

Absence of adaptive learning from the oviposition foraging behaviour of a checkerspot butterfly

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Abstract. A population of Edith's checkerspot butterfly, *Euphydryas editha*, laid eggs on two morphologically distinct host-plant species, one of which it had recently colonized. Search behaviour of two groups of females was compared in the field. 'Naive' females were experimentally deprived of both flight experience and host encounter, while 'experienced' females were observed without intervention. Three analyses failed to show evidence for adaptive learning that might have allowed the butterflies to increase their efficiency of host finding with experience: (1) proportions of alights on hosts were not different between the naive and experienced groups, (2) rates of alighting on hosts did not differ between the naive and experienced groups, and (3) probabilities of alighting on hosts did not increase during searching bouts. Both groups searched efficiently for their traditional host species, *Pedicularis semibarbata* (dwarf lousewort), and inefficiently for the novel host, *Collinsia torreyi* (blue-eyed Mary). There was also no evidence for behavioural differences among individuals of either group. The distribution among individuals of alight frequencies on *C. torreyi* appeared Poisson, with a single mode near the frequency expected from random alighting. This finding is consistent with the hypothesis that no females recognized *C. torreyi* as a host in flight, and that differences between butterflies in observed alight frequencies stemmed simply from random variation in the composition of the vegetation over which they flew. Thus, the absence of adaptive learning impeded the evolutionary incorporation of the novel host into the diet. These results complement previous findings that *E. editha* from the same population failed to learn to accept particular hosts after alighting and are in contrast to other studies of insect foraging, all of which have shown that learning is an important component of foraging behaviour, causing search efficiency to improve with experience. It is suggested that *E. editha* could be a model 'non-learning' insect in comparative studies that empirically test the role of learning in resource choice.

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Models of foraging by vertebrates assume that some form of adaptive learning assists individuals to respond to variation in availability and quality of resources and thereby increase their efficiency of resource finding (Stephens & Krebs 1986). Models developed for insects also stress learning but leave open the possibility of its absence (Ward 1987; Courtney et al. 1989; Jaenike & Papaj 1992; Mangel 1993). These models predict that the impact of learning on resource finding and acceptance will depend on interactions between effects of experience and genetic variation of host preference (Jaenike & Papaj 1992; Mangel 1993).

This stress on the role of learning in insect foraging is justified by several studies demonstrating learning in some form. Learning influences both the alighting frequencies in searches for

preferred resources (Rausher 1978) and the identities of resources that are preferred after alighting (Papaj & Prokopy 1989; Lewis 1993; Roitberg et al. 1993). Although the ability of insects to learn may be very restricted (Stanton 1984; Lewis 1986; Papaj 1986a), the existence of some type of learning in resource-gathering behaviour is the norm in published studies (Papaj & Prokopy 1989). Insects learn to prefer the resources they first encounter (Prokopy et al. 1982; Traynier 1984; Jaenike 1988) and to avoid those that cause them difficulty after ingestion (Dethier 1980; Bernays 1988). Insects become more efficient at finding resources by learning the timing of reward (Gould 1983; Dukas & Real 1993), location of plants (Gould 1983), colour and odour (Gould 1983; Prokopy et al. 1986), and shape of plants or plant parts (Rausher

1978; Gould 1983; Stanton 1984). Even the response to oviposition deterrent pheromones (which deter further eggs being laid at the same site) appears to be influenced by learning (Roitberg & Prokopy 1981; Chow & Mackauer 1986).

Ovipositing butterflies typically locate resources by some combination of vision (Traynier 1984) and olfaction (Feeny et al. 1989), then complete their assessment of host-plant quality by contact chemoreception (Feeny et al. 1983). Insects can use their contact chemoreception to assess host quality and availability, then restrict their search to those resources that are currently most rewarding. The classical example in butterflies is *Battus philenor*. Rausher (1978) proposed that learning was an adaptation to enable an oligophagous population (one which uses several plant species) of this butterfly to search preferentially for different host species in different generations. The relative abundance and quality of these host species was constant within generations but variable between them (cf. prediction by Stephens 1993). Additionally, Papaj (1986a) suggested that the existence of learning in a monophagous population of *B. philenor* is a means of increasing the efficiency of locating suitable individuals of the single host species, under conditions in which the visual characteristics associated with high suitability are somewhat unpredictable but can be assessed after alighting.

Much of the literature on insect learning, reviewed by Stephens (1993), has focused on the role of environmental predictability. If the environment is either totally unchanging or totally unpredictable from moment to moment, learning should have no value, compared to the most adaptive fixed behaviour (Stephens 1993). Stephens suggested that the maximum value of learning occurs when the environment is predictable within generations but unpredictable between generations.

We investigated the role of learning in host search in Edith's checkerspot butterfly, *Euphydryas editha*, which has a single brief (6-week) flight period per year, in which adult insects are exposed to very predictable hosts. The preferred host species does not change in density during the insect's flight season and has changed little in density over the past 15 years. Because these insects are sedentary (Ehrlich 1961), environmental unpredictability does not often

arise from migration of insects into habitats containing unusual combinations of potential hosts. This situation would lead both Rausher and Stephens to predict that learning would be relatively unimportant to host-finding by *E. editha*. However, a recent human-induced disturbance to our study site presented the insects with a novel potential host species that was highly suitable for larval development (Singer et al. 1993; see below). When such a novel potential host appears, insects that can learn to find it will be better able to colonize it, thus making such learning an important factor in the evolution of diet breadth.

We compared searching efficiencies of females experimentally deprived of experience (naives) with those of wild females whose prior experience had not been controlled, and whose age (judged from wing wear) indicated that they had indulged in several previous oviposition searches. We can be confident that these 'experienced' insects had previously encountered host plants, since they do so on average about once every 5 min during a daily oviposition search that usually lasts about 30 min (Mackay 1985). All test flights were performed in the natural habitat. We also looked for changes in search efficiency over time as naive females were exposed to host-plant stimuli and became more experienced, but we did not attempt to control the sequence in which they encountered the various plants on which they alighted.

This type of design has been criticized by Holliday & Hirsch (1986), who argued that demonstration of learning requires repeated measurements not only of individuals subjected to specific test stimuli but also of a control group housed identically to the test group but not subjected to 'learning' stimuli. While we agree that this rigorous design is appropriate for the testing of specific hypotheses on the nature of learning, it is not desirable for asking whether the organism learns anything at all in its natural habitat. By the very nature of the design favoured by Holliday & Hirsch, only one or very few stimuli can be presented, in order to 'ensure that each individual in a (treatment) group receives the same experience'. If these cues are taken out of context of the organism's natural history, they may not be recognized by the animal as cues for learning. Lack of a learning response in the test environment can lead to a false conclusion that the organism is unable to appropriately modify its

behaviour in its natural habitat (Tierney 1986). Our own approach has been to begin by asking whether changes in behaviour occur under natural conditions. If such changes were found, then the mechanisms responsible for them could be elucidated by specific studies in a more controlled environment.

METHODS

Study Organism and Habitat

We worked on *E. editha* at Rabbit Meadow on the Generals' Highway, Tulare County, California, where it is restricted to host plants in the Scrophulariaceae. The butterflies occupied a patchwork of two habitat types: clear-cuts that had been logged and burned, and rocky outcrops where no logging had occurred. Mark-release-recapture studies have shown some exchange of adults between outcrop and clear-cut habitats, but most individuals were recaptured in the same habitat type in which they were marked (C. Thomas & D. Boughton, personal communications).

We worked in adjacent outcrop and clear-cut sites that were used in previous studies (Singer 1983; Singer et al. 1992). In the clear-cut habitat (Rabbit Meadow area 1) most oviposition was on *Collinsia torreyi* (Singer 1983). In the adjacent outcrop habitat (Rabbit Meadow area 2), the sole host species was a prostrate, rosette-shaped perennial, *Pedicularis semibarbata*. Although *Collinsia* was also abundant on the outcrop, it did not receive eggs there. There is evidence that *Collinsia* has been incorporated into the diet of this insect population following clear-cutting in 1967, but that the use of *Pedicularis* is long-standing (Singer et al. 1992, 1993). Clear-cutting killed the *Pedicularis*, which is a hemiparasite on coniferous trees, and changed the phenology of the *Collinsia*, rendering it more suitable for the insects.

The oviposition behaviour of *E. editha* is divided into a pre-alighting (in-flight) component and a post-alighting phase in which the female tastes the plant on which it has alighted and responds to its chemical and physical properties (Singer 1986). A female searching for oviposition sites alights on all plant species present, both hosts and non-hosts, and tastes them by extending its atrophied foretarsi. Most alightings, even those on

a host species, result in rejection of the individual plant and continued searching (Rausher et al. 1981). We have never observed oviposition on non-host species, except those growing so close to hosts that the insect could taste the host while its ovipositor was pressed against the non-host. At Rabbit Meadow, eggs are laid in clusters of 15–130, and each butterfly normally produces one cluster per day (Moore 1987), starting on the second or third day of adult life.

Experimental Design

We identified oviposition search behaviour of *E. editha* from a characteristic flight pattern in which the insects flew low over the vegetation, making a series of brief alightings in which they 'tasted' the plants by extending their atrophied foretarsi.

We selected square study plots (30 × 30 m) in which to observe oviposition search behaviour. Within area 1, the clear-cut, we selected two plots. Plot 1A contained both the novel host, *Collinsia*, and a non-host (*Chaenactis douglasii*, Asteraceae) that visually resembled the long-standing host *Pedicularis*. Plot 1B contained *Collinsia* but not *Chaenactis*. Although both subareas were located within the larger area used by Mackay (1985), plot 1B was more typical of Mackay's study area. Our study site on the outcrop, area 2, contained the long-standing host, *Pedicularis*. Our study plot in area 2 was in the centre of the 'upper' area used by Rausher et al. (1981) and was located where Mackay's (1985) butterflies had concentrated their search flight.

We sampled the vegetation using randomly located line transects. Each transect initiation coordinate was chosen from a table of random numbers. From each point so chosen, three transects, each 3 m long, were thrown in random compass directions. Within each plot, we threw transects until the variances of ground-cover estimates were less than 10% of the mean for each host species present. We threw 36 3-m transects in plot 2, 50 in plot 1A and 61 in plot 1B.

We obtained naive females by finding mating pairs in the field and ascertaining by inspection that the females were general (newly emerged). All had developed naturally on *Collinsia*. At our study population, insect density was high enough to ensure that virtually all females mated within an hour of emergence, before they had flown at

all. A small proportion of females mated for a second time, when several days old. Loss of scales from the underside of the forewing occurs during flight and can be used to identify insects that are more than a day old. By examining insects for scale loss we were able to reject females that were mating for the second time. The remaining matings involved females that had not indulged in search for oviposition sites, and had almost certainly not flown at all. These were the 'naive' females that we used in our experiments.

We marked naive females on the upper surface for easy identification in flight, and held them in spherical cages of 0.5 m diameter until the test flight. Preliminary trials showed that release of naive insects on day 2 of their lives did not usually result in immediate search behaviour. Releases on day 3 proved satisfactory. When days 2 or 3 were very cold, we released on day 4. Releases were made at the centre of each study area. To ensure that our naive insects searched for oviposition sites (rather than nectar) on their first flight, we kept them well fed on a mixture of sugars and amino acids (Murphy et al. 1983) as well as natural nectar. When flight commenced, we recorded the sequence of plant species on which the insects alighted. The few insects that failed to taste the plants on which they alighted were assumed not to be searching for oviposition sites and were not included in the analysis. Any ovipositions were recorded. Since these insects do not oviposit more than once per day, an oviposition indicated termination of search.

We located 'experienced' searchers by observation of typical search behaviour in the field. We waited in our study areas for searching insects to enter them, and recorded alights until each insect left the area. We used only butterflies with visible wing wear that would have already alighted naturally on the abundant plant species at the site, and would have laid eggs at least once, on days prior to our observations. Because we wished to observe natural behaviour we did not mark the 'experienced' searchers. Searching flight is slow and butterfly density low at any given time and place, so there was no problem of confusion of identity during the observation time. In consequence, we may have accidentally observed the same individual more than once, on different days. However, because the population comprised many thousands of individuals, repeat observations are not likely.

One possible source of error is a systematic difference between flight paths of naive and experienced insects that could stem from our experimental design. We released each naive insect close to the centre of the study plot, in order to be able to record as many alights as possible before the insect left the plot. Releasing it at the edge of the plot would have risked its immediate departure, a problem because the number of naive insects we could obtain was limited. In contrast, alights of each experienced insect were recorded from the moment it entered the plot, often starting at a margin of the plot, not necessarily at the centre. This could have brought about systematic differences between the vegetational composition under the flight paths of naive and experienced insects. To minimize such effects, we chose study plots with very homogeneous vegetation and released naive insects onto patches of bare ground, not onto plants. The alternative experimental design would have been to control for initial starting position by catching experienced females the evening before their test time, holding them in cages overnight to allow them to calm down, and releasing them alongside the naives. However, we cannot be sure that learned behaviour would be robust to these manipulations. Because the time delay since having the experience with host plants, as well as the trauma of being caught (Singer & Wedlake 1981), are both known to affect butterfly behaviour and memory, we chose what we considered the lesser of two errors, the least invasive most natural design, for our experiment.

Analyses

Definitions of terms

Proportional alighting and alighting bias. We use 'proportional alighting' to mean the number of alights of an individual on plant species 'a' divided by the total number of alights on all plants by that individual. The term 'bias' is used to mean the proportional alighting of the individual (or group) on plant species 'a' divided by the proportion of species 'a' in the vegetation (estimated as the mean proportion of 'a' in random transects). Therefore, bias describes the difference between the observed proportion of alighting on a plant species and the proportion expected from random alighting. For individuals (or groups) flying over

Table I. Categories of plant species in area 1

Category	Definition	Plant species
Host	The host species	<i>Collinsia torreyi</i> Scrophulariaceae
Small erect	Small, erect plants with entire leaves, other than <i>Collinsia</i>	<i>Linanthus ciliatus</i> Polemoniaceae <i>Gayophytum diffusum</i> Onagraceae <i>Polygnum douglasii</i> Polygonaceae <i>Mimulus whitneyi</i> Scrophulariaceae <i>Plagiobothrys</i> sp. Boraginaceae
Chaenactis	Rosette growth, bipinnatifid leaves	<i>Chaenactis douglasii</i> Asteraceae
Rosette	Rosette growth, entire leaves	<i>Viola nuttallii</i> Violaceae <i>Calyptidium umbellatum</i> Portulacaceae <i>Eriogonum nudum</i> Polygonaceae
Large erect	Standing above the rest of the vegetation, leaves entire or pinnate	<i>Phacelia hydrophyloides</i> Hydrophyllaceae <i>Lupinus fulcratus</i> Fabaceae <i>Monardella villosa</i> Laminaceae <i>Aster occidentalis</i> Asteraceae <i>Erysimum perenne</i> Brassicaceae
Other	Rare plants that did not fit into above categories	<i>Ceanothus velutinus</i> Rhamnaceae <i>Sitanion hansenii</i> Gramineae <i>Allium campanulatum</i> Amaryllidaceae <i>Symphoricarpos parishii</i> Caprifoliaceae

the same area, proportions of plant species available are the same. Therefore, differences between such groups in proportional alighting will reflect differences in alighting bias. This rationale was used to justify our use of proportional alighting in our study plots to search for differences in alighting bias between naive and experienced insects.

Search efficiency. To avoid biasing our conclusions simply by our choice of definitions of efficiency, we performed several independent analyses on different aspects of the data set. We analysed efficiency both in terms of (1) proportional alighting on host plant species and (2) rate per min of alighting on host plant species. We looked for changes in efficiency both within an individual over time and between groups with very different levels of past searching experience.

Learning. For this study, learning is defined as change in efficiency with experience. Adaptive learning is defined as an increase in efficiency of finding host plants with experience.

Analysis 1: test for overall differences between naive and experienced groups

The null hypothesis is that naive and experienced females do not differ in their alighting frequencies on the set of available plant species.

Several plant species were both rare in transects and received infrequent alightings. Estimates of bias towards these species have high variance. To increase the power of the test to distinguish differences between naive and experienced butterflies, we lowered the variance in alightings among individuals by grouping some of the rare species and performing the test on pooled data. We reduced the 19 plant species present in plots 1A and 1B into six categories (Table I).

An analysis of deviance (ANODEV) was performed (GLIM software package). This analysis used the log-linear model

$$\log(E(y_{ijr})) = E(y_{ijr}) + b_i + p_j + x_r + (px)_{jr}$$

where y_{ijr} is the number of alightings of butterfly i of type r on plant j ; $E(y_{ijr})$ is the expectation of y_{ijr} ; b_i is the individual butterfly effect; p_j is the plant category effect; x_r is the effect of experience; and $(px)_{jr}$ is the interaction between effects of experience and plant categories.

Since alightings are counts, the model assumes that the data are from an approximate Poisson distribution and in particular that $\text{var}(y) \propto E(y)$. This hypothesis would be rejected by significance of the interaction term, which would be interpreted as showing that naive and experienced butterflies were different in their alighting frequencies on the six plant categories. Because a

Poisson distribution, rather than a normal distribution, is assumed, exact P -values cannot be assigned. A difference is considered significant if it is greater than two standard errors away from the mean. If the stated hypothesis is rejected, the means are compared between the plant categories by a multiple comparisons test to determine which categories contributed significantly to the overall differences between experienced and naive females.

Analysis 2: test for adaptive learning within the population

The null hypothesis is that the proportion of alights on hosts by experienced females is not greater than that by naive females.

The category of host plant is of particular interest, since significantly greater bias towards the host in experienced than in naive insects would constitute evidence that host-finding efficiency improves with experience in a manner consistent with adaptive learning to find hosts.

This hypothesis is rejected if the results from the multiple comparisons test from 'analysis 1' show that alights by experienced females are significantly more biased towards the host species in a given plot than alights by naive females.

Analysis 3: test for adaptive learning within the first searching bout of naive females

Plots 1A and 1B. The null hypothesis is that there is no consistent trend through time for an increase in the probability of alighting on the host *Collinsia*.

The techniques of time-series analysis were used to test whether there was any significant trend for an increase in the probability of alighting on the host, *Collinsia*, from the first alighting of the first search by naive females to the last alighting of that same search. Such a positive trend through time would be an indication of learning on the part of some of the individuals. Probability of the i th alighting being on *Collinsia* was estimated from the proportion of all naive females that alighted on *Collinsia* at that point in the search sequence. Thus, the first data point for the time series, x_1 , is the proportion of females that alighted on *Collinsia* on the very first alighting of their very first search of their life. x_2 to x_N is this proportion for the second to N th alightings of the

set of naive search sequences. Since the total number of alightings made before the searching bout ended varied between individuals, the data points in the time series are not all obtained with the same sample size. The sample size began at 30 individuals and decreased to three individuals by the 45th alighting, which was the last used in the analysis.

The 'boxjenk' procedure of the statistical package RATS (Regression Analysis of Time Series, version 4.0, Estima), was used to apply the Box-Jenkins methodology (Box & Jenkins 1976) to find the model which best fits the time series. Because the data points in a time series are not independent, they tend to show an autocorrelation structure which invalidates standard regression techniques, that is, there is a lag structure in which x_i tends to resemble, or depend on, x_{i-1} (or x_{i-2}) and so on). Time-series models explicitly take this structure into account by testing for the presence in the predictive model of lag-variables (variables which represent past data points) and testing for the need to difference the data (convert the series of data points to the difference between data points). The Box-Jenkins methodology is an interactive process requiring (1) interpretation of the autocorrelation and partial autocorrelation structure of the time series to suggest parameters for the initial model, (2) analysis of the model by non-linear least-squares regression, and (3) modification of the model based on interpretation of the autocorrelation and partial autocorrelation structure of the residuals. The final model should contain as few significant parameters as is needed to obtain residuals which fit a random, white noise process. Specifically, the residuals should exhibit no autocorrelation.

Plot 2. The null hypothesis is that there is no difference in the probability of alighting on a host plant between the first alighting of the first oviposition search and subsequent alightings of the same search.

In this area (plot 2), a strong bias towards the host had been previously demonstrated (Mackay 1985). Use of time-series analysis was not possible because the females oviposited so quickly into their search that the number of alightings available for the series was considerably less than the 50 data points required for a valid analysis. We sought simply, then, to determine whether the bias towards *Pedicularis* was as strong on the very first

Table II. ANODEV results for the comparison of naive and experienced females

Source	<i>df</i>	Deviance	Mean deviance	<i>F</i>	<i>P</i> †
Plot 1A					
Experience	1	81.7	81.70	50.00	*
Individual	22	128.9	5.86	3.63	*
Plant category	5	152.1	30.40	18.80	*
Experience*plant category	5	36.0	7.20	4.45	*
Error	110	287.3	2.61		
Plot 1B					
Experience	1	19.5	19.50	8.55	*
Individual	41	630.1	15.40	6.75	*
Plant category	4	645.6	161.40	70.80	*
Experience*plant category	4	40.0	10.00	4.5	*
Error	167	380.11	2.28		

*Effects are at least two standard deviations away from the mean and are therefore significant at $P < 0.05$.

†*P*-values cannot be calculated exactly because a Poisson distribution was assumed and tabled *F*-values are based on a normal distribution.

alighting of the very first search by an adult as it was averaged over all subsequent alightings.

A log-likelihood ratio test was performed on a 2×2 contingency table with columns 'host/non-host' and rows '1st alights/subsequent alights'.

Analysis 4: test for differences among groups in rates of alighting on hosts and non-hosts

The null hypothesis is that the rate of alighting (in counts per min) on a given plant category is not different among the naive and experienced groups in areas 1 and 2.

Separate ANOVAs were performed for each vegetational category of interest, with alighting rate as the dependent variable and group/area affiliation as the independent variable, followed by multiple comparisons tests if overall significance was found.

RESULTS

Forty naive females were followed in area 1 (plots 1A and 1B) for an average length of time of 28.7 ± 15.9 min. In plot 2, 27 naive females were followed for an average length of time of 10.8 ± 12.1 min. Thirty-seven experienced females were followed in area 1 (plots 1A and 1B) for an average time of 7.5 ± 6.9 min. In plot 2, eight experienced females were followed for an average

of 11.1 ± 2.6 min. For naives, significantly more of the searches resulted in ovipositions on *Pedicularis* in plot 2 than on *Collinsia* in plots 1A and 1B: 89% oviposited in area 2 and 20% in area 1 (Fisher's exact test: $P < 0.001$). Among experienced females, there was a non-significant trend in the same direction: 50% oviposited in area 2 and 14% in area 1 (Fisher's exact test: $P = 0.067$).

Because of variation in the quality of data between individuals, some females were eliminated from some of the following analyses. Some females were missing time data either partially or entirely, so could not be included in any rate analyses. Females that alighted fewer than five times were not included in the ANODEV, but some were included in the time-series analysis and distribution analysis.

Analysis 1: test for overall differences between naive and experienced groups

Naive females alighted differently overall from experienced females in plots 1A and 1B, as indicated by a significant interaction term for the effects of experience and plant category (Table II). The significant differences were: (1) in plot 1A, experienced females alighted more often on small erect plants and less often on large erect plants than did naive females; there were no significant differences in the other four categories; (2) in plot 1B, naive females alighted half as often as

experienced ones on the non-host 'rosette' category (comprised mainly *Calyptridium*), slightly less on small erect plants and slightly more often than experienced ones on both of the other non-host categories. Because only eight experienced individuals were tested in plot 2, and most of the data were from three individuals, no overall comparisons between naive and experienced groups were made there; we limited our analysis to alighting frequencies on the two host-plant species (analysis 2 below).

Naives in plot 1B alighted randomly with respect to all four non-host categories. All three other classes of butterfly in area 1 (plot 1A, naive and experienced; plot 1B, experienced) exhibited significant biases away from large erect plants and towards the non-hosts most resembling the host, *Pedicularis*, these being *Chaenactis* (strongest bias) and other plants having a rosette growth form (weaker bias). Naives in plot 2 showed a similar trend, alighting significantly more often than random on rosette-shaped plants and significantly less often than random on large erect plants.

Analysis 2: test for adaptive learning within the population

There was no support for the hypothesis that experienced females were more efficient in finding either host species. In plot 1A, there was no significant difference between the naive group and the experienced group in frequency of alightings on the host *Collinsia* (Table III). In plot 1B, experienced females alighted on *Collinsia* 12% of the time, significantly less often than naive females (at 16%; Table III). Two separate Student's *t*-tests were performed on proportional alightings (normalized by arcsine square-root transformations) on *Pedicularis* and *Collinsia* by naive and experienced females in plot 2 (Table III). Naive females were not significantly different from experienced in their alightings on either of the hosts. Naive females alighted 44% of the time on *Pedicularis* compared with 45% for experienced females ($N=27$ naive, 8 experienced, $P=0.92$). This corresponds to a bias of 4.8 for both naive and experienced butterflies. This value is exactly the same bias as found by Mackay (1985) for naturally searching (i.e. 'experienced') females in the same area. (Mackay's data were reformulated to examine only vegetational alightings; also, Mackay's flight path data were used to compute expected

values because the flight paths geographically corresponded to our 'plot 2', whereas his random transects extended into adjacent habitat.)

Experienced females in plot 1B and both classes of female in plot 1A showed trends towards avoidance of their local host, *Collinsia*. This trend reached significance only for experienced females in plot 1A (Table II) where *Collinsia* comprised 14% of the vegetation but received only 6% of the alightings by females. In plot 2, alights by both naive and experienced females were significantly biased towards the host *Pedicularis* (alighting nearly five times as often as random), but were random with respect to *Collinsia* (Table III).

Analysis 3: test for adaptive learning within the first searching bout of naive females

Area 1. The data set consisted of the proportions of alighting on the host plant *Collinsia* for each point of the sequence from the 1st to the 45th alighting of the first flight of naive females. Alight sequence data from 32 individuals from plots 1A and 1B were pooled to give the proportion of females that alighted on *Collinsia* at each alighting count. The actual time series is shown in Fig. 1.

The sequence itself showed significant autocorrelation (Ljung-Box $Q: Q_{20}=32.4, P<0.04$). The 95% out-of-bounds limits for the autocorrelations and partial autocorrelations was ± 0.30 . None of the autocorrelations was out-of-bounds and only one of 20 of the partial autocorrelations was out-of-bounds. These results indicate that the underlying process that generated the series is random (Chatfield 1989) and that there is no need to difference the series before performing the regression (i.e. there are no missing lag variables; Box & Jenkins 1976).

To determine the cause of the mild but significant autocorrelation of the series, the data were tested for fit to the non-linear model $y_t = \mu + e_t$, where y_t is the proportion of alights on *Collinsia* for the t th alighting, μ is a fixed mean, and e_t is the error term. The parameter reached convergence in two iterations giving a value of $\mu=0.07, P<0.001$. The resulting residuals showed no autocorrelation structure (Ljung-Box $Q: Q_{25}=35.1, P=0.09$). If a time parameter ' T ' is forced into this model, convergence is reached in 24 iterations and ' T ' comes out as non-significant at $P=0.93$. Thus, the best model is that of a fixed probability of alighting on *Collinsia* around which there is

Table III. Proportions of each of six plant categories in naive and experienced alightings and in random transects

	Pedicularis	Collinsia	Chaenactis	Rosette	Small erect	Large erect	Other	N
Plot 1A								
Naive	—	0.10 (0.02) ^{ab}	0.16 (0.05) ^a	0.14 (0.04) ^a	0.10 (0.01) ^a	0.42 (0.06) ^c	0.10 (0.03) ^a	12
Experienced	—	0.06 (0.03) ^a	0.21 (0.06) ^a	0.12 (0.06) ^a	0.30 (0.06) ^b	0.22 (0.07) ^a	0.08 (0.04) ^a	12
Random transects	—	0.14 (0.02) ^b	0.01 (0.004) ^b	0.02 (0.005) ^b	0.16 (0.02) ^a	0.63 (0.04) ^b	0.05 (0.02) ^a	34
Plot 1B								
Naive	—	0.16 (0.04) ^a	—	0.07 (0.03) ^a	0.48 (0.04) ^a	0.24 (0.03) ^a	0.05 (0.01) ^a	20
Experienced	—	0.12 (0.05) ^b	—	0.17 (0.03) ^b	0.54 (0.06) ^b	0.15 (0.05) ^b	0.02 (0.01) ^b	22
Random transects	—	0.14 (0.02) ^{ab}	—	0.04 (0.01) ^a	0.51 (0.03) ^{ab}	0.30 (0.02) ^a	0.01 (0.007) ^{ab}	36
Plot 2								
Naive	0.44 (0.07) ^a	0.14 (0.04) ^a	—	0.21 (0.05) ^a	0.06 (0.03) ^a	0.15 (0.03) ^a	0.004 (0.004) ^a	27
Experienced	0.45 (0.14) ^a	0.16 (0.12) ^a	—	0.11 (0.07)	0.11 (0.08)	0.17 (0.08)	0 (0)	6
Random transects	0.08 (0.03) ^b	0.24 (0.04) ^a	—	0.07 (0.02) ^b	0.09 (0.02) ^a	0.52 (0.05) ^b	0.007 (0.002) ^a	42

Standard errors are in parentheses. Superscript letters show significant differences ($P < 0.05$) between estimated proportions of each plant category in butterfly alights and/or transects (within each plot).

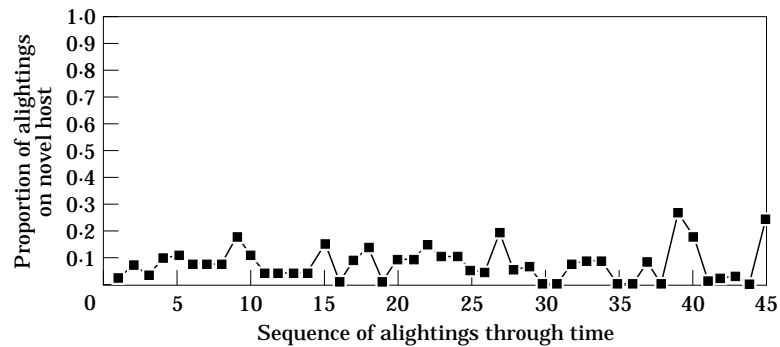


Figure 1. A Box–Jenkins time-series analysis was used to estimate changes through time in the probability of alighting on the host, *Collinsia*, estimated as the proportion of initially naive females that alighted on *Collinsia* at the M_h alighting of their first host search, where N is the number on the abscissa. We used data from 32 females in plots 1A and 1B, from the first alighting up to a maximum of the 45th alighting of the same search. There are fewer females represented at the right of the figure than at the left, because not all females were observed for 45 alightings; some either oviposited or left the study plot before this point in their search. We found no significant increase over time in the probability of alighting on *Collinsia* ($P=0.93$).

Table IV. Rates of alighting as counts per min on different vegetational categories

	Area 1 (plots 1A and 1B)		Plot 2	P	df
	Experienced	Naive	Naive		
On all vegetation	3.18 ^a	1.39 ^b	1.12 ^b	0.001*	2,81
On host, <i>Collinsia</i>	0.18	0.13	0.08	0.35	2,81
On host used in that area		0.13 (<i>Collinsia</i>)	0.38 (<i>Pedicularis</i>)	0.008*	1,54

Analyses were by ANOVA. Small letters which are the same in a row indicate no mean difference by Fisher's least significant difference multiple-comparisons test.

*Statistically significant.

random noise. These results indicate that the probability of alighting on *Collinsia* remains constant through time for an individual.

Area 2. Frequency of first alights on the host *Pedicularis* in plot 2 (35.7%), was not significantly different from the frequency in all subsequent alightings of the same search sequences (22.1%, $N=28$ butterflies, 164 total alights; $G=2.196$, $df=1$, $P=0.13$).

Analysis 4: differences among groups in rates of alighting on hosts and non-hosts

Because the abundance of *Collinsia*, the sole host present, was the same in plots A and B of area 1, individuals within groups were pooled. The results of all three analyses are shown in Table IV. With respect to all alightings on veg-

etation, the experienced group alighted significantly more often than the naive groups of either plots 1A and 1B or plot 2. The naive groups from the two areas did not differ significantly from each other. With respect to the host, *Collinsia*, there were no significant differences among groups. Between the naive groups, females in area 2 alighted significantly more often on the host used in that area, *Pedicularis*, than females in area 1 alighted on the host used in that area, *Collinsia*.

Post-hoc analyses: test for presence of a minority group of females in area 1

The null hypothesis that variation among individuals in the proportion of alights on *Collinsia* is random around a fixed mean probability of alighting on *Collinsia* was tested.

The three analyses looking for evidence of learning were concerned with average differences among groups or pooled data. Efficient search was found only for the host plant *Pedicularis*; no evidence for efficient search of the host *Collinsia* was found on any level. However, if there were two categories of females, those which alighted randomly on *Collinsia* and a minority that were biased towards *Collinsia*, the previous analyses might camouflage the presence of the minority. To look for the presence of a group of females that alighted preferentially on *Collinsia*, whether from learning or fixed preference, we wished to look at the distribution among individuals of the proportional alightings on *Collinsia* and test whether this distribution could have been generated from a random process. If all individuals had been watched for a fixed number of alightings, we could have viewed each alighting as a Bernoulli trial with 'success' being alighting on a *Collinsia* host plant and 'failure' as alighting on any other substrate. Each female would then have yielded k successes in N trials, and this distribution of k s could have been tested against a theoretical binomial distribution of k s in N trials with a fixed probability of success, P . Because N is different for each female, however, two alternative analyses were used.

Analysis 5

Although we cannot compare proportional alightings of all females to a single binomial distribution, we can ask whether the proportional alightings on *Collinsia* by each individual treated separately lies within the 95% confidence interval of a binomial distribution with a given P and N . If all individuals are behaving according to the same rules, and conclusions from analyses 1–4 are correct (that females do not recognize *Collinsia* as a host in flight and alight on it only by random chance), then the probability of alighting on *Collinsia* for each Bernoulli trial (each alighting) should be equal to the proportional abundance of *Collinsia* in the habitat. Therefore, we took $P=0.14$ as the theoretical probability value against which we tested j sets of trials ($j=66$ females) for the probability of k successes over N_i trials ($i=1$ to j). Software developed by Bill Engels, University of Wisconsin, was used to calculate the two-tailed probabilities of getting k or a more extreme value. Since we did j such tests, we used a Bonferonni correction for the α -value of

each set to give an overall $\alpha=0.05$. None of the 66 females exhibited a number of alightings on *Collinsia* that was significantly different from that expected from a fixed probability of alighting on *Collinsia* of $P=0.14$.

Analysis 6

If P is small and N is large, counts of events occurring in discrete intervals will be distributed as Poisson. Our data set approximately fits this scenario if we view the intervals as values of proportional alightings on *Collinsia* and the counts as numbers of females which fall into those intervals. Our null hypothesis is that alightings on *Collinsia* are random and that the probability P of alighting on *Collinsia* is governed by the proportion of *Collinsia* in the habitat, which is the same for plot 1A as plot 1B and equals 0.14. Since P is the same for plots 1A and 1B, we combined naive and experienced individuals into one data set giving $N=66$. Thus, our data fit the criteria of small P and large N , with the only potential problem being that, as the intervals represent proportions, they are truncated at 1.0 instead of extending into infinity as in a theoretical Poisson distribution. We did not judge that this truncation invalidated the analysis. Females were categorized according to the proportion of alightings on *Collinsia* and the distribution of these proportions was plotted. The null hypothesis predicts that this distribution should resemble a Poisson distribution with a fixed mean probability of alighting on *Collinsia*, about which individuals vary randomly. The presence of a set of females which are different from the rest in having a real bias towards alighting on *Collinsia* would pull this distribution to the right and result in a more normal or even a bimodal (Rausher 1978) distribution.

The test statistic used was variance $\times (N-1)/$ mean $\sim \chi^2 (N-1)$ (Cox & Lewis 1966). Visual inspection of the distribution (Fig. 2) shows that it is clearly not bimodal and that, in fact, the null hypothesis that the distribution is Poisson is accepted ($\chi^2=15.29$, $df=65$, $P>0.995$).

DISCUSSION

Evidence Against Adaptive Learning in Foraging by *E. editha*

By three criteria, the butterflies failed to show evidence of adaptive learning. First, the only

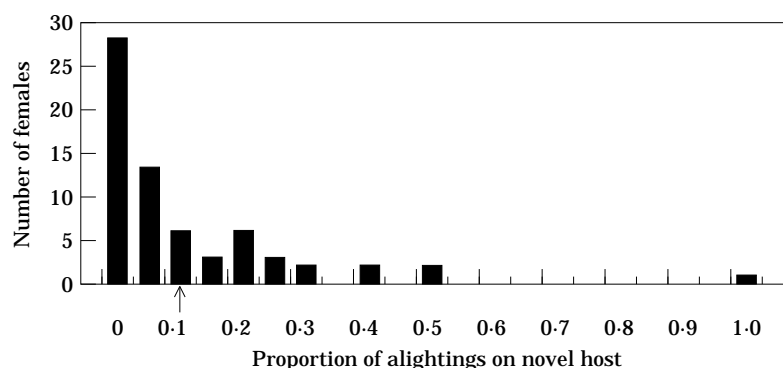


Figure 2. Distribution of the proportion of alightings on *Collinsia* by all females ($N=66$) in area 1 (naive and experienced in both plots 1A and 1B). This distribution does not differ from Poisson ($P>0.995$). X-axis numbers are the lowest value included in that interval. The arrow represents the mean of the data.

significant difference between naive and experienced insects in alighting bias towards either of the two host species was in the opposite direction to that predicted if insects learn to find hosts: in plot 1B, experienced females alighted on the host, *Collinsia*, 12% of the time, significantly less often than did naive females (16%; Table III). Second, naive and experienced females did not differ in the rate per min of finding host plants (Table IV). Finally, no evidence of improvement in finding either host species was shown in the time trajectories of alighting bias by individual naive females as experience increased from the first host search alighting of their lives (Fig. 1, see below).

The probability of alighting on the novel host, *Collinsia*, began at a low value and remained constant throughout the alighting sequence (Fig. 1). The probability of alighting on the traditional host, *Pedicularis*, was high in both naive and experienced insects. Because single-trial learning is known in insects (Traynier 1984; Papaj 1986b), we asked whether *E. editha* searching among *Pedicularis* learned to find this species after a single alighting on it. These insects may have had an evolved ability to associate the shape of their long-standing host plant with a fixed internal chemical template (Papaj 1986a), using only a single encounter. In this study, however, a female was just as likely to land on the attractive host, *Pedicularis*, on the very first alighting of her life as she was subsequently. This finding fails to support the hypothesis of single-trial learning. In fact, the non-significant trend in our data set is in the opposite direction to that expected if efficiency of finding improved after the first alighting.

These results are all consistent with the hypothesis that the probability of alighting on each host species was fixed prior to the first alighting, rather than increasing as a consequence of host encounter. Previous work testing influence of experience on oviposition by *E. editha* has been concerned only with post-alighting preference (Singer 1986; Thomas & Singer 1987). Using insects from Rabbit Meadow, these workers asked whether a series of staged encounters with either *Collinsia* or *Pedicularis* affected subsequent insect responses. They could find no effect of experience on acceptance of encountered plants.

Possible Cause of Differences in Alights on Non-hosts

In both plots 1A and 1B, there were significant differences in proportional alighting between individuals within a group. This finding, however, is probably trivial, resulting simply from the fact that different individuals followed different flight paths that took them over different sets of plants. This argument does not account for the significant differences between alighting biases of naive and experienced insects towards some categories of non-host plants. Because we found these differences, we cannot state that no learning occurred, but merely that any learning did not result in increased efficiency of host-finding, that is, it was not adaptive.

Results in Light of Learning Theory

None of the butterfly species that has been studied visited its eggs after oviposition. Hence,

they receive no feedback about the consequences of their decisions for offspring fitness. Thus, less information can be obtained during oviposition than during feeding, when the organism receives internal feedback relevant to its fitness. A female butterfly derives no obvious benefit from a learned post-alighting preference for a resource on which it has already laid eggs (Rosenheim 1993). However, if during oviposition the insect learns to handle the resource more efficiently, an increased preference for that resource could be a benefit in terms of lower time costs, increased rates of oviposition and decreased risk of predation. Some butterfly species do learn to find preferred oviposition sites (Rausher 1978; Stanton 1984; Traynier 1984), but we know of no evidence that they learn how to exploit those sites after finding them, as do butterflies feeding on nectar (Lewis & Lipani 1990). Hence, the sole established reason for learning during oviposition search is that the learned associations between visual and chemical stimuli increase the rate of host encounter, as in *B. philenor*.

Possible Reasons for the Lack of Adaptive Learning in *E. editha*

If the arguments of Rausher (1978) and Stephens (1993) are correct, the restriction of *E. editha* to a single short flight season and the history of high environmental predictability at Rabbit Meadow lead us to expect that learning should be less important in our study than in others. Roitberg et al. (1993) predicted that learning should occur when many decisions are made, each with a small effect on fitness. Fixed behaviour is expected when few decisions are made, each with a large effect on fitness. This prediction also fits our findings, because Rabbit Meadow *E. editha* make only one oviposition decision per day (Moore 1987), each of which has a large effect on fitness (Moore 1989).

Implications for Evolution of Diet Breadth

Both naive and experienced butterflies showed consistent strong bias towards their long-standing host, *Pedicularis*, and the non-host that resembled it, *Chaenactis*. Where *Pedicularis* was present, nearly one-half of the females' alightings were on this host, although this plant species only comprised 8% of the vegetation. Similarly, where

Chaenactis was present, females alighted on this species up to 20 times more often than random, and did not learn to avoid it, although they never oviposited on it. Thus, the insects that lived in patches of *Collinsia* (such as area 1 of our study) wasted time and energy alighting on *Chaenactis*. This tendency of insects in a subpopulation using a novel host to alight on plants resembling the ancestral host must be a constraint to the evolutionary expansion of diet. In this case, colonization of *Collinsia*, in spite of failure to find it efficiently, requires that it be present abundantly in large patches, as it is at Rabbit Meadow. Since most of the *E. editha* in area 1 did recognize *Collinsia* as a host after alighting (Singer et al. 1992), associative learning similar to that of *B. philenor* would assist the colonization of the novel host. Because such learning would increase efficiency of search for *Collinsia*, it would increase fitness of insects using this host and thereby assist in the maintenance of populations on the novel host in the face of gene flow from areas (such as area 2) where the traditional host is still used. So, although associative learning may have been of little use to Rabbit Meadow *E. editha* when they were monophagous on *Pedicularis* prior to human intervention, its potential usefulness has recently increased. The evolutionary constraint on expansion of diet breadth resulting from lack of learning would be mitigated if the population contained genetic variation for alighting bias towards *Collinsia*. Such variation would allow evolution of alighting bias in response to selection for efficient host search. Although we do not have genetic evidence, there is no evidence for the presence of a minority phenotype that perceives *Collinsia* as a host in flight (Fig. 1).

This constraint appears to operate only in the short term. Parmesan (1991) showed that another population of *E. editha*, known as Schneider's Meadow, was able to evolve the ability to search efficiently for the host *C. parviflora*, a visually similar species to *C. torreyi*. Additionally, this population had the ability to alight better than randomly on a second host, the introduced weed *Plantago lanceolata*, which they had colonized within the past 100 years. The implications of this study are that (1) the inability of *E. editha* to learn to recognize *C. torreyi* in flight is not due to an inherent difficulty with perceiving that particular visual stimulus and (2) at the population level, it is possible to find efficient search for more than one

host species, even when these species are very dissimilar in visual appearance. If these two populations are representative of the abilities of the species as a whole, then the inability to learn new visual stimuli associated with hosts represents a short-term constraint to host switches. Failure to learn impedes use of novel hosts within an individual's lifetime, but does not necessarily impede the incorporation of the novel host into the population's diet over a long-term evolutionary time scale.

Conclusion

No other examples of absence of adaptive learning in insect foraging have been described (Papaj & Prokopy 1989). We do not know whether this is because no similar examples have been found, or because such findings have been considered uninteresting and have remained unpublished. Rosenheim (1993) argued that failure to publish such 'negative' results could have caused major bias in the literature on insect learning. One possible reason for the lack of similar findings is that most other work has been done under controlled conditions rather than in the field. Insects that learn in the laboratory in response to relatively simple stimulus-configurations may fail to show detectable adaptive learning in the much more complex field environment.

Jaenike & Papaj (1992) presented a model that predicts diets of insects in which post-alighting preferences are variable, and may or may not be influenced by learning. The properties of their 'non-learning' insect correspond quite well to those known for *E. editha*. The model predicts how learning and non-learning insects will differ in their responses to variable encounter rates with hosts of variable acceptabilities. These predictions can be tested by empirical comparisons between learning and non-learning insects. We suggest that *E. editha*, in which learning appears to be absent or insignificant in both pre- and post-alighting host choice, would make an excellent candidate for a non-learning insect in which models such as that of Jaenike and Papaj could be tested.

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