



Article

No Effect of Early Adult Experience on the Development of Individual Specialization in Host-Searching Cabbage White Butterflies

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Abstract: Individuals in a population often use unique subsets of locally available resources, but we do not entirely understand how environmental context shapes the development of these specializations. In this study, we used ovipositing cabbage white butterflies (*Pieris rapae*) searching for host plants to test the hypothesis that early experience with an abundant resource can lead to later individual specialization. We first exposed naïve butterflies to one of three environments with different relative abundances of host plants of comparable nutritional quality, cabbage and radish. The next day, we observed butterflies from all treatments searching for hosts in a common environment where cabbage and radish were equally abundant. We predicted that the butterflies would preferentially visit the host plant that had been abundant during their previous experience, but instead found that butterflies from all experience treatments visited cabbage, a likely more visually salient host, more often than radish. In this experiment, behavioral plasticity in current conditions outweighed developmental experience in shaping individual resource use. We argue that these butterflies potentially respond to particularly salient search cues and that the discriminability of a resource may lead to specialization bias independent of early life experiences with abundant resources.

Keywords: plant-insect interactions; individual specialization; behavioral plasticity; learning



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1. Introduction

Resource use is an important component of most ecological and evolutionary processes. Within populations, individuals may specialize in specific resources, using only a fraction of the population niche width [1]. Individual specialization is widespread across taxa [2]: for example, some birds and frogs show consistent individual differences in diet [3,4], predatory wasps specialize on certain prey species [5], and foraging bees specialize on certain flower species, even when equally valuable flowers are also available [6,7]. Understanding the causes of such intraspecific variability in resource use is relevant to understanding ecological interactions [8,9], ecosystem functioning [10] and evolutionary dynamics [11]. Inter-individual variation in resource use can sometimes be explained by age, sex, or morphology [12–14], but there is still variation in resource use specialization within these categories [15–17]. It is quite possible that individual variation in an ecological context could explain this further variation in individual specialization [18]. This research builds on recent efforts to begin to understand how experience shapes the development and maintenance of individual specialization [2,19].

Early life experiences may shape the development of individual specialization. A handful of existing studies have shown that early experience with a given resource assemblage can shape later foraging preferences, most likely through learning. For example, in birds, earlier experiences with specific prey types or foraging modes can shape later life foraging specializations [20,21]. In otters, the diet specializations of individuals more closely

resembles those of their mothers than other members of the population [17]. Such examples of experience-dependent resource specialization are likely explained by learning—developmental plasticity in behavior [22]. Learning can affect foraging behavior through more efficient handling time or resource search [23–25]. If experience with a certain resource ultimately leads to increased foraging or digestive efficiency over time, this resource may become preferred [26,27]. In some ways, individuals develop behavioral, morphological, or physiological “expertise” with particular resources, such that initial experience biases subsequent preference and performance [28]. For example, in swallowtail butterflies, it has been suggested that early adult experience with a given locally abundant host plant species leads to learned search images for different leaf shapes and divergent individual specializations [29,30].

This research builds on existing studies on how experience shapes resource use, with a case study on butterfly host searching. We test the hypothesis that individual variation in resource use can be explained by early life differences in resource abundance. If a particular resource is abundant relative to others and is thus encountered more frequently, these encounters could lead to positive reinforcement of the cues or handling behavior associated with the common resource. Insects, for example, can change preference in response to encounter rates through learning [31–33]. Because learning new information or new skills requires time and energy, when animals encounter new environments or experience a change in their environment, they may retain preferences from earlier environments. Learned resource preferences can be maintained over the course of a foraging bout, a season, or even a lifetime [5,34,35]. Even within a group of animals, there is variation in the time course of resource specialization; for instance, some individual bees maintain pollen specializations for hours, and some for their lifetime [36]. By experimentally contrasting the effects of previous versus current resource environment, we can build a more general understanding of why experience shapes individual specialization over diverse time courses.

We tested the hypothesis that early experiences in environments with different relative resource abundances can produce individual specializations in a common environment. More specifically, we predicted that naïve individuals would form preferences for resources that were abundant in their early adult environment and preferentially visit those resources in subsequent environments where resources were equally abundant. We tested these predictions by observing the host plant choices of individual cabbage white butterflies (*Pieris rapae*) in environments where two different species of host plants (radish and cabbage) varied in their relative abundance. We then observed these same butterflies in a common environment, where radish and cabbage were equally abundant. Cabbage whites are a good model to explore the effects of early adult experience on host choice because associative learning plays a role in host searching, with individuals remembering color cues over multiple days [24,37,38]. Cabbage whites often show individual variation in host plant and floral preferences [39,40] and they are experimentally tractable in terms of controlled lab rearing and adult behavioral observations [40,41]. Given that these butterflies use associative learning to discriminate host plants from non-host plants, we predicted that the butterflies would learn the cues associated with the most abundant host in their early environment and retain those cues on their second day of foraging, preferentially landing on that host over others.

2. Methods

2.1. Overview

To manipulate a butterfly’s experience with different relative host abundances, we allowed mated, naïve female butterflies to search for host plants in one of three “treatment” arrays: one where cabbage was abundant and radish was rare (3:1 ratio), one where cabbage and radish were equally abundant (1:1 ratio), and one where radish was abundant and cabbage was rare (1:3 ratio). After 24 h, butterflies from all three treatments were allowed to search for host plants in a common “test” array where cabbage and radish were equally

abundant. During both the treatment phase on Day 1 and the test phase on Day 2, a single observer (MKS) recorded the number of landings a single butterfly made on host and non-host plants while searching.

2.2. Care for Experimental Butterflies

The butterflies used in this experiment were host-naïve offspring of wild-caught cabbage whites (*Pieris rapae*) captured in June and July 2015 on the Saint Paul campus of the University of Minnesota. To rear these experimental individuals, wild-caught females were placed inside a mesh 60 × 60 × 60 cm “bug dorm” and allowed to lay eggs on store-bought organic cabbage leaves with a non-host plant for humidity and a sponge soaked in 10% honey water for food. Leaves with eggs were transferred to a climate chamber (23 degrees Celsius, 14L:10D, 60% relative humidity) and, after 7 days, early second instar caterpillars were transferred to artificial diet [40]. Caterpillars remained in the climate chamber on artificial diet until they emerged as adults. Each adult was given a unique ID number, written in fine-tipped black sharpie on its wings. Each butterfly was then placed in a glassine envelope and stored in a refrigerator at 6 °C for up to 3 days. Butterflies were then transferred to the bug dorms (10 males, 10 females) for mating for 48 h. From there, mated female butterflies were removed and observed in one of three treatment arrays. After observation, these female butterflies were retired to a bug dorm with a honey water sponge and non-host plant for the evening and then observed in the test array the following day. All experimental females had no host plant experience when they first entered the test arena.

2.3. Care for Plants

We used two host plants (cabbage: *Brassica oleraceae* var. *Earliana* and radish: *Raphanus sativus* var. *Cherry Belle*) and four non-host plants (Swiss chard: *Beta vulgaris* var. *Foordhook Giant*, basil: *Ocimum basilicum*, tomato: *Solanum lycopersicum* var. *Patio Princess Hybrid* and red lettuce: *Lactuca sativa* var. *Rouge d’Hiver*) in our experiment, all grown from seed in greenhouse facilities at the University of Minnesota. We planted seeds in small trays and, after two weeks, transferred seedlings to larger 5” × 5” × 2.65 L pots with Sunshine® Professional Growing Mix 15/LC15. One day after transfer, plants were fertilized with 6 g of Osmocote® Classic 14-14-14 N:P:K fertilizer and treated with 1/3 tsp of OHP Marathon 1% Granular pesticide to protect plants from greenhouse pests. The first seeds were planted in late May and a new cohort of seeds was sown every two weeks through early July in order to have fresh plants for butterfly choice. Plants were used in experimental arrays when they were approximately 40 days old. Although all six species of plants were relatively similar sizes and heights, any non-host plants that were markedly higher than others were cut to size to standardize structural complexity of the environment in all assays.

2.4. Experimental Arrays

In all treatment and test arrays, 24 potted plants were arranged in a 6 × 4 array inside a 2 m × 3 m × 1.6 m (height) flight cage. Absolute host abundance was constant across arrays: there were always 12 host plants and 12 non-host plants (3 plants each of basil, Swiss chard, tomato and red lettuce). To avoid forming patches due to random placement of plants, we systematically assigned locations to all hosts and non-hosts. All host plants always had adjacent non-host neighbors and diagonal host neighbors. All non-host plants were placed such that individuals of the same species were as far from each other as possible (Figure 1). In treatment arrays where cabbage and radish were equally abundant, host plants had diagonal neighbors of a different species (Figure 1A). In treatment arrays where one host was rare, the three individuals of that host were placed such that there was one in every other row and all were never in the same column (Figure 1B). The Day 2 test array was exactly the same as the Day 1 treatment array, where cabbage and radish were equally abundant.

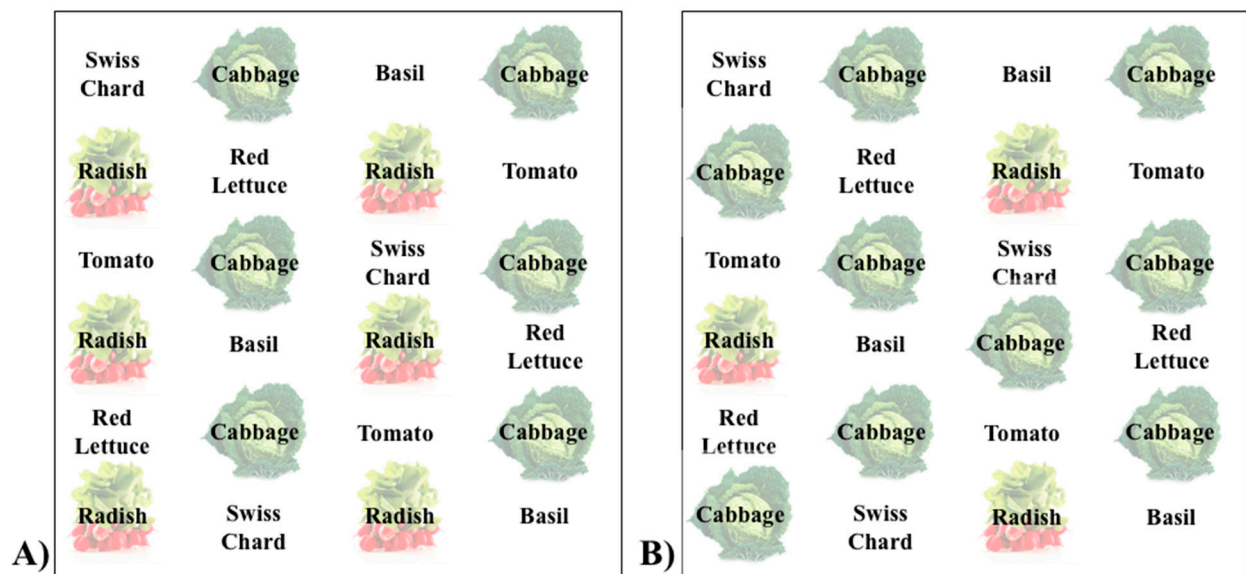


Figure 1. Arrangement of host plants (cabbage and radish) and non-host plants (red lettuce, Swiss chard, tomato, basil) in experimental arrays. (A) This arrangement was used for the Day 2 test array and for the Day 1 treatment array where cabbage and radish were equally abundant. (B) This arrangement was used for the Day 1 treatment arrays when a host was rare, in this case with radish as the rare host.

2.5. Behavioral Measurements

Behavioral observations were the same across all treatment and test arrays. An observer (MKS) sat inside the experimental flight cage and released individual females into the cage by placing them on a randomly assigned host plant in order to motivate host search behavior. If a butterfly did not immediately begin to search for host plants, it was excluded from the study. If the butterfly began to search, it was allowed to continue until it had made 20 landings on host plants. A “landing” was identified as tarsal drumming on the leaf of a plant, a behavior indicating that butterflies are evaluating plant chemistry using contact chemoreception [38]. Tarsal drumming on a host plant is usually followed by “oviposition” which was scored separately from “landing” because the former is a pre-alighting choice (largely visual) and the latter, a post-alighting choice (largely tactile). The likelihood that butterflies will oviposit on a host plant after landing on it (“acceptance rate”) is similar for both radish and cabbage [40]. The observer continuously recorded landings and ovipositions, the species of plant each behavior was associated with, and the time they occurred using the software, Jwatcher, on a laptop computer [42]. All observations were completed between 10 am and 3 pm on sunny days in July and August, 2015.

To quantify a butterfly’s tendency to land on cabbage vs. radish, we calculated a “landing preference”, defined here as the likelihood that a butterfly will land on cabbage upon encountering it, assuming that butterflies encounter resources in proportion to their abundance in the environment. “Landing preference” during a foraging bout of 20 host landings was calculated by scoring cabbage landings as “1” and radish landings as “0” and calculating an overall probability of landing on cabbage. In our graphs, however, we chose to leave “landing preference” as the raw number of cabbage landings in 20 total host landings to make interpretation more visually intuitive.

2.6. Statistical Analysis

All statistical analyses were performed using R version 3.3.3. We used generalized linear mixed effects models using the lme4 package [43] to model the probability of landing on cabbage on Day 2 as a function of Day 1 treatment with individual as a random effect. To understand whether butterfly landing patterns departed from the ratio of host plants in each of the relative abundance treatments, we calculated the mean proportion of cabbages

that butterflies visited in each treatment and compared those values to the proportion of cabbages in the environment. We created 95% bootstrapped confidence intervals around the mean proportion of cabbage landings for each treatment and looked at whether the proportion of cabbage in the environment (0.25, 0.50 and 0.75 respectively) fell within these confidence intervals. To explore how butterfly landing preferences and foraging ability changed with experience, we restricted our analysis only to butterflies that experienced the same resource environment over two days: those in the treatment where cabbage and radish was equally abundant. We modeled (1) probability of landing on cabbage as a function of Day with individual as a random effect and (2) a butterfly's accuracy (number of non-host landings in 20 host landings) as a function of Day with individual as a random effect.

3. Results

A total of 65 butterflies completed behavioral trials across two days. On Day 1, 20 of these butterflies searched in environments where cabbage was abundant, 20 butterflies searched in environments where cabbage and radish were both equal and 25 butterflies searched in environments where radish was abundant. On Day 2, all 65 butterflies searched in environments where cabbage and radish were equally abundant.

3.1. Day 1: Confirming That Butterflies Have Different Host Plant Experiences across Treatments

We first sought to confirm that our treatments resulted in differences in experience with the two host plant species (Day 1). Butterflies searching in the cabbage-abundant environment exhibited a higher probability of landing on cabbage than butterflies searching in the environment where both hosts were equally abundant ($B = 0.894$, $p < 0.001$) and where radish was abundant ($B = 1.750$, $p < 0.001$). Butterflies foraging in environments where both hosts were equally abundant exhibited a higher probability of landing on cabbage than in environments where radish was abundant ($B = 0.856$, $p < 0.001$). Taken together, these results indicate that the butterflies were more likely to land on cabbage as it increased in abundance in the environment (Table 1, Figure 2—day 1), confirming that our environmental manipulations provided the butterflies with different experiences with host plants.

Table 1. Results of post hoc Tukey comparisons predicting a butterfly's probability of landing on cabbage. On Day 1, butterflies foraged in one of three environments that differed in the relative abundance of host plants radish and cabbage. On Day 2, these same butterflies foraged in a common environment where the two hosts were equally abundant.

Relative Abundance Comparisons	β	SE	z	p-Value
Day 1: Different Environments				
Cabbage Abundant-Equal Abundance	0.894	0.144	6.230	<0.001
Equal Abundance-Radish Abundant	0.856	0.146	5.866	<0.001
Cabbage Abundant-Radish Abundant	1.750	0.147	11.870	<0.001
Day 2: Common Environment (comparisons refer to Day 1 experiences)				
Cabbage Abundant-Equal Abundance	0.062	0.141	0.440	0.899
Equal Abundance-Radish Abundant	0.098	0.147	0.662	0.785
Cabbage Abundant-Radish Abundant	0.160	0.140	1.139	0.490

We additionally tested whether the butterflies exhibited any kind of preference for one host type over another by testing whether the butterflies landed on cabbage in proportion to their abundance. The butterflies landed on the expected number of cabbages when cabbage was abundant (exp = 0.75; 95% conf = 0.68–0.79) and when both hosts were equally abundant (exp = 0.5; 95% conf = 0.44–0.64). However, when radish was abundant and cabbage was rare, the butterflies landed on cabbage more often than expected by chance given its proportion in the environment (exp = 0.25; 95% conf = 0.26–0.43, Figure 2—day 1).

These results suggest that butterflies may have slightly preferred cabbage in some of these experimental arrays.

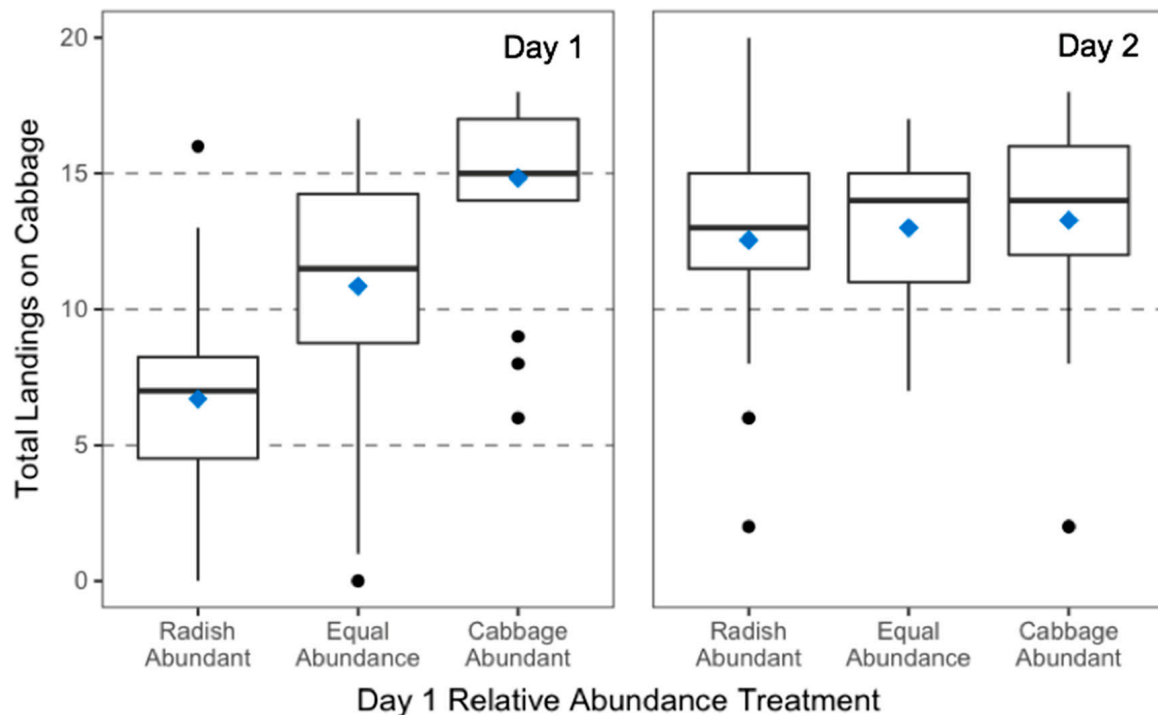


Figure 2. Total landings on cabbage made by butterflies that experienced different relative host abundances of cabbage and radish on Day 1 and a common environment with equal abundance of both hosts on Day 2. Box plots are constructed using the median (center line) and first and third quartiles (lower and upper lines respectively). Whiskers extend to the largest value no further than $1.5 \times \text{IQR}$. Blue diamonds represent means and dots represent outlying points plotted individually. Dashed lines represent the expected number of cabbage landings based on the proportion of cabbages in the environment: 15 for cabbage-abundant, 10 for equal abundance, and 5 for radish-abundant environments. Note: This graph differs from our analysis, which used binomial regression to model cabbage (1) and radish (0) landings.

3.2. Day 2: Previous Experience Did Not Affect Subsequent Resource Specialization

To explore the effects of previous experience on subsequent resource choices, we asked whether the relative host plant abundance the butterflies experienced on Day 1 influenced their choices on Day 2 in a common environment, where both hosts were equally abundant. On Day 2, the butterflies exhibited the same probability of landing on cabbage regardless of the relative host environment they experienced on Day 1 ($\text{chisq} = 1.302$, $\text{df} = 2$, $p = 0.522$, Table 1, Figure 2—day 2).

We also explored whether the butterflies landed on hosts in proportion to their abundance in the environment on Day 2. The butterflies with all three types of Day 1 experiences visited cabbage more often than expected given its abundance in the environment (Figure 2—day 2). The proportion of cabbage plants in the environment (0.5) fell below the 95% confidence intervals of butterfly landings when cabbage was abundant ($\text{conf} = 0.58\text{--}0.74$), when both hosts were equally abundant ($\text{conf} = 0.59\text{--}0.71$), and when radish was abundant ($\text{conf} = 0.53\text{--}0.72$). These results indicate that, although butterfly landings on Day 2 did not differ based on Day 1 experience, the butterflies on Day 2 did not merely visit the host plants in proportion to their abundance in the environment (i.e., random landings).

3.3. Change between Days: Butterflies Increased Visits to Cabbage and Improved Their Accuracy

Because we tracked individuals over the course of two days, we were also interested in how landings and search accuracy changed over time. We evaluated the host landing preference and accuracy of butterflies that experienced equal abundance of cabbage and radish over two days. On Day 2, the butterflies exhibited a higher probability of landing on cabbage ($B = 0.444 + 0.086 \text{ SE}$, $p < 0.001$) and landed on fewer non-hosts than on Day 1 ($B = -0.338 + 0.062 \text{ SE}$, $p < 0.001$; Figure 3), indicating that landing host preference and accuracy changed with experience.

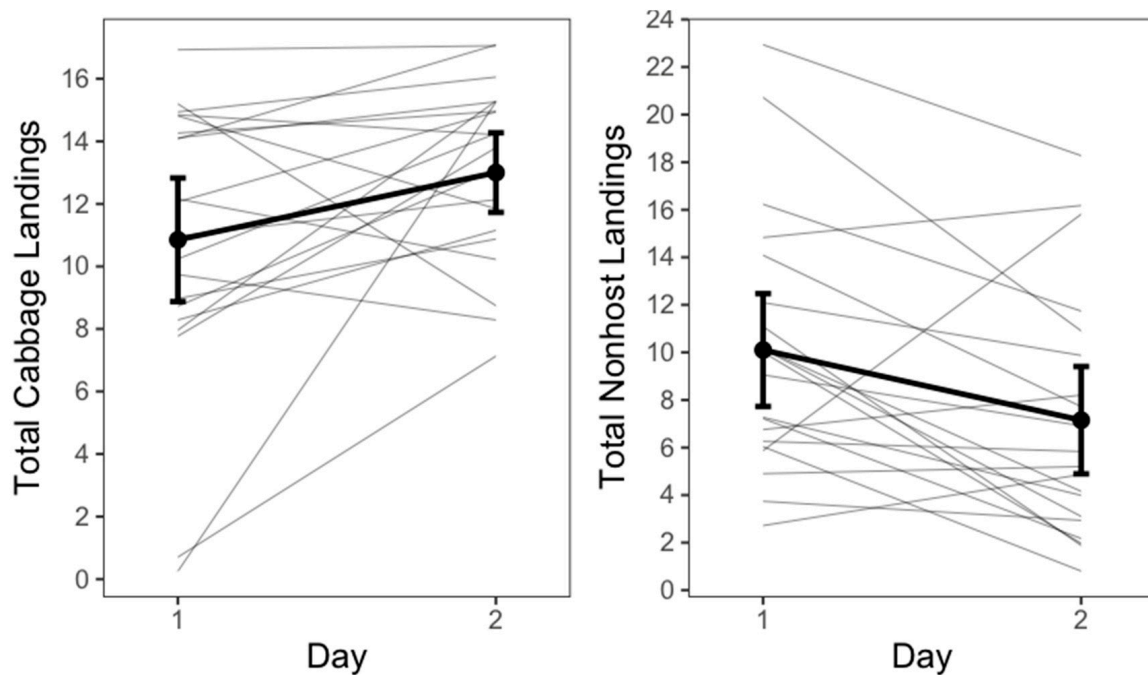


Figure 3. Butterfly host landings and host-finding accuracy over the course of two days. Butterflies increased their visits on cabbage from Day 1 to Day 2 (left). Butterflies decreased their landings on non-hosts from Day 1 to Day 2 (right). Points and bars represent means and + 1.96 SE. Light gray lines connect data from individual butterflies and are slightly jittered for easier visualization.

4. Discussion

Overall, our results do not support the hypothesis that early experiences with different relative host plant abundances lead to individuals with different host landing specializations. Current experiences outweighed the effect of prior experience: in other words, context-dependent behavioral plasticity determined resource choice more than developmental behavioral plasticity (*sensu* [44]). Although the butterflies were exposed to and visited different relative abundances of host plants when they were naïve, these early host landings did not influence subsequent host landing preference in a common environment. Instead, butterflies from all treatment experiences were more likely to land on one particular host, cabbage, on the second day. Consequently, although experience searching for hosts led to a landing preference for a particular host, it did not lead to individuals developing distinctly different specializations from each other.

Our results are surprising given that there are many examples in previous research suggesting that learning and early experiences are mechanisms through which individual specializations develop [5,17,19,20,39,45]. Our results are also surprising given that, in insects, encounter rate often leads to changes in preference through learning [31–33]. Still, we have evidence consistent with learning in this study: the butterflies improved their ability to discriminate between hosts and non-hosts over the course of two days. However, this learning did not lead to individual differences in host choice. Rather, all butterflies increased their likelihood of landing on only one of our hosts, cabbage, over time.

There are several reasons why experience in all three of our treatment search arrays could have resulted in a higher probability of landing on cabbage than radish in our test array. First, according to the preference-performance hypothesis, ovipositing female insects should be more likely to lay eggs on host plants that are most suitable for larval development (review [46]). However, at least for the growing conditions in these experiments, cabbage white larvae develop at a faster rate on radish than on cabbage, indicating that the butterflies did not preferentially visit cabbage because of its higher nutritional quality [40]. Alternatively, cabbage white butterflies could have a genetically based population-level preference for cabbage because the host maximizes some other element of larval survival (e.g., enemy-free space, disease resistance, reduced competition) or has been a reliable host over many generations. However, our previous work documented that naïve individual butterflies do not all immediately land on cabbage: some visited primarily radish, some visited primarily cabbage, and others visited a mixture of both [40]. The butterflies increased their probability of landing on cabbage both within a foraging trial (20 host landings) and over the course of two days, indicating that a butterfly's landing preference for cabbage is, in part, a product of experience.

We propose, instead, that butterflies from all treatment arrays might preferentially visit cabbage because it can be visually easier to discriminate from non-hosts than radish. For visual foragers, searching for resources that are extremely discriminable from the background community can save time and improve foraging performance [47–49]. Such visual discrimination tasks, coupled with short-term memory constraints, can even explain why some bees specialize in certain flowers (“floral constancy” [50]). Cabbage whites use primarily visual cues to make immediate pre-alighting host choices [38]. Over time, butterflies learn to associate the host plant “reward” (the presence of oviposition-inducing chemicals on the leaf surface) with host plant cues, such as color or shape [37]. Cabbage is likely more visually discriminable than radish in comparison to our chosen non-hosts because cabbage leaves reflect UV wavelengths, whereas radish and the non-host plants do not [40]. If cabbage is more visually salient to the cabbage white, our results suggest that host saliency may sometimes override the importance of repeated exposure to an abundant resource in butterfly host learning. A highly discriminable resource may be present in very low abundances and still be preferentially visited, as suggested by our observation that butterflies visited cabbage more often than expected in the treatment array when it was rare and radish was abundant. However, more controlled experiments, such as with artificial host models (e.g., [51]) are needed to test this hypothesis experimentally.

5. Conclusions

In this study, it was found that experience with an abundant resource does not necessarily lead to intra-population variation in individual resource use. Instead, experience with different host abundances led to a landing preference for only one host, cabbage, possibly because this host was more visually discriminable and learning resulted in a common directional host preference rather than diverse individual host preferences. How do we reconcile the present results with well-studied examples of individual resource specialization shaped by learning and differences in experience with different resources [5,17,19,20,39,45]? We hypothesize that perhaps individual specialization may be more likely when resource experience involves a greater range of motor tasks, rather than primarily a sensory task. In a theoretical model, Tinker et al. [22] propose that the co-existence of such different specializations is likely to occur when resources are associated with complex capture and handling techniques that require time to learn. Indeed, the idea of the development of “expertise” in a task or resource emphasizes motor learning [28,52] and empirical examples in insects suggest switching between complex motor patterns in different resources creates a performance cost [7,39,53,54]. It is also possible that more complex visual search tasks could favor individual specialization and intrapopulation variation, such as hosts that are more cryptic against a visually complex or color matched background (e.g., [55]). Future work that manipulates the difficulty of search and complexity of handling tasks

will further reveal how learning and experience shape the development of individual resource specializations.

Author Contributions: M.K.S. led the conception and design of the work, with discussion with E.C.S.-R., M.K.S. directed all experimental work, statistical analyses and initial writing, with input from E.C.S.-R. throughout. E.C.S.-R. updated and revised subsequent manuscript drafts with input from M.K.S. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors have no conflict of interest to declare.

Ethics Statement: All butterflies used in this study were obtained with minimal impact to wild populations, although note this is a non-native species. All individuals reared in the lab were treated with care and respect and, at the conclusion of the work, were sacrificed at -20°C .

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