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The cost of polyphagy: oviposition decision time vs error rate in a butterfly

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Neural constraints on information processing have emerged as a possible general explanation for why a majority of plant-feeding insects are relative specialists. According to the hypothesis, acquiring and processing information necessary to make fast and accurate oviposition decisions will carry a cost. As plants constitute a vast but diverse resource, the cost can be expected to increase with increasing host range. The cost can be paid in two currencies: time or accuracy. Both types of costs have been demonstrated, using a variety of taxa including butterflies. However, all studies have measured either one of the two currencies. Hence, there is the possibility that a decrease in one of the currencies can be compensated by an increase in the other, in which case the net outcome may not be a cost at all. Poor oviposition decisions could then be counterbalanced by shorter decision times, which could lead to higher realized fecundity. Using two strains of butterflies (*Polygonia c-album*) with different degrees of specificity, I test the hypothesis that the previously reported higher error rates in the more polyphagous butterflies are compensated by shorter decision times at oviposition. Post-alighting decision times were measured while the females evaluated a preferred plant (*Urtica dioica*) for oviposition. Contrary to the expectations, the polyphagous butterflies actually had longer decision times than the specialized butterflies, giving no support for the quality vs. quantity hypothesis. Instead, the results suggests that the polyphagous butterflies do pay a real cost for their wide host range and thus gives increased support for the information processing hypothesis as a general explanation for the widespread host specificity among plant-feeding insects.

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While relative generalists certainly exist in most insect groups, specialization is a very general rule among plant feeding insects (Bernays and Chapman 1994, Thompson 1994, Schoonhoven et al. 1998). One explanation for this pattern that has received renewed interest in recent years is that searching for and evaluating a large number of potential host plants can carry a substantial information cost (reviewed in Bernays 2001).

In a previous set of experiments with five species of nymphaline butterflies, we documented lower error rates for more specialized species compared with less specialized relatives, when given a choice of conspecific host plants of different quality (Janz and Nylin 1997). The study also included a comparison between females of *Polygonia c-album* of different origin, that differed in degree of specialization and the difference in error rates was evident even on this intraspecific scale. Hence, relative generalists appeared to pay for their ability to discriminate between several host plant species with a lower ability to discriminate between individuals of the same host species. A second experiment, using the same categories of *P. c-album* females, also demonstrated a similar difference when they were given a choice between the preferred host *Urtica dioica* and the non-host *Lamium album* that is similar in visual appearance (Nylin et al. 2000). While the more polyphagous swedish females sometimes accepted the lethal *L. album*

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for oviposition, the more specialized english females did not. They always laid all their eggs on *U. dioica*.

Other studies on the effect of neural limitations on host specificity have typically used decision times, rather than accuracy of decision, as unit of measurement (Bernays 1998, 1999, Bernays and Funk 1999). As no study thus far has measured both these components of the decision process, there is a possibility that a reduced capacity along one axis is compensated by an increased capacity along the other. In this case the higher error rates of the polyphagous butterflies could be seen as an alternative strategy that favors time at the expense of accuracy.

The tendency among the swedish butterflies in the experiment described above to accept *L. album* for oviposition is especially striking since the similarity between the plants is limited to visual appearance. It could therefore be argued that the generalist females in the experiment used less time and resources on post-alighting plant evaluation, as a means to achieve higher oviposition rate. It has been suggested that increasing the effort to assure good oviposition sites can be seen as a form of maternal care, where the female increases offspring survival at the expense of oviposition rate (Wiklund and Persson 1983, Janz 2002). It would thus be possible to view specialists and generalists as representing different outcomes of a trade-off between quality and quantity of offspring. In this case we should expect the polyphagous females to spend less time investigating and evaluating each host.

In this paper, I have investigated this hypothesis using the same categories of females (english and swedish *P. c-album*) used in the previous studies, in order to test if the more specialized females had longer decision times than the less specialized, while evaluating their preferred host *U. dioica* for oviposition.

Methods

Study species

Polygona c-album, the comma butterfly, is distributed across much of the Palearctic region, from Spain and the British Isles in the west all the way to China and Japan in the east. It is considered to be a polyphagous butterfly, feeding on plants from seven families in four orders, represented by the genera *Urtica*, *Humulus*, *Ulmus*, *Salix*, *Ribes*, *Betula* and *Corylus*. As with most other phytophagous insects these plants are ordered in a preference hierarchy, with highest preference for the species in Urticaceae, especially *Urtica*, intermediate preference for *Salix*, and *Ribes*, and low preference for *Betula* and *Corylus* (Nylin 1988, Janz et al. 1994). Offspring performance generally matches oviposition preferences fairly well, although there is individual variation (Janz et al. 1994).

Even if the hierarchy appears to be similar across populations (Nylin 1988, Nylin and Janz unpubl.), the level of specificity is variable. Some populations are highly specialized on *Urtica dioica* (e.g. southern England), while some populations use all plants in the repertoire (e.g. southern Sweden). This difference in degree of specialization between english and swedish females has been documented several times (Janz and Nylin 1997, Janz 1998, Nylin 1988, Nylin et al. 2000) and creates an ideal opportunity to study the dynamics of host plant specialization. The difference in specificity is thus well established, and appears to be largely determined by genes on the paternally inherited X-chromosome (Janz 1998).

The females used in this experiment came from overwintered laboratory stocks, with the same origin as the females used in a previous study on specialization and oviposition error rates (Nylin et al. 2000). Experiments were conducted during June 1999 and July 2000.

Experimental setup

Naïve, mated females were flown individually in $1 \times 1 \times 1$ m cages at the butterfly lab of Stockholm University. Each female had access to one fresh stalk of *U. dioica*, standing in aquaculture in the center of the cage and they were supplied with diluted sugar solution from a sponge. The cages were illuminated by free-hanging 75 W light bulbs hanging approximately 50 cm above the transparent cage roof. Decision times were measured with a stopwatch by taking time from landing on the plant to successful oviposition. Only observed landings resulting in oviposition were included in the analysis, as there was no way of determining whether a landing without oviposition represented a rejection or a landing for other purposes than laying eggs.

Decision times were recorded for 10 successful ovipositions for each of 28 females of swedish origin and 10 females of English origin, and were analyzed with repeated measures ANOVA. The unbalanced design was caused by poor availability of butterflies of english origin. Females of this species spend most of the time sitting inactive, probably relying on their strong crypsis to avoid detection by enemies. This inactivity is interrupted by relatively short bouts of activity when the females search for oviposition sites or sources for adult feeding. Observation of a particular cage thus started when the female showed signs of activity.

Results

After landing on a potential host plant, females inspect the plant by drumming the leaf surface with the forelegs and tapping it with the antennae. Females of english and swedish origin showed no difference in the type of behavior expressed during host plant evaluation.

Table 1. Repeated measures ANOVA table for log-transformed values of decision time at oviposition. Decision time was measured 10 times for each female as the time between landing and oviposition. "Origin" refers to females of swedish and english origin, representing generalist and specialist genotypes, with 28 females in the swedish and 10 females in the english category. $R^2 = 0.2694$, Adjusted $R^2 = 0.1640$.

Source	Partial SS	df	MS	F	Prob > F
Model	23.6529554	46	0.514194683	2.56	0.0000
Origin	1.04166373	1	1.04166373	5.18	0.0235
Female	20.6524561	36	0.573679335	2.85	0.0000
Measurement	2.22850771	9	0.247611968	1.23	0.2748
Residual	64.1462406	319	0.201085394		
Total	87.799196	365	0.240545742		

There was a statistically significant difference between specialist and generalist females in decision time. There was also a significant individual variation between females, but no significant difference between measurements (repeated measures ANOVA, Table 1). Both categories of females made their oviposition decisions relatively fast, with a mean decision time for the swedish females of 2.30 s (SE = 0.08, SD = 1.23), compared to 1.98 s (SE = 0.10, SD = 0.96) for the english females. Thus, contrary to the prediction from the "quality vs quantity" hypothesis, it was the more polyphagous swedish females that had longer decision times. Consequently, it seems fairly safe to conclude that the more generalist swedish females cannot compensate for their higher oviposition error rates demonstrated in previous studies with shorter decision times. Instead, the generalist females appear to pay a real cost for being polyphagous: not only do they make more oviposition mistakes, but they also use more time for host plant evaluation prior to making the oviposition decision. The fact that the analysis found significant effects of both origin and individual females but not of measurements within female suggests that there exists genetic variation for this trait both between and within these categories of females.

Discussion

This is, to my knowledge, the first study that is able to compare error rates with decision times in oviposition choice for the same species. The results did not support the hypothesis that the polyphagous females should be able to compensate their lower accuracy with a shorter decision time (Table 1). Even though the difference was rather small, the swedish butterflies had a significantly longer decision time than the more specialized english females. This makes it more difficult to interpret the lower accuracy of the polyphagous females as an alternative strategy to maximize offspring quantity over quality. Instead, it strongly suggests that polyphagous females do pay a real cost for their wider host range.

The decision that is measured in this study is only the last in a series of decisions needed to be made in the process of host choice, including the choice of habitat, the decision to approach a plant from a distance and the decision to land on a potential host plant. Judging from the short decision times reported here, post-alighting decisions may not impose the most severe time-cost of these, but they were where it seemed most likely that the generalists could possibly have had an advantage over the specialists. Measuring the other parts of this process will be more difficult, but certainly not impossible. It seems unlikely though, that generalists should be better at finding any given host than specialists, even though total host encounter rates could be expected to increase with a wider host range (Dukas and Clark 1995).

The costs of having higher error rates and decision times at oviposition are potentially very high for a plant-feeding insect, and the neural limitation hypothesis is rapidly becoming a major candidate for a general explanation of host specificity. However, such a general explanation also necessitates the search for fitness advantages of a wider host range that could potentially counterbalance these information-processing costs, such as risk spreading, increased encounter rates etc. We need to ask under what circumstances these costs and benefits will weigh over in favor of wider host ranges, allowing for the occasional host range expansions that evidently do occur.

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