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Preference or Desperation? Distinguishing Between the Natal Habitat's Effects on Habitat Choice

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3 **Preference or desperation? Distinguishing among the natal habitat's effects on**
4 **habitat choice.**

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10 DAVIS: NATAL EXPERIENCE AND HABITAT CHOICE
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45

46 Abstract

47 While the effect of natal experience on habitat and host selection has long been of
48 interest to evolutionary biologists, the adaptive consequences of this effect have only
49 recently been explored. The natal habitat provides dispersing individuals with
50 information that can potentially improve estimates of three parameters important in
51 sequential habitat search: habitat quality, habitat encounter rate, and total time available
52 for search. The estimates that are changed by natal experience will determine the
53 ecological consequences of the individual variation that results from natal experience. In
54 this paper, I demonstrate methods for examining habitat acceptance during sequential
55 search that allow discrimination amongst the potential effects of natal experience. I then
56 discuss the results of an experiment that used these methods to determine which habitat
57 search parameter estimates are most influenced by natal experience in the vinegar fly,
58 *Drosophila melanogaster*. I find that the natal habitat's effect on estimates of time
59 available for search is largely responsible for differences in breeding site acceptance
60 between individuals from different natal habitats. This type of effect is likely to be
61 common in nature, and future tests of how natal experience influence habitat selection
62 should take care to distinguish between this and other potential effects of natal experience.

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64 Keywords: Habitat Selection, Sequential Search, Learning, *Drosophila melanogaster*

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66 There is growing evidence that individual differences in the use of resources such
67 as hosts and habitats are both common in natural populations and have important
68 implications for the ecology and evolution of species (Bolnick et al. 2003). Natal
69 experience has been recognized as a potential source of this variation (Immelmann 1975)
70 and has its own unique consequences, including implications for speciation (Beltman et
71 al. 2004), metapopulation dynamics (Hanski & Singer 2001), conservation efforts
72 (Watters et al. 2003; Stamps & Swaisgood in press), and biological control (Gandolfi et
73 al. 2003).

74 While natal experience has been shown to affect habitat and host preferences in a
75 broad range of taxa (Davis & Stamps 2004), the strength of this effect is variable across
76 species (Barron 2001; Davis 2006). This may represent adaptation to the species-specific
77 challenges of habitat search (Dukas 2004; Davis 2006; Stamps & Davis in press).
78 Therefore, an understanding of the adaptive nature of natal habitat effects is needed to
79 develop realistic models of the consequences of individual variation in resource use.

80 A potential first step in developing such an understanding is to consider how
81 information in the natal environment can change estimates of the parameters that affect
82 habitat search behaviour, thereby allowing individuals to make adaptive choices during
83 dispersal (Stamps & Davis in press). In this paper, I will discuss the results of an
84 experiment on *Drosophila melanogaster* designed to distinguish amongst changes in the
85 parameter estimates that should most influence habitat search.

86 Models of sequential habitat search, in which animals must decide whether to
87 accept a given habitat or to continue searching, suggest that three parameters are most
88 important in adaptive decision making: time available for search, encounter rate with

highly preferred habitats and the relative quality of habitats (Ward 1987; Baker & Rao 2004; Stamps et al. 2005). ‘Time available for search’ is the amount of time an animal has to continue searching without, for example, substantially increasing its risk of starvation (Stamps et al. 2005). ‘Encounter rate with highly preferred habitats’ is the likelihood per unit time of encountering a habitat that is highly preferred. ‘Habitat quality’ is the fitness that an individual is expected to have after settling in that type of habitat. Estimates of all three of these parameters can be improved by experience in the natal habitat.

Following models of sequential search (Ward 1987; Stamps et al. 2005), Stamps and Davis (in press) predict that relative to a hypothetical disperser with no natal experience (reared in absence of any cues relevant to natural habitats):

1) Natal experience can influence a disperser’s estimate of the natal habitat’s quality, typically increasing it (Davis 2006), so that a given habitat type is more likely to be accepted by dispersers whose natal habitat was of the same type.

2) Natal experience may decrease a disperser’s estimate of the quality of novel habitats making it less likely to accept all non-natal habitat types.

3) If highly attractive habitats are rare and dispersers are unlikely to encounter many habitats during search (i.e. sampling during dispersal is limited), natal experience with a highly preferred habitat-type might indicate that that habitat is currently present in the environment and hence increase the disperser’s estimated encounter rate with that habitat-type. This should increase the selectivity of disperser (i.e. decrease the acceptability of less attractive habitat types).

111 4) Natal experience can influence the physiological condition of the disperser and hence
112 its estimate of time available for search. Acceptance of less preferred habitats will
113 increase when estimated time available for search is low (Stamps 2006).

114 The habitat search parameters, time available for search and encounter rate, are
115 only relevant during sequential search. Therefore ‘one-choice tests,’ which simulate
116 sequential search by exposing individuals to only one habitat at a time and measuring
117 their response to that habitat, are most appropriate for measuring how natal experience
118 changes all three habitat search parameter estimates. In this type of test, the effect of the
119 natal habitat on habitat use will appear as a statistical interaction between natal habitat
120 and the habitat-type offered, on the measured response (e.g. latency to accept the habitat,
121 time spent in proximity to the habitat, etc.).

122 Standard protocols for measuring the effect of experience on habitat use can
123 detect whether or not the natal habitat has an effect, but the results of these experiments
124 often do not tell us which habitat search parameter estimates have changed as result of
125 experience. For example, figure 1A depicts the results of a one-choice experiment in
126 which individuals reared in a given habitat type, X, are more likely than individuals
127 reared in another habitat, Y, to accept habitat X within a given amount of time. These
128 results indicate that natal experience influences acceptance of habitat X, but can be
129 explained by all four of the hypotheses discussed above.

130 In order to test which of these hypotheses best explains how natal experience
131 influences habitat choice, an estimate of the response to habitat X in individuals that are
132 ‘naïve’ with respect to natural habitat cues is needed. The changes in response due to
133 experience can then be considered relative to the response of these naïve individuals.

Moreover, determining naïve individuals' acceptance rates of more than one habitat type further assists in interpretation of experience effects. While it is impossible to determine exactly what these naïve responses are, by rearing subjects in environments that lack cues relevant to their natural habitat, an estimate of response to each habitat can be calculated. The difference in response to a habitat relative to the naïve response therefore provides a measure of the magnitude and direction of change in response to a habitat that is due to a given natal experience.

Measuring the acceptance rates of individuals with particular experiences relative the acceptance rates of naïve individuals assists in testing each of the 4 hypotheses.

- To demonstrate Hypothesis 1: Experience in habitat X increases the estimated quality of X,
Requires that: Individuals reared in habitat X accept X at a higher rate than naïve individuals and individuals reared in any other habitat (Fig. 1B and D).
- To demonstrate Hypothesis 2: Experience in Y decreases the estimated quality of novel habitats,
Requires that: Individuals reared in habitat Y accept all non-Y habitats at a lower rate than naïve individuals (Fig. 1C).
- To demonstrate Hypothesis 3: Experience in Y increases the expected encounter rate with Y,

Requires that: A. Naïve animals accept habitat Y at a high rate and, B. Individuals reared in habitat Y accept habitats that naïve individuals accept at a low rate (including X), at an even lower rate (Fig. 1C and 1E).

- To demonstrate Hypothesis 4: Experience in habitat X decreases estimated time available for search,

Requires that: A. Naïve individuals accept habitat X at a low rate relative to acceptance rate of other habitats, B. Evidence that individuals reared in some habitats have a shorter time available for search (smaller size, less resistant to starvation) than naïve individuals and individuals reared in other habitats and C. Individuals from all habitats (e.g. habitat X) that provide a lower estimate of time available for search accept habitat X at higher rate than individuals from habitats that provide a longer estimate of time available for search (e.g. habitat Y)(Fig. 1B and 1E).

By measuring the responses of ‘naïve’ individuals to multiple habitat types and using the criteria described here, researchers can distinguish among the hypotheses for potential effects of natal experience on habitat choice. To illustrate this, I will describe an experiment that measures the variables needed to determine how different natal experiences may be affecting the habitat selection behaviour in *Drosophila melanogaster*. Specifically, this experiment determined how experience with different fruit species upon emergence from pupae changed both the flies’ physiological condition and acceptance of potential breeding sites relative to flies that emerged from their pupae in a habitat that lacked fruit-associated cues. This methodology allowed me to determine which parameter

estimate changes are most likely responsible for changes in habitat selection observed in wild flies.

METHODS

Overview

In this experiment, I determined how the response of flies to traps baited with one of three fruits (apple, banana or kiwi) was influenced by natal experience. Because it has been demonstrated previously that only experience after eclosion influences fruit preference in *Drosophila melanogaster* (Jaenike 1983; Barron & Corbet 1999), all experience treatments in this experiment started at eclosion from the pupa, and lasted for approximately 24 hours. In order to estimate the response to each of these fruits in naïve individuals, I measured the response of flies that had only been exposed to Bloomington-recipe *Drosophila* media (hereafter referred to as ‘control flies’). Bloomington media is composed of water, yeast, soy flour, yellow cornmeal, malt extract, agar, corn syrup and propionic acid.

Experimental Flies

All experiments were performed using flies derived from five crosses between ten randomly selected isogenic lines of *Drosophila melanogaster*. These isolines were established by Dr. Sergey Nuzhdin from flies captured in Wolfskill experimental orchard in Winters, CA (for details, see Stamps *et al.* 2005). Crosses were prepared by placing five virgin females from one isoline with four males from another isoline in 2 x 9.5 cm vials with approximately 10 mL Bloomington *Drosophila* media. Crosses were

maintained at 24.5 -26° C and on an 11:13 L:D cycle. 12-14 days after the crosses were prepared, pupae nearing eclosion were removed from the sides of the vials, washed with distilled water and female pupae were identified and collected for use.

Provision of natal experience

Fruit: To provide newly emerged females with experience with fruit cues that were comparable to those that newly emerged flies typically experience in the wild, ‘conditioned’ food (fruit or Bloomington media that was actively being used as a larval resource) was used as the natal environment in these experiments. Thus, fruit was supplied by maintaining population cages of a single isogenic line on each fruit type (organic kiwi, banana or Braeburn apples). These fruits developed an active community of yeast and bacteria (Judy Stamps, unpublished data). Fruit that contained 3rd instar larvae but no pupae was collected from the cages to provide natal experience to experimental females. Similarly, natal experience with Bloomington recipe media was provided using media collected from 200 mL bottles containing 3rd instar larvae of a single isoline.

Experience - Flies used in these experiments eclosed in isolation from other adult flies. Natal experience vials were prepared by placing approximately 1 mL of hand-mixed conditioned fruit pulp or media in a 14 mL vial. Female pupae from each cross were individually affixed, ventral side down, to a piece of plastic screen with juice from the used fruit they were to experience upon emergence. Each screen was individually placed in a prepared vial stoppered with cotton. Vials were placed in the room where all experiments were run and kept at an average temperature of 25.8 ± 1.5 °C and $78.1 \pm$

6.8% relative humidity. Fluorescent ceiling lights were turned on at 0900 hours each morning and turned off at 2000 hours. To better mimic the natural light cycle, additional incandescent spotlights were turned on from 1000 to 1800 hours.

One-choice tests of attraction

Individual flies' response to fruit cues were tested by placing them individually in a chamber that contained a single trap baited with sliced fresh apple, banana or kiwi and observing the latency to trap entrance. Experimental chambers consisted of a 36 x 21 cm Masonite® floor (smooth side up) and a modified 34 x 21 x 10.5 cm Rubbermaid® shoebox, open-side down, serving as ceiling and walls. The ceiling of the chamber contained two 10 x 13 cm fine mesh windows. A strip of polyester costume fur was affixed to the lip of the shoebox to fill in spaces between the walls and floor.

Traps were constructed from 8 oz. transparent plastic Solo® cups, the bottom of which had been removed and replaced with a plastic screen funnel 5 cm in diameter and 3 cm deep. The tip of the funnel was cut off so that there was a 0.5 cm diameter entry way. This cup was then placed open-side down over an 8 cm Petri dish that contained ~ 10 g of ripe kiwi, banana or braeburn apple. This design allowed visual and olfactory access to flies outside the trap and was efficient in retaining flies that entered it. A single baited trap was placed in the middle of the floor of each experimental chamber.

The afternoon after collected flies emerged from their pupae (1700 hours, ~7 hours post-emergence), the vials were set inside the experimental chambers to allow the flies to acclimate to the light and temperature conditions. At 0830 the next morning, while the experimental room was still dark, the cotton stoppers were removed from each

vial allowing the flies to enter the experimental chamber. Fifteen minutes later the vials were removed from the chambers. Nearly all flies had left the vials by that time, and those few that hadn't (~1 in every 30) did so as the vial was being removed from the chamber. Every hour for the next 11 daylight hours (1000 – 2000 hours) and an hour after “nightfall” (2100 hours), all chambers were checked to see which flies had entered the traps. At 0900 and 1300 hours the next day (24 and 28 hours after release) two final observations were made.

Two individual pupae were prepared for each genotype by fruit experience by bait group in each of the 32 trials of this experiment, however, not all individuals emerged from their pupae. Therefore, the sample size for each of the 45 genotype by fruit experience by bait combinations fell between 36 and 58. Data from all trials was pooled because 2 or fewer individuals from each treatment were tested in each trial. Control flies were tested simultaneously with fruit experienced flies during the last 18 trials. Between 21 and 34 of these control flies were tested for each of the 15 genotype by bait combinations.

Analysis of attraction data

A large proportion of flies (30%) entered the trap between 2000 and 2100 hours (i.e. just after nightfall) the day they were released, leading to an extremely non-normal distribution of trap times. Therefore, analysis of trap entry data was conducted after dichotomizing fly response into early entry (before 1730 hours, ≤ 8.5 hours after release) and late entry (after 1730 hours). The cutoff point was selected because it was the midpoint of my observations. For control flies, differences in the rate of entry into traps

with different baits were analyzed using chi-square tests. For flies with fruit experience, I used backwards and forwards elimination to determine which factors (genotype (GENO), experience (EXP), bait (BAIT) and the interactions between them (GENO*BAIT, GENO*EXP, EXP*TRAP and GENO*TRAP*EXP) significantly improved the fit of a nominal logistic regression model explaining the proportion of flies entering before and after 1730. I repeated these steps using 1830, 1930 and 2030 hours as cut off points for data dichotomization and found qualitatively similar results (data not shown).

Starvation tests to assess physiological condition

In order to determine the effect of genotype and rearing conditions on the physiological state of flies, I reared individuals in the same way as described above and then measured time to starvation. As above, flies spent their first 24 hours after eclosion on conditioned fruit or media. After 24 hours, flies were aspirated individually from their rearing vials and into empty 20 mL glass vials that were then stoppered with a cotton ball. These flies were maintained in the same rooms as in the one-choice experiment (25.8 ± 1.5 °C and $78.1 \pm 6.8\%$ rh). The state of each fly (alive or dead) was checked every three daylight hours until all flies had died.

Between 45 and 64 flies from each genotype by fruit experience combination was tested across 8 trials. Across the final 4 trials, between 25 and 30 flies from each genotype were tested after being reared only with Bloomington media. The time of starvation was estimated as the midpoint between the observation when the fly was last observed alive and the observation that it was observed to be dead. Analysis of variance

(SPSS v. 14.0) was performed on these midpoints, with genotype and natal experience as fixed factors and trial as a random factor.

Testing alternative hypotheses

After analyzing the trap entry of control flies and the starvation resistance of flies that emerged with different fruits and confirming that natal fruit experience influences the acceptance rates of different baits, I re-categorized experience and bait treatments along 4 axes: attractiveness of bait (BAIT-ATTR: High or Low), attractiveness of experienced fruit (EXP-ATTR: High or Low), physiological effect of early experience (EXP-COND: High or Low) and match between experience and trap bait (MATCH: Yes or No). I used these categorical variables to construct statistical models that corresponded to the 4 hypothetical effects of natal experience on habitat acceptance described in the introduction. These model terms were added and removed to determine if they improved the fit of the logistic model and Akaike information criteria were used to determine the optimal model to describe how natal experience affected the likelihood that flies entered traps early.

RESULTS

Bait acceptance in control flies

Apple was the least acceptable trap for control flies. Within 8.5 hours of release, 35% ($\pm 4.2\%$) of control flies were trapped in banana-baited traps, 31% ($\pm 4.1\%$) of control flies were trapped in kiwi-baited traps and 11% ($\pm 2.8\%$) of control flies were trapped in apple-baited traps. (Apple vs. Banana bait, $\chi^2_1 = 20.23$, $P < 0.001$; Apple vs. Kiwi bait, $\chi^2_1 = 14.67$, $P < 0.001$; Banana vs. Kiwi bait, $\chi^2_1 = 0.56$, $P = 0.48$)

Natal experience affects starvation resistance

The time it takes flies to starve can be used as an indicator of relative differences in time available for search. Both genotype and experience upon emergence affected the number of hours it took for flies to starve (natal experience: ANOVA: $F_{3,914}=29.37$, $P<0.001$, genotype: ANOVA: $F_{4,914}=29.75$, $P<0.001$). There was no interaction effect on starvation between these two factors indicating that the physiological effect of natal experience was similar for flies of all genotypes tested (genotype*exp: ANOVA: $F_{12,914}=0.797$, $P=0.69$). Control flies and flies reared on banana lived longer than flies reared on kiwi or apple (All p-values for these differences were less than 0.001 in Tukey post-hoc comparisons)(Control: 43.68 hrs $\pm$ 0.79; Banana: 43.58 hrs $\pm$ 0.55; Apple: 40.52 hrs $\pm$ 0.55; Kiwi: 40.52 hrs $\pm$ 0.55). Banana-exposed and control flies did not differ significantly in starvation time, nor did flies exposed to kiwi and apple. Given these differences, experience upon emergence should cause flies eclosed on kiwi or apple to have shorter estimates of time available for search than banana-eclosed and control flies.

Natal fruit experience affects acceptance rates

If natal fruit experience differentially influences the response to traps baited with different fruits, then the fit of a model describing how factors influence the proportion of flies entering the trap early should be significantly improved by the inclusion of an interaction term between trap bait and natal experience (BAIT by EXP). The data on the proportions of flies that were trapped within 8 hours of release (Fig. 2) best fit a logistic model that included the main effect of genotype and an interaction effect between bait and natal experience (difference in fit between null model and one containing GENO $\chi^2_4 = 126.0$, $P<0.001$, difference in fit between model containing only main effects and one

containing a BAIT by EXP interaction term $\chi^2_4 = 12.894$, $P=0.012$). The addition of other interaction terms (EXP*GENO, TRAP*GENO or EXP*TRAP*GENO) did not significantly improve the fit of the model. This suggests that natal experience did influence the flies' relative acceptance of different baits, but does not distinguish between the hypotheses discussed in the introduction. Also this model indicates that genotype influenced the time it took the flies to enter traps, but that this effect was independent of the bait or experience (i.e. genotypes did not differ in their relative attraction to the different baits nor in the extent to which natal experience influenced trap acceptance).

Testing the alternative hypotheses

Using the results from the starvation experiments and the responses of control flies to different baits, I re-categorized the treatments into dichotomous categories that could be used test which hypothesis for the effect of natal experience best explained why an interaction between experience and bait improved the fit of the logistic model. Banana and kiwi were classified as attractive (EXP-ATTR=High, BAIT-ATTR=High) and apple was categorized as unattractive (EXP-ATTR=Low, BAIT-ATTR=Low). Flies with experience on apple and kiwi were categorized as starvation prone (EXP-COND=Low), while flies exposed to banana were starvation resistant (EXP-COND=High). Finally, flies that were provided with the same fruit for both experience and trap bait were categorized as matched (MATCH=Yes). Those flies that received a bait that was different from their natal experience fruit were classified as unmatched (MATCH=No).

Hypotheses 1. Experience increases the estimated quality of the natal habitat

If natal experience increases the estimated quality of the natal habitat, individuals should more often accept the offered bait early if it matches their natal habitat. Therefore the fit of the data to the model should be significantly improved by the inclusion of MATCH as an explanatory factor.

Hypothesis 2. Experience decreases the estimated quality of novel habitats

If this hypothesis is true then acceptance of baits not experienced upon emergence should be decreased relative to control flies. Flies with any fruit experience accepted all baits earlier than control flies (Fig. 2) This suggests that fruit experience does not decrease the estimated quality of novel habitats. This hypothesis (hypothesis 2) will therefore, not be considered further.

Hypothesis 3. Experience in attractive habitats increases the estimate of encounter rate with that habitat

If this hypothesis is true, then experience in an attractive habitat (banana or kiwi) should decrease acceptance of the least attractive habitat (apple) relative to control flies. The fit of the data to the model should be significantly improved by the inclusion of an EXP-ATTR by BAIT-ATTR interaction (an interaction between attractiveness of the experienced fruit and the attractiveness of the bait).

Hypothesis 4. Experience in the natal habitat changes estimates of time available for search

If this hypothesis is true, natal experience with apple or kiwi should increase the acceptance rate of the least attractive bait (apple) relative to control (and banana experienced) flies. The fit of the data to the model should be significantly improved by the inclusion of a BAIT-ATTR by EXP-COND interaction (an interaction between the attractiveness of the trap bait and the effect of experience on starvation resistance).

Comparing the hypotheses

_____ In a nominal logistic regression model with forced entry of GENOTYPE and BAIT terms, I introduced the terms MATCH, EXP-ATTR by BAIT-ATTR and BAIT-ATTR by EXP-COND, and determined which terms significantly improved the fit of the model. The addition of an EXP-ATTR by BAIT-ATTR interaction to the model did not significantly improve the model ($\chi^2_2 = 2.802$, $P=0.25$), indicating that improved estimates of encounter rate are unlikely to account for the effect of natal experience on habitat acceptance. The inclusion of MATCH or of a BAIT-ATTR by EXP-COND interaction improved the fit over a model including only GENOTYPE and BAIT main effects. (MATCH: $\chi^2_1 = 4.75$, $P=0.025$, BAIT-ATTR by EXP-COND: $\chi^2_2 = 12.689$, $P=0.002$). However, while the addition of the BAIT-ATTR by EXP-COND interaction to a model already containing MATCH significantly improved the fit of the model ($\chi^2_2 = 10.252$, $P=0.006$), the addition of MATCH to model already containing the BAIT-ATTR by EXP-COND interaction did not significantly improve fit ($\chi^2_1 = 2.313$, $P=0.128$). This suggests that natal experience's effect on habitat choice in this experiment can best explained by its effect on estimated time available for search. This is confirmed by the fact that among tested models, the one containing only GENOTYPE and the BAIT-

ATTR by EXP-COND interaction is optimal according to Akaike information criteria, an index of the amount variation explained by a model, weighted by the number of model parameters included (Burnham & Anderson 2002) (Table 1).

Physiological Condition and Timing of Trap Entrance

From the analysis above, it appears that the effect of natal experience on habitat acceptance was largely due to the natal habitat's effect on time available for search estimates. Models of habitat search suggest that as time available for search increases, acceptance of less preferred habitats should decrease while acceptance of highly preferred habitats should remain the same (Ward 1987; Stamps et al. 2005). Therefore, in this experiment, the natal habitat's effect on physiological condition should affect acceptance of apple baited traps, but not banana-baited traps. To test this prediction, I created scores of the effect of natal experience on both starvation time and response to trap baits for each genotype - experience combination. This was done by calculating the standardized residuals on genotype of both mean starvation time and proportion of individuals entering each trap early. These scores indicate the magnitude and direction of the effect of natal experience on both starvation time and proportion of flies entering traps early. Plotting these scores against each other, therefore, reveals the relationship between the change in estimated time available for search caused by natal experience and the responses to each bait. As predicted by models of habitat selection, while there is a strong negative relationship between the change in estimated time available for search and acceptance of apple-baited traps ($F_{1,19}=12.628$, $\beta=-0.682$, $P=0.002$), there is no relationship between time available for search and acceptance of banana-baited traps

($F_{1,19}=2.739$, $\beta=-0.119$, $P=0.389$), which are consistently accepted at a higher rate than apple-baited traps (Fig. 3). Furthermore, the relationship between acceptance of the intermediately preferred kiwi-baited traps and estimated time available for search available is negative, but not as strongly so as when traps were baited with apple ($F_{1,19}=14.914$, $\beta=-0.419$, $P=0.001$).

DISCUSSION

Using a framework of adaptive habitat search (Stamps & Davis in press), I used the results from these one-choice experiments to determine which parameter estimates important in sequential habitat search (time available for search, habitat encounter rates and/or habitat quality) changed the most as a result of natal experience in *Drosophila melanogaster*. The data best fit the pattern expected when natal experience influences estimates of time available for search, making individuals less selective (accepting less preferred habitats at higher rates) when they are reared in habitats that decrease estimated time available for search by reducing condition.

Much of the insight gained in this experimental design is a consequence of the inclusion of an estimate of the acceptance of different fruits by 'naïve' individuals. However, one concern is that if chemical cues in fly media were similar to one of the three tested fruits, estimates of 'naïve' response would be biased, and lead to misinterpretation of the data. However, three lines of evidence suggest that the cues from the three tested fruits are much more similar to each than any one fruit's cues is to Bloomington media. First, preference for fruit over Bloomington media is very strong (Judy Stamps, unpublished data), indicating that the media is unlikely to contain

attractive cues that will affect subsequent response to fruit. Similarly, the yeast communities that grow on the three fruits tested, and which probably create some proportion of the chemical cues that influence fly attraction, are very similar to each other, while the yeasts that grow on Bloomington media are distinct from those that grow on fruit. (Judy Stamps, unpublished data). Finally, the fact that the flies in this experiment accepted all fruits faster when they were previously exposed to fruit indicates that there may have been cues that all fruits shared, but that the media lacked.

While this experiment demonstrated that physiological condition played the largest role in changing habitat acceptance patterns in *Drosophila*, it probably underestimated the natal habitat's effect on physiology. All flies were raised as larvae on the same high quality diet and were only exposed to different fruits after eclosion. Had the flies been reared from egg to adult on different fruits, their physiological differences, and hence differences in their patterns of habitat acceptance would have most likely been larger. Preliminary results indicate flies reared from egg to adult on kiwi and apple are indeed significantly smaller than flies reared on banana or Bloomington media (Anh Quoc Nguyen and Jeremy Davis, unpublished data).

To my knowledge, there is only one other experiment that has demonstrated this type of physiologically-mediated influence of the natal habitat on habitat choice. In this experiment, conducted by Bjorksten and Hoffman (1998), the effect of rearing species on the acceptance of three species of host eggs was tested in the egg parasitoid *Trichogramma nr. brassicae*. Individuals reared on two less-preferred hosts demonstrated an increase in the acceptance of the least-preferred species relative to individuals reared on the most-preferred species. The authors note that individuals reared on the most

preferred host were substantially larger than individuals from the other two hosts, and that this probably afforded them the ability to be more choosy, i.e. larger wasps were able to locate more hosts per unit time, effectively increasing time available for search.

Because the habitat in which an animal develops can often have an effect on its condition upon natal dispersal, this mechanism of natal influence on habitat selection may often be important.

Although experimental evidence is lacking, it is likely that the natal habitat or host influences a number of physiological states that are likely to influence selectivity in a diverse range of species. Therefore, the natal habitat's effect on physiologically mediated selectivity is likely to be both common and important in nature. This can cause predictable differences in the habitat selection behaviour of individuals dispersing from different types of habitats and can have important ecological and evolutionary implications. For example, it could affect metapopulation dynamics by forcing individuals reared in low quality habitats to accept low quality habitats during dispersal. Such a pattern would reduce effective population size, since lineages of animals from high quality habitats will consistently contribute more to the gene pool (Gunnarsson et al. 2005).

Furthermore, the type of natal habitat effect found here will have different evolutionary consequences than the type of natal habitat effect most often considered in models of sympatric speciation and the maintenance of genetic variation (e.g. Beltman et al. 2004). Natal habitat preference induction (NHPI), in which individuals' preferences, rather than selectivity, change as a result of natal experience (reviewed in Davis & Stamps 2004), is expected when experience increases the estimated quality of the natal

habitat or host. As a result of strong NHPI, subpopulations of individuals can form and local adaptation to that habitat will only strengthen the effect of natal experience on habitat use (Davis & Stamps 2004). This is can lead to host race formation and/or sympatric speciation (Beltman et al. 2004). On the other hand, a subpopulation breeding on a low quality habitat as result of the physiologically-mediated natal habitat effect found here is unlikely to become locally adapted to that habitat type because any mutation that improves performance in that habitat will increase the mutant individuals' estimated time available for search, and hence decrease the likelihood that they will return to that habitat type.

Finally, it is important to note that the experimental design described here tests for the effects of natal experience on behaviour during purely sequential search. At smaller spatial scales or during certain stages of search (e.g. host search after settling in a patch) individuals can return to previously visited habitats or even simultaneously compare habitats. Habitat choices made at this scale may not depend as heavily on time available for search and encounter rate, and should be made based largely on expected fitness (Stamps & Davis in press). Indeed, other experiments on *Drosophila* indicate that when presented with two choices in relative proximity to each other, natal experience influences habitat choices in a manner more consistent with shifts in the estimated quality of habitats (Jaenike 1983; Stamps & Blozis 2006), while at larger scales, the physiological consequences of natal experience play a larger role (Hoffmann 1985; Hoffmann & Turelli 1985). Similarly, models of the evolutionary and ecological consequences of natal habitat and host effects must take into account the spatial scale at which habitat and host choice occur, and the search strategy used during habitat selection.

In this paper, I have demonstrated that in one-choice experiments that test sequential search tactics, the most important effect of the natal environment on habitat selection in *Drosophila melanogaster* is its effect on physiological condition, which in turn influences its acceptance of typically unpreferred breeding sites. This would not have been evident without estimating the acceptance rates of naïve individuals and measurements of starvation time. The methodology presented here, with the adaptive framework laid out in Stamps and Davis (in press), should produce a richer understanding of the ways in which natal experience can influence habitat and host use, and the consequences of the individual differences that result from these effects.

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Table 1. Akaike information criteria (AIC) for alternative models of the influence of natal experience on the acceptance of different fruit baits by *Drosophila*^a

Model Terms	AIC	w
GENOTYPE	250.39	0.00
GENOTYPE, BAIT	233.60	0.00
GENOTYPE, MATCH	248.07	0.00
GENOTYPE ,BAIT, MATCH	231.05	0.02
GENOTYPE, BAIT-ATTR*EXP-COND	224.04	0.53
GENOTYPE, BAIT BAIT-ATTR*EXP-COND	225.11	0.31
GENOTYPE, BAIT-ATTR*EXP-ATTR	233.89	0.00
GENOTYPE, BAIT BAIT-ATTR*EXP-ATTR	234.99	0.00
GENOTYPE, MATCH BAIT-ATTR*EXP-COND	245.05	0.00
GENOTYPE, MATCH BAIT-ATTR*EXP-ATTR	233.09	0.01
GENOTYPE, MATCH BAIT-ATTR*EXP-ATTR BAIT-ATTR*EXP-COND	226.76	0.13

^aLower values of AIC indicate that increased efficiency in predicting acceptance rates. The Akaike weight, w, ranges from 0 to 1 and indicates the relative support for each model. Models with greatest degree of support are shaded.

Figure 1. A demonstration of the utility of estimation of attraction in ‘naïve’ individuals.

A) In this example, the acceptance of habitat X is greater in individuals previously exposed to habitat X compared to individuals exposed to habitat Y. This acceptance rate could have been affected positively by experience with X or negatively by experience with Y. By estimating habitat acceptance in naïve individuals (in shaded area), and calculating the change in acceptance of habitat i by individuals exposed to j relative to naïve acceptance, the researcher can distinguish between these two possibilities. In situation B, low naïve acceptance of X indicates that experience with X increases acceptance of X either through a decrease in its estimate of time available for search available, or by increasing its estimate of the quality of habitat X. In situation C, high naïve acceptance of X indicates that experience with Y decreases the acceptance of habitat X in response to either an increased estimate of the encounter rate with habitat Y, or a decreased estimate of habitat X’s quality. When the responses to habitat X are combined with responses to habitat Y, (panels D and E), the specific effect of natal experience on habitat search parameters can be surmised (see text)

Figure 2. The effect of natal experience on the proportion of flies entering early into traps baited with apple (white bars), kiwi (black bars) and banana (hatched bars). Flies having natal experience with Bloomington fly media were used to estimate measures of bait acceptance in the absence of natal experience with fruit cues (shaded area). Arrows indicate a statistically significant change in the proportion of individuals entering traps baited with a particular fruit relative to naïve individuals (χ^2 -test, where $\alpha=0.006$ after bonferroni corrections).

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635 Figure 3. The relationship between starvation time and acceptance of three baits. (Bait:
636 Apple - *, Kiwi - ●, Banana - Δ) Standardized starvation scores are the standardized
637 residual starvation times of each genotype-experience combination after controlling for
638 genotype. Similarly, standardized response scores are the standardized residual
639 proportions of each genotype-experience combination entering a trap early, after
640 controlling for genotype. (Apple bait: $\beta = -.682$, $t = -3.55$ $P = .002$; Kiwi bait: $\beta = -.419$, $t =$
641 -3.862 , $P = .001$; Banana bait: $\beta = -.119$, $t = 0.833$, $p = .389$).

Figure 1.

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Figure 2.