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

JEREMY M. DAVIS

Animal Behavior Graduate Group, University of California-Davis

DAVIS: NATAL EXPERIENCE AND HABITAT CHOICE

Jeremy M. Davis
Department of Ecology & Evolutionary Biology
The University of Arizona
P.O. Box 210088
Tucson, AZ 85721
davisj@email.arizona.edu
Word Count: 5,181

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.

63

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

65

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

89 highly preferred habitats and the relative quality of habitats (Ward 1987; Baker & Rao
90 2004; Stamps et al. 2005). ‘Time available for search’ is the amount of time an animal
91 has to continue searching without, for example, substantially increasing its risk of
92 starvation (Stamps et al. 2005). ‘Encounter rate with highly preferred habitats’ is the
93 likelihood per unit time of encountering a habitat that is highly preferred. ‘Habitat
94 quality’ is the fitness that an individual is expected to have after settling in that type of
95 habitat. Estimates of all three of these parameters can be improved by experience in the
96 natal habitat.

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

- 100 1) Natal experience can influence a disperser’s estimate of the natal habitat’s quality,
101 typically increasing it (Davis 2006), so that a given habitat type is more likely to be
102 accepted by dispersers whose natal habitat was of the same type.
- 103 2) Natal experience may decrease a disperser’s estimate of the quality of novel habitats
104 making it less likely to accept all non-natal habitat types.
- 105 3) If highly attractive habitats are rare and dispersers are unlikely to encounter many
106 habitats during search (i.e. sampling during dispersal is limited), natal experience with a
107 highly preferred habitat-type might indicate that that habitat is currently present in the
108 environment and hence increase the disperser’s estimated encounter rate with that
109 habitat-type. This should increase the selectivity of disperser (i.e. decrease the
110 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.

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

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

143

- 144 • To demonstrate Hypothesis 1: Experience in habitat X increases the estimated quality
145 of X,

146 Requires that: Individuals reared in habitat X accept X at a higher rate than naïve
147 individuals and individuals reared in any other habitat (Fig. 1B and D).

148

- 149 • To demonstrate Hypothesis 2: Experience in Y decreases the estimated quality of
150 novel habitats,

151 Requires that: Individuals reared in habitat Y accept all non-Y habitats at a lower rate
152 than naïve individuals (Fig. 1C).

153

- 154 • To demonstrate Hypothesis 3: Experience in Y increases the expected encounter rate
155 with Y,

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

159

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

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

169

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

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

181

182 METHODS

183 Overview

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

194

195 Experimental Flies

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

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

205

206 Provision of natal experience

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

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

225 6.8% relative humidity. Fluorescent ceiling lights were turned on at 0900 hours each
226 morning and turned off at 2000 hours. To better mimic the natural light cycle, additional
227 incandescent spotlights were turned on from 1000 to 1800 hours.

228

229 One-choice tests of attraction

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

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

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

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

255 Two individual pupae were prepared for each genotype by fruit experience by bait
256 group in each of the 32 trials of this experiment, however, not all individuals emerged
257 from their pupae. Therefore, the sample size for each of the 45 genotype by fruit
258 experience by bait combinations fell between 36 and 58. Data from all trials was pooled
259 because 2 or fewer individuals from each treatment were tested in each trial. Control flies
260 were tested simultaneously with fruit experienced flies during the last 18 trials. Between
261 21 and 34 of these control flies were tested for each of the 15 genotype by bait
262 combinations.

263

264 Analysis of attraction data

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

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

278

279 Starvation tests to assess physiological condition

280 In order to determine the effect of genotype and rearing conditions on the
281 physiological state of flies, I reared individuals in the same way as described above and
282 then measured time to starvation. As above, flies spent their first 24 hours after eclosion
283 on conditioned fruit or media. After 24 hours, flies were aspirated individually from their
284 rearing vials and into empty 20 mL glass vials that were then stoppered with a cotton ball.
285 These flies were maintained in the same rooms as in the one-choice experiment (25.8
286 ± 1.5 °C and 78.1 $\pm 6.8\%$ rh). The state of each fly (alive or dead) was checked every
287 three daylight hours until all flies had died.

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

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

295

296 Testing alternative hypotheses

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

309

310

RESULTS

311 Bait acceptance in control flies

312 Apple was the least acceptable trap for control flies. Within 8.5 hours of release,
313 35% ($\pm 4.2\%$) of control flies were trapped in banana-baited traps, 31% ($\pm 4.1\%$) of
314 control flies were trapped in kiwi-baited traps and 11% ($\pm 2.8\%$) of control flies were
315 trapped in apple-baited traps. (Apple vs. Banana bait, $\chi^2_1 = 20.23$, $P < 0.001$; Apple vs.
316 Kiwi bait, $\chi^2_1 = 14.67$, $P < 0.001$; Banana vs. Kiwi bait, $\chi^2_1 = 0.56$, $P = 0.48$)

317 Natal experience affects starvation resistance

318 The time it takes flies to starve can be used as an indicator of relative differences
319 in time available for search. Both genotype and experience upon emergence affected the
320 number of hours it took for flies to starve (natal experience: ANOVA: $F_{3,914}=29.37$,
321 $P<0.001$, genotype: ANOVA: $F_{4,914}=29.75$, $P<0.001$). There was no interaction effect on
322 starvation between these two factors indicating that the physiological effect of natal
323 experience was similar for flies of all genotypes tested (genotype*exp: ANOVA:
324 $F_{12,914}=0.797$, $P=0.69$). Control flies and flies reared on banana lived longer than flies
325 reared on kiwi or apple (All p-values for these differences were less than 0.001 in Tukey
326 post-hoc comparisons)(Control: 43.68 hrs \pm 0.79; Banana: 43.58 hrs \pm 0.55; Apple: 40.52
327 hrs \pm 0.55; Kiwi: 40.52 hrs \pm 0.55). Banana-exposed and control flies did not differ
328 significantly in starvation time, nor did flies exposed to kiwi and apple. Given these
329 differences, experience upon emergence should cause flies eclosed on kiwi or apple to
330 have shorter estimates of time available for search than banana-eclosed and control flies.

331 Natal fruit experience affects acceptance rates

332 If natal fruit experience differentially influences the response to traps baited with
333 different fruits, then the fit of a model describing how factors influence the proportion of
334 flies entering the trap early should be significantly improved by the inclusion of an
335 interaction term between trap bait and natal experience (BAIT by EXP). The data on the
336 proportions of flies that were trapped within 8 hours of release (Fig. 2) best fit a logistic
337 model that included the main effect of genotype and an interaction effect between bait
338 and natal experience (difference in fit between null model and one containing GENO χ^2_4
339 = 126.0, $P<0.001$, difference in fit between model containing only main effects and one

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

348

349 Testing the alternative hypotheses

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

361

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

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

367

368 Hypothesis 2. Experience decreases the estimated quality of novel habitats

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

374

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

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

382

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

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

390

391 Comparing the hypotheses

392 _____ In a nominal logistic regression model with forced entry of GENOTYPE and
393 BAIT terms, I introduced the terms MATCH, EXP-ATTR by BAIT-ATTR and BAIT-
394 ATTR by EXP-COND, and determined which terms significantly improved the fit of the
395 model. The addition of an EXP-ATTR by BAIT-ATTR interaction to the model did not
396 significantly improve the model ($\chi^2_2 = 2.802$, $P=0.25$), indicating that improved estimates
397 of encounter rate are unlikely to account for the effect of natal experience on habitat
398 acceptance. The inclusion of MATCH or of a BAIT-ATTR by EXP-COND interaction
399 improved the fit over a model including only GENOTYPE and BAIT main effects.
400 (MATCH: $\chi^2_1 = 4.75$, $P=0.025$, BAIT-ATTR by EXP-COND: $\chi^2_2 = 12.689$, $P=0.002$).
401 However, while the addition of the BAIT-ATTR by EXP-COND interaction to a model
402 already containing MATCH significantly improved the fit of the model ($\chi^2_2 = 10.252$,
403 $P=0.006$), the addition of MATCH to model already containing the BAIT-ATTR by
404 EXP-COND interaction did not significantly improve fit ($\chi^2_1 = 2.313$, $P=0.128$). This
405 suggests that natal experience's effect on habitat choice in this experiment can best
406 explained by its effect on estimated time available for search. This is confirmed by the
407 fact that among tested models, the one containing only GENOTYPE and the BAIT-

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

411

412 Physiological Condition and Timing of Trap Entrance

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

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

436
437
438

DISCUSSION

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

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

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

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

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

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

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

484 Although experimental evidence is lacking, it is likely that the natal habitat or
485 host influences a number of physiological states that are likely to influence selectivity in
486 a diverse range of species. Therefore, the natal habitat's effect on physiologically
487 mediated selectivity is likely to be both common and important in nature. This can cause
488 predictable differences in the habitat selection behaviour of individuals dispersing from
489 different types of habitats and can have important ecological and evolutionary
490 implications. For example, it could affect metapopulation dynamics by forcing
491 individuals reared in low quality habitats to accept low quality habitats during dispersal.
492 Such a pattern would reduce effective population size, since lineages of animals from
493 high quality habitats will consistently contribute more to the gene pool (Gunnarsson et al.
494 2005).

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

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

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

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

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- 548 **Baker, M. B. & Rao, S.** 2004. Incremental costs and benefits shape natal dispersal:
549 Theory and example with *Hemilepistus reaumuri*. *Ecology*, 85, 1039-1051.
- 550 **Barron, A. B.** 2001. The life and death of Hopkins' host-selection principle. *Journal of*
551 *Insect Behavior*, 14, 725-737.
- 552 **Barron, A. B. & Corbet, S. A.** 1999. Preimaginal conditioning in *Drosophila* revisited.
553 *Animal Behaviour*, 58, 621-628.
- 554 **Beltman, J. B., et al.** 2004. Learning and colonization of new niches: A first step toward
555 speciation. *Evolution*, 58, 35-46.
- 556 **Bjorksten, T. A. & Hoffmann, A. A.** 1998. Separating the effects of experience, size,
557 egg load, and genotype on host response in *Trichogramma* (Hymenoptera:
558 Trichogrammatidae). *Journal of Insect Behavior*, 11, 129-148.
- 559 **Bolnick, D. I., et al.** 2003. The ecology of individuals: incidence and implications of
560 individual specialization. *American Naturalist*, 160, 1-28.
- 561 **Burnham, K. P. & Anderson, D. R.** 2002. *Model selection and multimodel inference: a*
562 *practical information-theoretic approach*. New York: Springer-Verlag.
- 563 **Davis, J. M.** 2006. The Influence of Natal Experience on Habitat Selection., Ph.D. thesis,
564 University of California-Davis
- 565 **Davis, J. M. & Stamps, J. A.** 2004. The effect of natal experience on habitat preferences.
566 *Trends in Ecology & Evolution*, 19, 411-416.
- 567 **Dukas, R.** 2004. Evolutionary biology of animal cognition. *Annual Review of Ecology*
568 *Evolution and Systematics*, 35, 347-374.
- 569 **Gandolfi, M., et al.** 2003. Mechanisms of behavioral alterations of parasitoids reared in
570 artificial systems. *Journal of Chemical Ecology*, 29, 1871-1887.

571 **Gunnarsson, T. G., et al.** 2005. Seasonal matching of habitat quality and fitness in a
572 migratory bird. *Proceedings of the Royal Society B-Biological Sciences*, 272,
573 2319-2323.

574 **Hanski, I. & Singer, M. C.** 2001. Extinction-colonization dynamics and host-plant
575 choice in butterfly metapopulations. *American Naturalist*, 158, 341-353.

576 **Hoffmann, A. A.** 1985. Effects of experience on oviposition and attraction in
577 *Drosophila*: comparing apples and oranges. *American Naturalist*, 126, 41-51.

578 **Hoffmann, A. A. & Turelli, M.** 1985. Distribution of *Drosophila melanogaster* on
579 alternative resources: effects of experience and starvation. *American Naturalist*,
580 126, 662-679.

581 **Immelmann, K.** 1975. Ecological significance of imprinting and early learning. *Annual*
582 *Review of Ecology and Systematics*, 6, 15-37.

583 **Jaenike, J.** 1983. Induction of host preference in *Drosophila melanogaster*. *Oecologia*,
584 58, 320-325.

585 **Stamps, J. A.** 2006. The silver spoon effect and habitat selection by natal dispersers.
586 *Ecology Letters*, 9, 1179-1185.

587 **Stamps, J. A. & Blozis, S. A.** 2006. Effects of natal experience on habitat selection when
588 individuals make choices in groups: a multilevel analysis. *Animal Behaviour*, 71,
589 663-672.

590 **Stamps, J. A. & Davis, J. M.** in press. Adaptive effects of natal experience on habitat
591 selection by dispersers. *Animal Behaviour*,

592 **Stamps, J. A., et al.** 2005. Search costs and habitat selection by dispersers. *Ecology*, 86,
593 510-518.

594 **Stamps, J. A. & Swaisgood, R. R.** in press. Someplace like home: experience, habitat
595 selection and conservation biology. *Applied Animal Behavior Science*,
596 **Ward, S. A.** 1987. Optimal habitat selection in time-limited dispersers. *American*
597 *Naturalist*, 129, 568-579.

598 **Watters, J. V., et al.** 2003. Phenotype management: a new approach to habitat
599 restoration. *Biological Conservation*, 112, 435-445.

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604 Table 1. Akaike information criteria (AIC) for alternative models of the influence of natal

605 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

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607 ^aLower values of AIC indicate that increased efficiency in predicting acceptance rates. The Akaike weight,

608 w, ranges from 0 to 1 and indicates the relative support for each model. Models with greatest degree of

609 support are shaded.

610

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

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

626

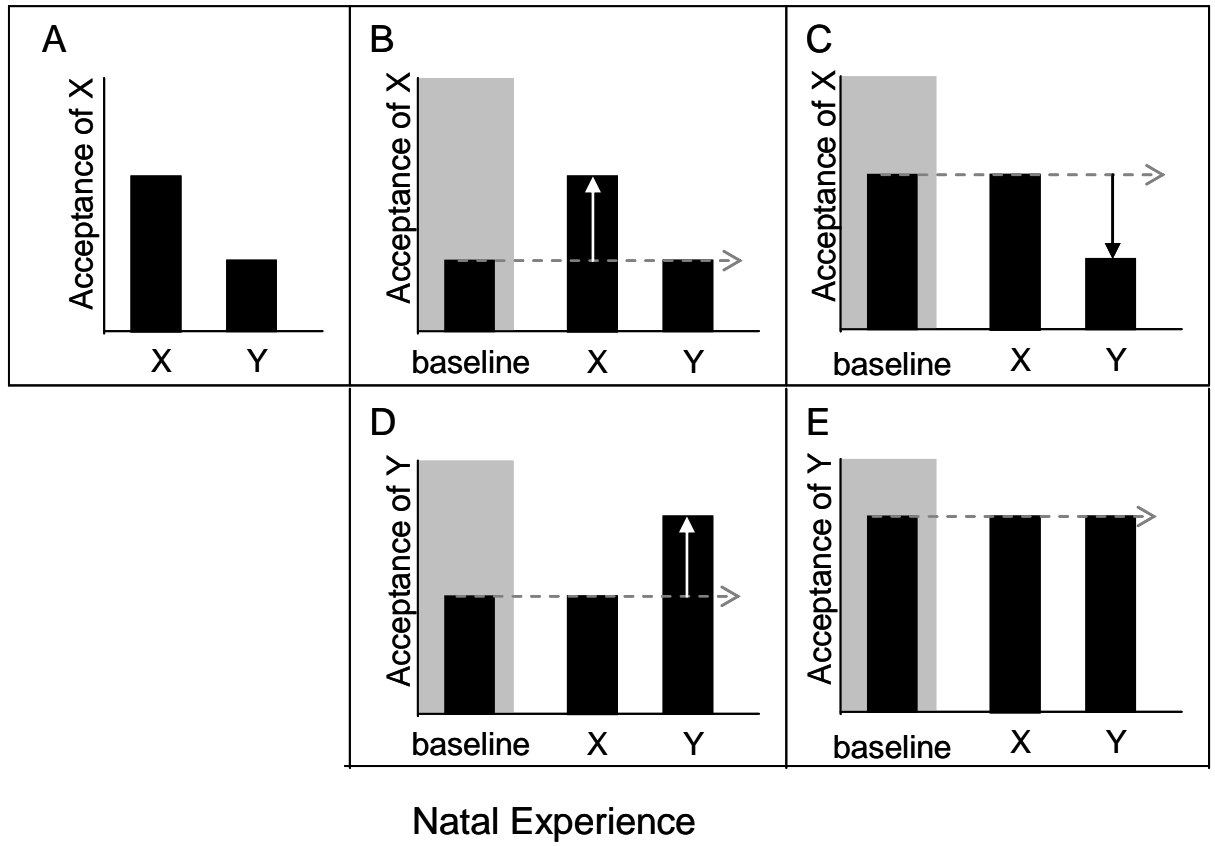
627 Figure 2. The effect of natal experience on the proportion of flies entering early into traps
628 baited with apple (white bars), kiwi (black bars) and banana (hatched bars). Flies having
629 natal experience with Bloomington fly media were used to estimate measures of bait
630 acceptance in the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

634

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: $\beta = -.119$, $t = 0.833$, $p = .389$).

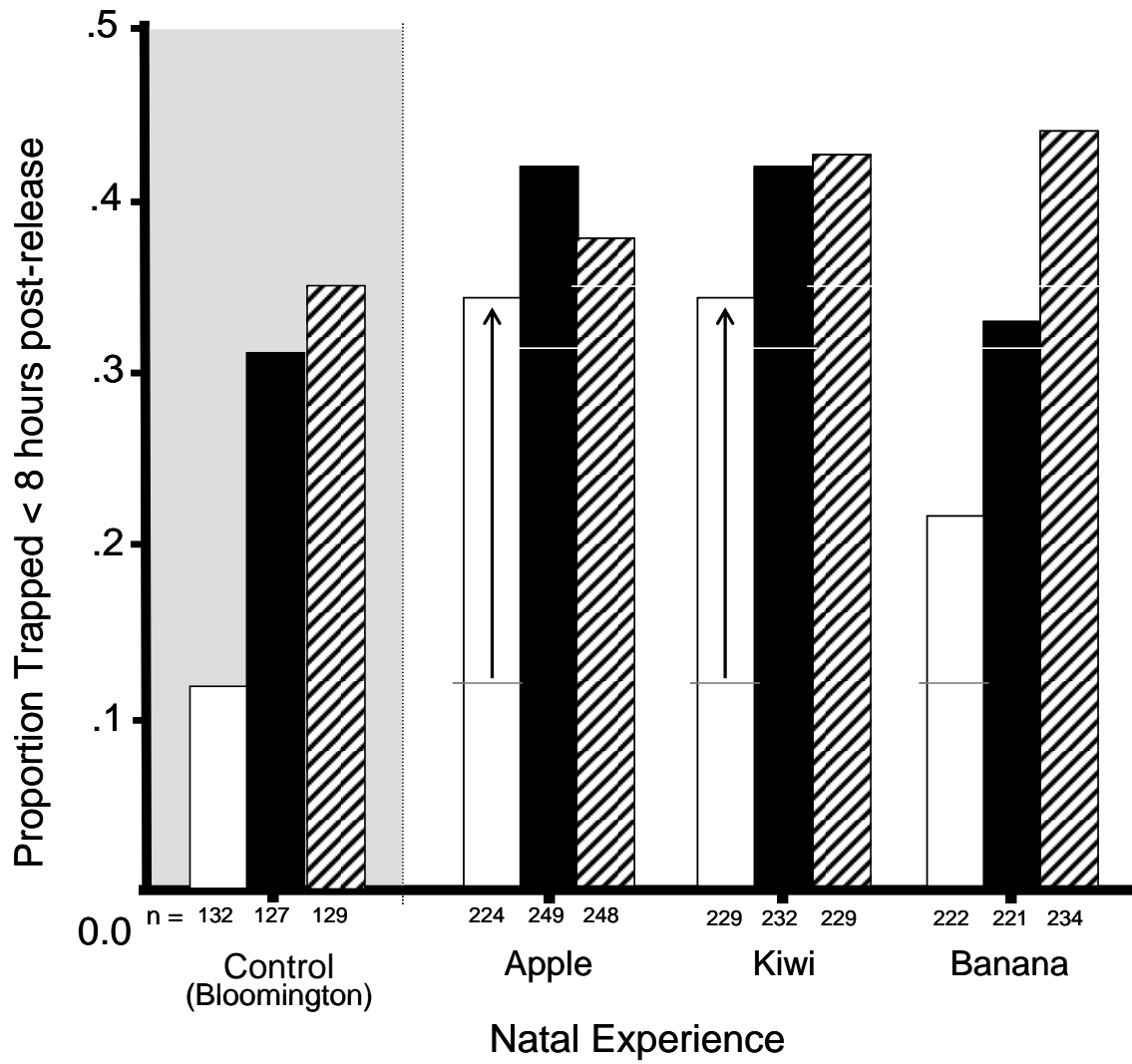
642 Figure 1.

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Figure 2.



668 Figure 3.

