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**Adaptation to a novel environment drives female habitat preference, not mate choice**

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**Abstract**

Understanding the factors that contribute to reproductive isolation is essential to understanding the process of speciation. Populations can undergo reproductive isolation when experiencing divergent selection after introduction to a novel environment. In this study, we looked for evidence of the evolution of premating isolation in the host generalist grain pest, red flour beetle (Coleoptera: Tribolium castaneum) after adaptation to a novel environment. Through mate and habitat preference assays, we support the preference-performance hypothesis that females will preferentially lay eggs on hosts that increase offspring performance. We found evidence that T. castaneum may have evolved host specialization as well as incomplete behavioral premating isolation based on female habitat preference.

**Introduction**

According to the theory of ecological speciation, populations experiencing divergent selection after undergoing a host shift can evolve reproductive isolation (Schluter 2000). Premating isolation can evolve as a “by-product” when mating or environmental preferences are genetically correlated with the traits under divergent natural selection. Moreover, the preference-performance hypothesis posits that females should evolve preference for the habitat in which their offspring have the best performance (Levins and MacArthur 1969, Jaenike 1978). Understanding the factors that contribute to reproductive isolation after selection in a novel environment is critical to our understanding of the process of speciation.

In this study, we looked for evidence of the evolution of premating isolation in several populations of the red flour beetle (Coleoptera: *Tribolium castaneum*) after selection in a novel environment. *T. castaneum* are ubiquitous, generalist grain and stored food product pests. Understanding whether they might adapt and diversify as a result of introduction to a new environment (*i.e.* stored food product) is of great economic importance. Adaptation to a new environment and host specialization could lead to costly problems for grain producers. We will use mate and habitat choice assays to determine whether premating reproductive isolation has evolved as a result of adaptation to a novel environment.

## Methods

### *Experimental populations*

We used 40 populations of soy flour adapted *T. castaneum* which originated from 11 wheat flour adapted lines with up to 5 replicates of each population. These soy adapted populations were founded by a sample of 20 beetles from the wheat adapted lines and maintained on soy flour for 40 weeks (~10 generations). At week 40, a soy performance index (PI40) was calculated for each soy adapted population (Figure 4, Table 1). PI40 is a weighted count of the combined number of offspring of three females 28 days after one day of oviposition. Weightings were based on developmental class (adults=3, pupae=2, larvae=1).

*Preference Assays*

To determine the reproductive isolation between the wheat and soy adapted populations, we set up 4 preference assays: (1) female mate choice between wheat adapted and sympatric males, (2) female mate choice between sympatric and allopatric males, (3) male habitat choice between wheat and soy flour, and (4) female habitat choice between wheat and soy flour. In mate choice assays, soy adapted female beetles were given a choice between 2 different males. Wheat adapted males were sampled from the female's ancestral stock line, sympatric males were sampled from the female's population, and allopatric males were sampled from other soy adapted populations that shared a common ancestral stock line with the female. In habitat choice assays, wheat and soy adapted male and female beetles were given a choice between soy and wheat flour. Choice was recorded by their position in relation to their options (options were positioned at -4 and 4, 0 was half way between), which was recorded every 5 minutes for a total of 25 minutes.

*Statistical Analysis*

Mate choice assays were analyzed by testing if the mean female position differed from 0 using a two-tailed t test. The habitat choice assays were analyzed by testing if the difference between the sample means of soy adapted lines and wheat adapted lines was greater than 0 using a one-tailed t-test. All analyses were conducted with R v. 2.14 (2011).

## Results

In both mate choice assays, the soy adapted females did not show a preference for soy adapted versus wheat adapted males ($t = -0.0192$, p-value = 0.9848; Figure 1) or for allopatric versus sympatric males (two-tailed t-test, $t = 1.7614$, p-value = 0.08643; Figure 1). In the habitat choice assays, soy adapted males did not prefer soy flour more that wheat adapted males (one tailed t-test, $t = -0.4662$, p-value = 0.676; Figure 2). However, soy adapted females did have a higher preference for the soy flour environment than the wheat adapted females (one-tailed t-test, $t = 2.0412$, p-value = 0.02915; Figure 3). Based on these results, we ran a test to determine whether habitat preference and soy performance were correlated. We found a significant correlation between habitat choice and performance on soy (PI40) (Pearson's $r= 0.39$, p-value = 0.014; Figure 4).

## Discussion

*T. castaneum* are considered to be host generalists, as they are found on a wide variety of processed food products. Based on soy adapted female habitat preference for soy (a formerly unfavorable habitat), we can infer that these populations have evolved host specialization. This could have important and costly implications for stored food products because it shows that when *Tribolium* are introduced to new food products, they can adapt and even become specialized.

Our results also support the preference-performance hypothesis. Females were not allowed habitat choice in soy adapted populations. Therefore, habitat preference and soy performance are likely genetically correlated.

We did not find evidence of premating isolation from mate choice or male habitat preference assays. However, soy adapted females prefer soy flour to wheat flour. Divergent selection on wheat and soy flour resulted in populations with increased performance on soy and, as a by-product, females with increased preference for soy. This preference could result in behavioral premating isolation between soy and wheat selected lineages which could drive their diversification. Given the inferred genetic correlation between soy performance and female soy preference, we could extrapolate that as performance on soy increases over time, behavioral premating isolation will also increase.

*Future directions*

Mate choice could evolve over time, so it would be beneficial to re-evaluate mate choice preferences after another 10 generations of selection. This re-evaluation would also allow us to determine whether habitat preferences have increased over time. In this study, we only explored female choice because *Tribolium* males often do not show mate choice preferences and because female mate choice preferences have been detected in *T. confusum* (Wade *et al* 1993; 2005). However, it would be interesting to determine if male choice has evolved in these populations. Additionally, future studies examining hybrid fitness between wheat and soy adapted populations would determine whether post-mating isolation has evolved.

**Acknowledgements**

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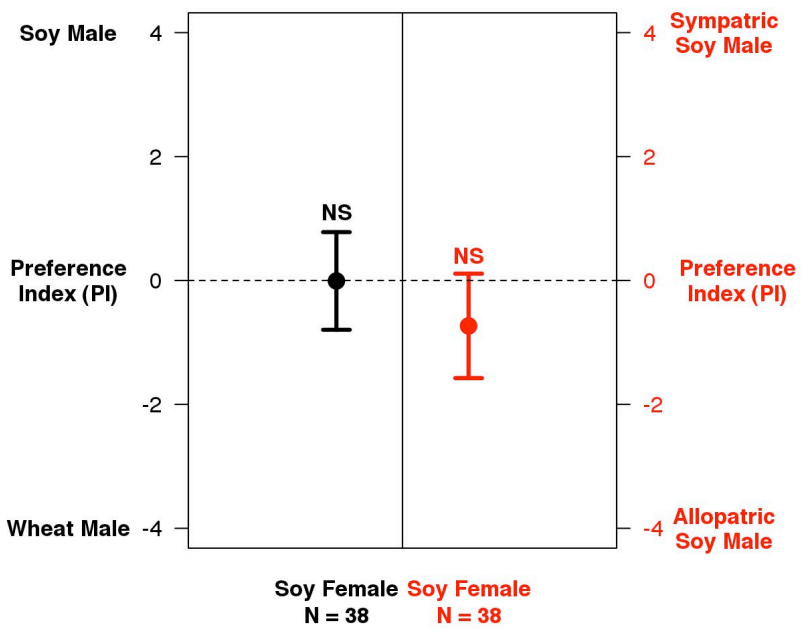


Figure 1:
Preference index measures choice of mate based on position of female relative to the two males. A) Soy adapted females were given a choice between soy adapted males from their own population and wheat adapted males from their ancestral wheat adapted population. Females showed no preference. B) Soy adapted females were given a choice between soy adapted males of their own population (sympatric) and soy adapted males of a different soy adapted population from their ancestral wheat adapted population (allopatric). Females showed no preference.

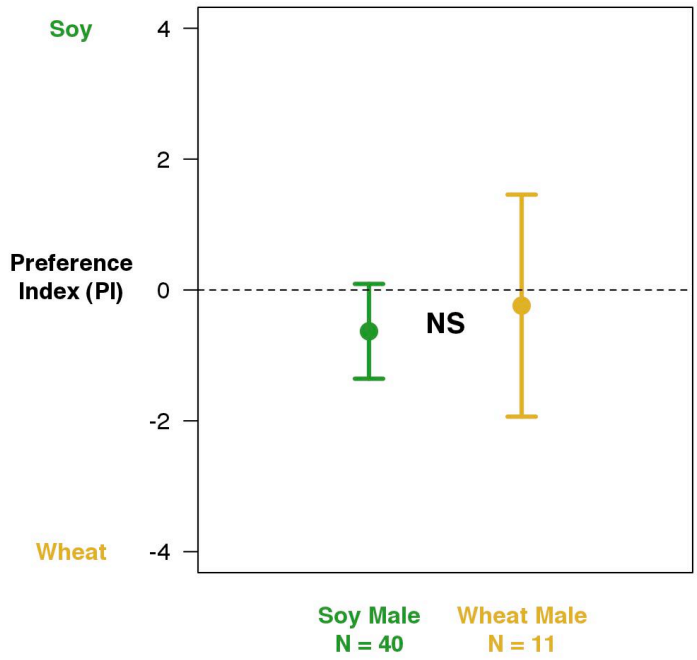


Figure 2:
As in Figure 1, preference index measures choice based on position of male relative to the two flours. Males from soy adapted (left) and wheat adapted (right) populations were given a choice between soy flour and wheat flour. Soy adapted males did not have a greater preference for soy than wheat adapted males.

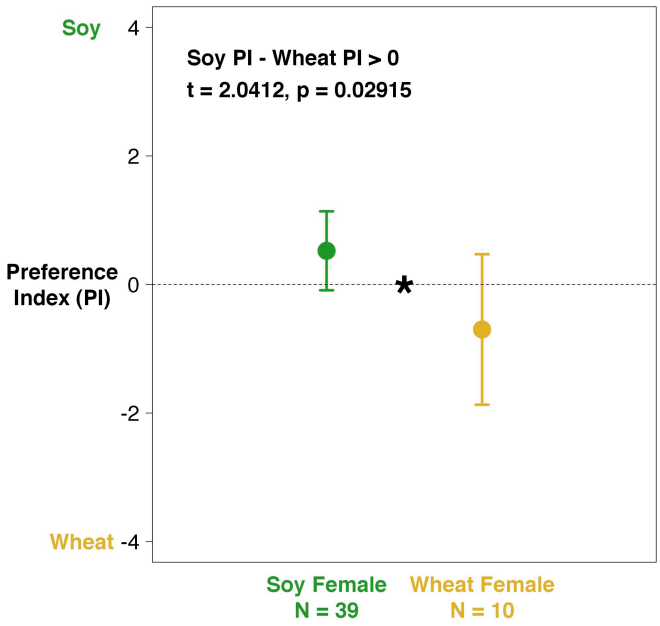


Figure 3:
Preference index measures choice based on position of female relative to the two flours. Females from soy adapted (left) and wheat adapted (right) populations were given a choice between soy flour and wheat flour. Soy adapted females have a greater preference for soy than wheat adapted females.

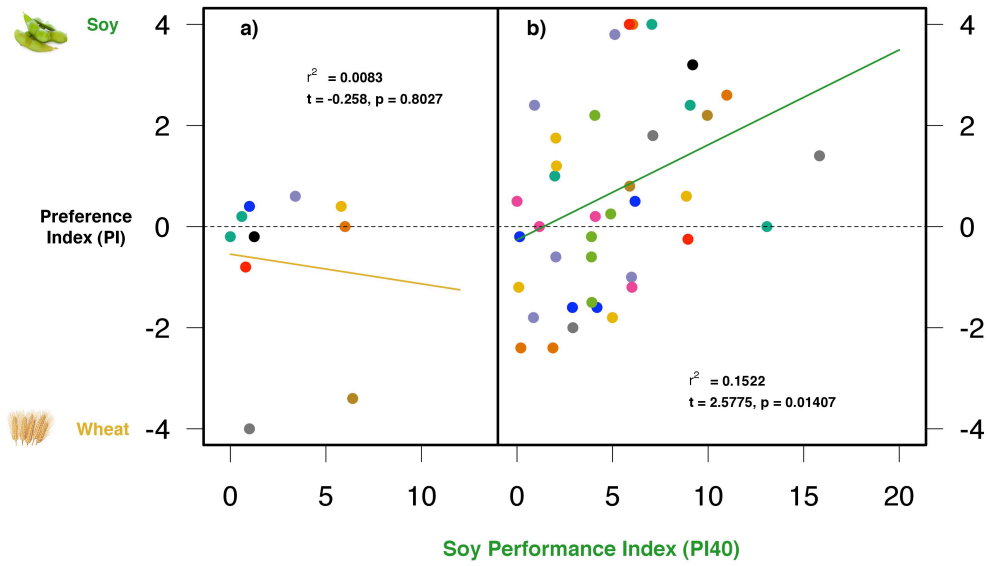


Figure 4:
PI40 is a weighted count of the combined number of offspring of three females 28 days after one day of oviposition. Weightings were based on developmental class (adults=3, pupae=2, larvae=1). PI40 was assessed in soy adapted populations after 40 weeks of selection on soy flour. Performance index was measured as in Figure 3. We looked at wheat adapted populations (a) and soy adapted populations (b). There is a correlation between soy performance and soy preference in the soy adapted populations. Colors refer to the ancestral wheat adapted populations (Table 1, right). Data points were jittered to avoid masking points with the same values.

| Population | Rep | PI40 |
|---|---|---|
| Colombia (corn) | 1 | 18 |
| TX, USA (corn) | 1 | 16 |
| Tanzania (?) | 4 | 13 |
| TX, USA (rice) | 3 | 11 |
| India (wheat) | 2 | 10 |
| TX, USA (corn) | 2 | 9 |
| India (wheat) | 1 | 9 |
| Tanzania (?) | 2 | 9 |
| TN, USA (wheat) | 1 | 9 |
| India (rice) | 2 | 7 |
| TX, USA (rice) | 1 | 7 |
| India (rice) | 3 | 6 |
| TX, USA (rice) | 2 | 6 |
| Tanzania (?) | 1 | 6 |
| Tanzania (?) | 5 | 6 |
| Japan (rice) | 5 | 6 |
| Colombia (corn) | 2 | 6 |
| TX, USA (corn) | 5 | 5 |
| TX, USA (rice) | 5 | 5 |
| TN, USA (wheat) | 2 | 5 |
| India (?) | 1 | 4 |
| TX, USA (corn) | 4 | 4 |
| India (wheat) | 5 | 4 |
| TX, USA (rice) | 4 | 4 |
| TN, USA (wheat) | 4 | 4 |
| TN, USA (wheat) | 5 | 4 |
| India (rice) | 5 | 3 |
| Tanzania (?) | 3 | 3 |
| India (?) | 2 | 2 |
| India (?) | 3 | 2 |
| India (?) | 5 | 2 |
| Colombia (corn) | 5 | 2 |
| Singapore (rice) | 5 | 2 |
| India (rice) | 4 | 1 |
| TX, USA (corn) | 3 | 1 |
| Colombia (corn) | 3 | 1 |
| India (wheat) | 4 | 0 |
| Japan (rice) | 3 | 0 |
| Japan (wheat) | 3 | 0 |
| Japan (wheat) | 5 | 0 |

Table 1:
Population refers to the geographic origin of the ancestral wheat adapted lines. The grain the population was originally collected from is in parentheses. Up to 5 replicates were initially made from each ancestral population for selection on soy. Pi40 is calculated as in Figure 4 (see methods).