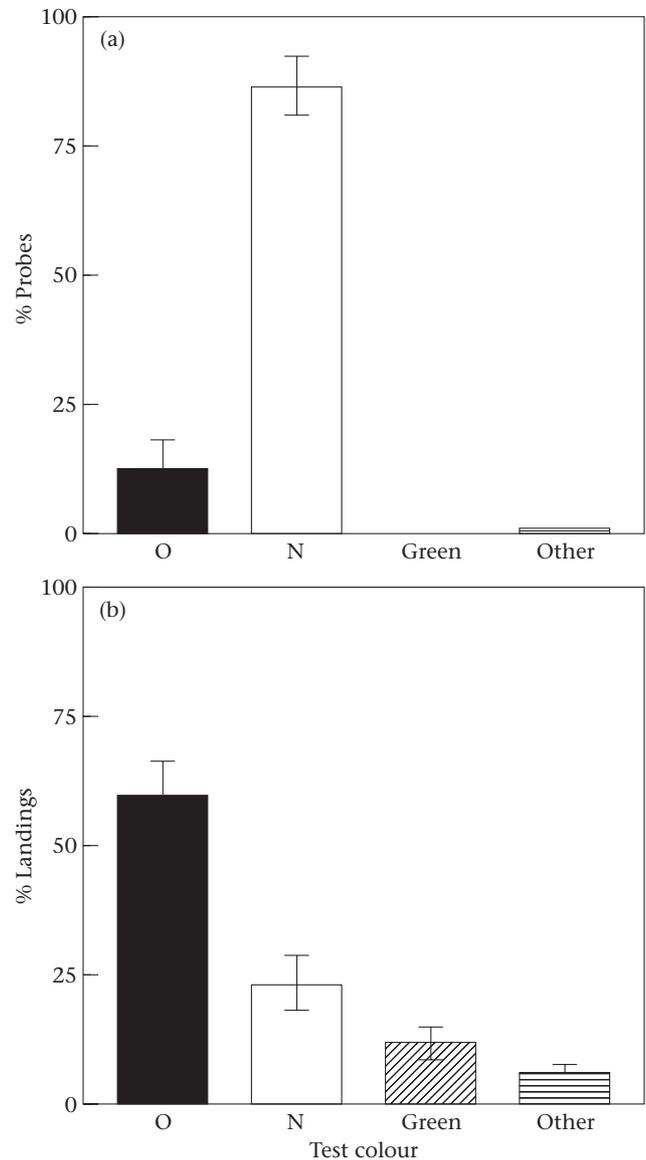

Figure 4. Summary of mean probes and landings ($\pm$SE) by 15 dual-trained butterflies on trained oviposition colour (O), trained nectar colour (N), green, or the alternative colour (Other). (Butterflies trained to green oviposition are not included.)

two trained to green oviposition ($N=15$ butterflies) and then tabulated visits as to whether they were made to the same-context training colour, the alternative-context training colour, green, or the remaining colour (Fig. 4). Two interesting patterns emerged. First, in the contexts of both probing and landing, visits to nontrained colours were made most often on the alternative-context training colour. That is, probes not made on the trained nectar colour were made most often on the oviposition training colour and landings not made on the trained oviposition colour were made most often on the nectar training colour. Second, almost no butterflies probed on green (with the mean number of probes on green being less than the mean on the remaining test colour); in contrast, butterflies trained to other colours landed on

green relatively frequently (with the mean number of landings on green being greater than the mean on the remaining test colour).

To test for the significance of these patterns, we used a repeated measures ANOVA with the type of nontrained visit (alternative-context colour, green or remaining colours) as a random effect. For probes on nontrained colours, the model was highly significant, explaining almost 72% of the overall variance. The between-subjects effect (which indicates degree of variation among females in nontrained probes) was not significant ($F_{6,12}=0.84$, NS). The visit type effect, by contrast, was highly significant ($F_{2,12}=12.88$, $P<0.001$). In particular, probes on the alternative-context colour were significantly more frequent than either green probes ($F_{1,12}=21.39$, $P<0.0005$) or probes on the remaining colours ($F_{1,12}=17.02$, $P<0.001$). Probes on green when trained to any other colour were no more common than probes on the remaining colours ($F_{1,12}=0.25$, NS).

The model was also highly significant in terms of accounting for landings on nontrained colours, explaining almost 69% of the overall variance in such landings. The between-subjects effect (which indicates variation among females in landings on nontrained colours) was significant ($F_{13,26}=2.92$, $P<0.01$). The visit type effect was highly significant ($F_{2,26}=9.67$, $P<0.001$). Once again, alights on colours trained in the alternative context were significantly more frequent than alights on the remaining nontrained colours ($F_{1,26}=19.03$, $P<0.0002$). Alights on colours trained in the alternative context were again more frequent than alights on green, although the difference was far less significant than it was for probes on colours trained in the alternative context ($F_{1,26}=7.09$, $P<0.01$). Landings on green were not significantly more frequent than landings on the remaining colours ($F_{1,26}=2.88$, $P=0.10$). Finally, landings on green were significantly more common than probes on green (paired t test: $t_{14}=4.02$, $P<0.001$).

In summary, for animals trained to colours other than green, there was a tendency for visits to green to be more frequent in the oviposition context than in the nectar context. However, the predominant result in either behavioural context was a distinct bias for visits to the colour trained in the alternative context. Indeed, visits to the alternative-context training colour occasionally outnumbered visits to the same-context training colour. In each of four cases in which the trained oviposition colour did not receive the most landings, the nectar colour did (see butterflies 75, 114, 104 and 81 in Table 1). In the one case in which the trained nectar colour did not receive the greatest number of probes, the oviposition colour did (see butterfly 111 in Table 1).

Range of behaviour patterns

Probing and landing data for three pairs of individual butterflies trained to opposite sets of colours illustrate the range of observed behaviour patterns (Fig. 5).

Yellow/Blue. Butterfly 116 (Bn/Yo) and butterfly 84 (Yn/Bo) both made the highest number of probes on
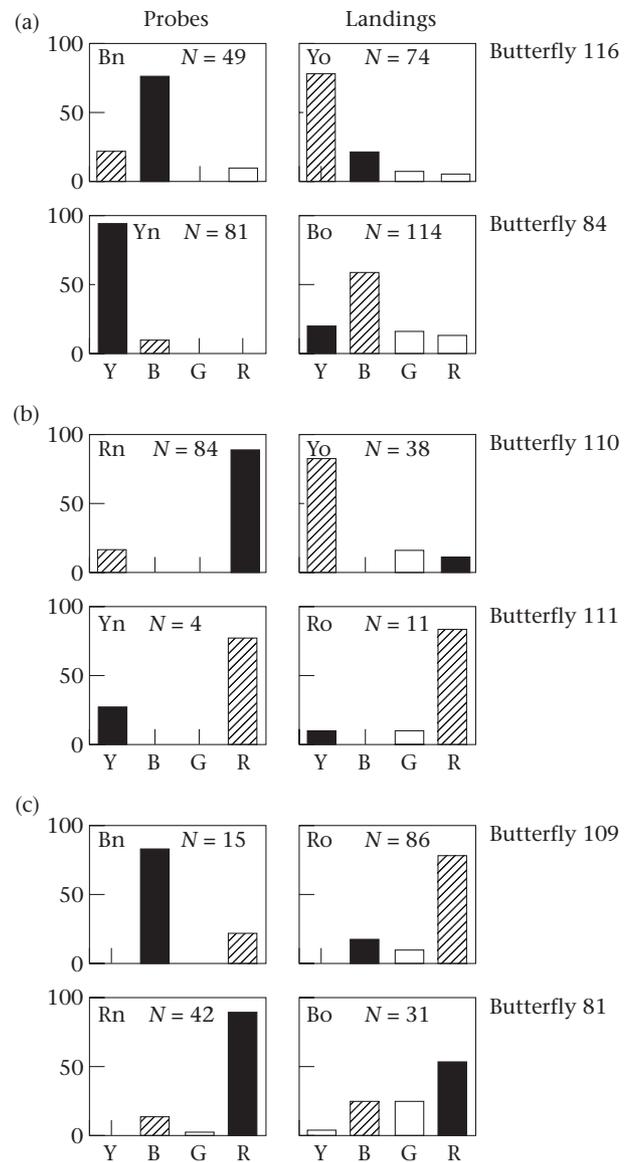

Figure 5. Comparison of nectar probes (n) and oviposition landings (o) on flower models by three pairs of butterflies trained to opposite sets of colours (Y: yellow; B: blue; R: red). Sample sizes are the number of probes or landings made by each individual. In all cases, black bars show the nectar training colour; hatched bars show the oviposition training colour. (a) Butterflies 116 and 84 made the greatest number of probes on their trained nectar colour (B and Y, respectively) and alights on their trained oviposition colour (Y and B, respectively). (b) Butterfly 110 made the greatest number of probes on her trained nectar colour (R) and alights on her trained oviposition colour (Y); butterfly 111 made the greatest number of probes and alights on her trained oviposition colour (R). (c) Butterfly 109 made the greatest number of probes on her trained nectar colour (B) and alights on her trained oviposition colour (R); butterfly 81 made the greatest number of probes and alights on her trained nectar colour (R).

their trained nectar colours and the highest number of landings on their trained oviposition colours (Fig. 5a).

Red/Yellow. Butterfly 110 (Rn/Yo) made the highest number of probes on her trained nectar colour and the

highest number of landings on her trained oviposition colour; butterfly 111 (Yn/Ro) made the highest number of probes on her trained oviposition colour, followed by her nectar colour; she made the highest number of landings on her trained oviposition colour (Fig. 5b).

Blue/Red. Butterfly 109 (Bn/Ro) made the highest number of probes on her trained nectar colour, followed by her oviposition colour and the highest number of landings on her trained oviposition colour, followed by her nectar colour. Butterfly 81 (Rn/Bo) made the highest number of probes on her trained nectar colour, followed by her oviposition colour; she made the highest number of landings on her trained nectar colour, followed by equal numbers of landings on her trained oviposition colour and on green (Fig. 5c).

DISCUSSION

Learning in Two Contexts

Battus philenor butterflies have previously been shown to associate colour with a nectar reward (Weiss 1997) and leaf shape with an oviposition reward (Rausher 1978; Papaj 1986; Allard & Papaj 1996). This paper provides a clear demonstration that butterflies can learn distinct cues in each of two behavioural contexts and can express the appropriate colour preference whether motivated to search for hosts or for nectar.

A capacity for learning colour cues more or less simultaneously in nectaring and oviposition contexts is likely to be relevant for butterflies in nature. Both flowers and hosts vary unpredictably with respect to colour. Flowers of a range of colours may be rewarding at various times and in various places. In southern Arizona, *B. philenor* butterflies appear to probe for nectar opportunistically on whatever species of flower is currently abundant. Presumably an individual would benefit by learning the colour of the currently rewarding flower type (Weiss 1997). Similarly, leaf colour, while generally green, nevertheless varies considerably in nature. In southern Arizona, the leaves of *B. philenor*'s host plant, *Aristolochia watsoni*, range in colour from reddish-purple to green.

In the present study, single-trained *B. philenor* butterflies trained to green oviposition models made proportionately fewer visits to other colours than butterflies trained to blue, red or yellow models. At first glance, this result seems consistent with the notion of a 'preparedness' to learn green. However, our error analysis indicated that the relatively poor performance on blue, red and yellow in oviposition training was due in large part to a tendency for butterflies trained to those colours to land on green regardless of their training. Thus, what might appear to be a preparedness to learn green seems instead to reflect an innate disposition to respond to green regardless of training.

If our inference is correct, we would expect that naïve butterflies searching for oviposition sites would show a congenital preference for green. Data on this point are not available. Such a preference would not be surprising, since *Aristolochia* leaves, like those of most higher plants, reflect strongly in the green part of the spectrum. It is worth noting that phytophagous insects that lack a red visual receptor commonly show a stronger preference for yellow than for green (Prokopy & Owens 1983), while butterflies with a red receptor (as *Battus* likely has) prefer colours for oviposition that appear green to the human eye (Kelber 1999). By contrast, in the context of nectar foraging, *B. philenor* butterflies show an innate preference for yellow and appear to avoid green. In an earlier study, naïve males and females offered unrewarding paper flowers in six colours made approximately 67% of their first nectar visits to yellow and 30% to blue and purple together, while green models received no visits (Weiss 1997). We might anticipate still other innate colour preferences in the context of mate recognition or courtship (Magnus 1958).

'Mistakes' versus Shifts in Context

Visits to green regardless of oviposition training colour arguably make functional sense. Visits to other unrewarded colours, in the context of either oviposition or nectar foraging, seem more likely to be 'mistakes'. In dual-training experiments, it can be difficult to distinguish between a mistake made in a given behavioural context and a shift in the type of reward that a subject is seeking. In the Lewis & Takasu work cited in the Introduction, for example, what can be made of the occasional hungry wasp that flew to the oviposition-associated odour instead of the food-associated odour? Was the wasp making a mistake, or was she foraging for oviposition sites despite her food hunger? In that work, the same response to odour (upwind flight towards an odour source) was assayed in each foraging context, making it difficult to distinguish between a 'mistake' and a shift in motivational state. However, our butterflies behaved differently towards models in each context, as they do towards host plants and flowers in the field. When foraging for nectar, they extended and inserted their proboscides into model wells. When searching for oviposition sites, in contrast, they landed briefly on models and sometimes drummed their tarsi on model surfaces. By categorizing visits as probes or landings, we could thus distinguish mistakes from shifts in what dual-trained females were seeking. Our data indicate that, while female butterflies can keep two things in mind at once, they are not perfect at it and are prone to making 'cross-contextual' mistakes.

Cross-contextual Mistakes

Many studies have shown that external contextual cues (e.g. colour, location, shape) can be used to indicate to an animal how to respond appropriately to other cues present in the environment (Bouton 1993). Colborn et al. (1999), for example, found that bumblebees can acquire a new response to a pair of visual stimuli at a feeder without disturbing an established response to the same stimuli at the nest entrance. The absence of interference when bees are trained in different contexts contrasts with the

marked interference found when bees are trained on two motor tasks in the same context (Chittka & Thomson 1997). Colborn et al. (1999) speculated that the contexts themselves offer cues that can prevent interference.

We have found that butterflies too can learn two cues in two different contexts, although in our study, the contexts were behavioural, rather than external to the animal. Our results also suggest that learning in one context may interfere to some degree with learning in another context. By using more colours during testing than during dual-training contexts, we were able to compare visits made to never-rewarded colours in a given context with visits made to colours rewarded in the alternative context. Our data indicate that visits in one context to other than the rewarded colour were consistently biased towards the colour learned in the alternative context.

These cross-contextual mistakes hint at an information-processing constraint in our butterflies, the nature of which is uncertain. We can imagine two possible sources of such a constraint. First, cross-contextual mistakes could occur when there is a time lag between shifts in motor pattern and shifts in attended colour. A change in motivational state (from hunger to oviposition, or vice versa) may cause shifts both in motor pattern and in the colour attended to. Cross-contextual mistakes may occur when a butterfly shifts her attention from one motor pattern to the other, but does not immediately shift attention from one colour to the other. Alternatively, the butterfly may shift from one colour to another more quickly than she shifts motor patterns. In either case, attention to the appropriate colour is not synchronized with motor action.

Second, it is possible that cross-contextual mistakes are due to a limitation on the selectivity of recall, independent of motor control. Under this scenario, a butterfly attends mainly to the appropriate colour in a given context, but maintains some degree of attention towards a colour rewarded in an alternative context. This hypothesis makes no presumptions about time lags.

Both explanations imply limits on memory, a concept often invoked in explanations of floral constancy, whereby pollinators are more specialized on a given floral resource than expected based on available alternatives (Lewis 1986; Waser 1986; Dukas & Real 1993; Chittka et al. 1999). Lewis (1986) found that for *Pieris rapae*, learning to extract nectar from flowers of a second species interfered with the ability to extract nectar from the first. Memory constraints have also been invoked in search behaviour for host plants. Stanton (1984) determined that when *Colias* spp. females interspersed visits to host and nectar plants, they were less accurate at landing on host plants after periods of nectar feeding, suggesting a trade-off between the two searching modalities, perhaps due to the dynamics of short-term learning.

Whatever the nature of the constraint that generates cross-contextual mistakes, 'constraint' does not necessarily translate to reduced fitness in nature. It is likely that a butterfly in the field would rely on a range of other cues (e.g. shape, odour, location, etc.) to discriminate between flowers and host plant leaves. Thus, the task we gave our butterflies was probably more difficult than one that they would face in the field, and it is possible that the confusion of contexts observed here would not be manifested under more natural conditions.

Even if some confusion of contexts did occur in nature, mistakes like those observed here might be more than offset by benefits of this pattern of organization of learning; such benefits might be related to the rate of processing. Bernays (1996) has argued that limiting attention to a stimulus benefits an animal by improving its rate of response to that stimulus (see also Dukas 1998). By extension, limiting attention to a couple of stimuli may increase the overall rates of responses to both stimuli. By focusing attention on one colour in a given context but maintaining some degree of attention to an alternative-context colour, a butterfly may be well prepared to shift rapidly from foraging in one context to foraging in another. The fact, as noted above, that our butterflies commonly intermingle nectaring bouts and oviposition bouts in nature suggests that a preparedness to shift behavioural contexts, as hosts and flowers are encountered in turn, might be of advantage in this species. In short, cross-contextual mistakes, even if they occur in nature, may persist so long as their cost is more than offset by a benefit associated with rapid and effective shifts in the mode of foraging.

A fruitful point of comparison on these issues may eventually be found among species of solitary insects that vary in the degree to which behavioural contexts are mingled in time. Some species of butterflies, beetles and flies intermix foraging, mating and oviposition activities over time scales as short as minutes (Faegri & van der Pijl 1979; Stanton 1984; Young 1986). Other insects tend to forage in discrete modes; the wood white butterfly, *Leptidea sinapsis*, for example, spatially separates its nectar and oviposition searches (Wiklund 1977). Are animals that intermingle tasks particularly effective at learning cues in several contexts more or less at once and at retrieving context-specific memories relatively rapidly? Alternatively, are the costs of 'confusion' for animals that intermingle tasks simply lower than for those that forage in discrete modes? Answering these questions will require studies of the learning abilities of additional species of solitary insects, as well as careful analyses of patterns of foraging by those species in nature.

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