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Specialists make faster decisions than generalists: experiments with aphids

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Theoretical studies and a few recent experimental reports suggest that the evolution of diet breadth in herbivorous insects is constrained by a limited neural ability to efficiently process large amounts of information in short periods of time. This neural-constraints hypothesis predicts that generalist herbivores should make slower or poorer decisions than specialists when selecting plants, because generalists must discriminate and decide among stimuli from a wider variety of potential hosts. The present study compares the speed with which host-associated decisions are made in specialist versus generalist populations of the aphid *Uroleucon ambrosiae*. Populations of *U. ambrosiae* from eastern North America are highly specific to the host plant *Ambrosia trifida* (Asteraceae), whereas those from the American south-west also feed on a variety of other taxa from the Asteraceae. Experiments with winged (alate) and wingless (apterous) individuals showed that host-finding, host-selection, host-acceptance, host-sampling and host-settling were more efficiently performed by the eastern specialists. These very consistent results provide evidence that strongly supports the neural-constraints hypothesis.

Keywords: diet breadth; herbivory; host-plant discrimination; neural constraints; *Uroleucon ambrosiae*

1. INTRODUCTION

Why are most of the myriad herbivorous insect species relatively specialized in their tastes, feeding and living on only a small proportion of the plant species available to them? This question has been a major focus of evolutionary ecology in recent decades (see, for example, Futuyma & Moreno 1988; Jaenike 1990). One potential explanation has none the less received rather little attention. This is the idea that the evolution of generalism is constrained by the increased neural sophistication required for generalists to behave as efficiently as specialists, which live in an effectively simpler world (Levins & MacArthur 1969; Bernays & Wcislo 1994). To date, limited evidence indicates that generalists and specialists may differ in the ability to discriminate among hosts of different quality or in the speed with which decisions are made (Janz & Nylin 1997; Bernays 1998).

This study examines the efficiency of host-selection behaviours in the aphid *Uroleucon ambrosiae*. Previous work indicates that *U. ambrosiae* specializes on the giant ragweed, *Ambrosia trifida*, in the eastern United States (Moran 1985). However, host records (Knowlton 1983) and recent collections indicate that this aphid is more generalized in the south-western United States (N. Moran and D. J. Funk, unpublished data), as well as in South America (Carvalho *et al.* 1998), where it uses hosts from several genera and tribes in the Asteraceae. Laboratory studies demonstrated significant differences between eastern and south-western aphids in their willingness to use species from four genera in the Asteraceae, with the eastern aphids exhibiting more

restricted patterns of acceptance (D. J. Funk and E. A. Bernays, unpublished data).

Here, we make use of this geographic variation in host specificity to test the hypothesis that a more specialized diet is associated with more efficient decision-making. We do so by assaying host-associated aphid behaviours spanning multiple stages in the complex process of host-plant selection and acceptance.

2. MATERIALS AND METHODS

Aphids were collected from a number of *Ambrosia trifida* plants at each of five localities, two representing the temperate forest habitats of the eastern USA (Mississippi and Minnesota) and three representing the arid south-western USA (all in south-eastern Arizona). Just as alates of *U. ambrosiae* regularly make decisions to leave poor-quality plants in search of better hosts, so too do the long-legged and highly mobile apterae (Moran 1986); both forms were evaluated in this study. The *A. trifida* plants used to test and propagate these aphids were grown from seeds harvested at an Arizona locality where this host is used by *U. ambrosiae*.

Using five kinds of behavioural assays, we tested the relative efficiency with which eastern versus south-western aphids find and use the *A. trifida* plant. Here, these assays are described in the order in which the associated host-selection behaviours would naturally occur. Individual field-collected adult female apterae were tested in experimental assays §2c and §2e below and then used to establish clonal colonies. Multiple eastern (including both Mississippi and Minnesota) and south-western clones were tested in each of the other assays to include genetic diversity. The non-parametric statistical methods used to analyse data sets are indicated in the results.

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(a) Host-finding by alatae: wind-tunnel experiments

Ten experiments were performed at 22 °C in a horizontal wind tunnel made of Plexiglass (3 m × 1 m × 1 m) within a laboratory at the University of Arizona. A fan pushed air through activated charcoal to remove volatile chemicals in the room, and through baffles and white nylon net screen to smooth the airflow, thus providing a wind speed of 0.2–0.4 m s⁻¹ in the tunnel. One to three potted plants of *Ambrosia trifida* were placed close to the screen to provide an odour source and a visual target for aphids. Double-sided adhesive tape around each plant pot ensured that aphids could only reach a plant by air.

In each experiment, between 16 and 40 recently moulted alates (30-h-old or less) from one eastern and from one south-western clone were simultaneously released 1 m downwind of test plants after being deprived of food for up to 5 h. Five hours after release the proportions of eastern and south-western aphids that had successfully arrived on the host were calculated. Aphids from the two regions were distinguished either by natural variation in pigment (shades of red or brown) or by preliminary dusting with fluorescent powder of two different colours. Four eastern and three south-western clones were tested.

(b) Host-selection by apterae: short-term tests in the presence of non-hosts

In each of three experiments, six aphids from each of four eastern and four south-western clones were tested in a greenhouse at 22–26 °C, between 07.30 and 12.00. All test aphids were removed from clonal colonies immediately before testing, and each of the 24 replicate trials in each experiment simultaneously evaluated one aphid from each of the two regions. In each trial, the aphid pair was placed at the top of a wooden dowel that emerged from a bouquet of similarly sized cuttings of *Ambrosia trifida* (the principal host of all aphids) and two non-hosts, presented together in a vial of water. The time required for each aphid to reach the host (i.e. place two tarsi on *A. trifida*) was recorded.

In experiment 1, non-host cuttings were the odoriferous *Mentha spicata* (Lamiaceae) and *Peucedanum graveolens* (Apiaceae), obtained from potted plants in the greenhouse. In experiment 2, non-hosts were Arizona herbs from the same family as the principal host plant (Asteraceae), *Macheraanthera asteroides* and *Solidago wrightii*, the first obtained from plots near to the University of Arizona campus and the second from potted plants in the greenhouse. Experiment 3 used the herbaceous plants *Sisymbrium altissimum* (Brassicaceae) and *Lupinus sparsiflorus* (Fabaceae) collected from the field in regions where *U. ambrosiae* occurs.

(c) Host-acceptance by apterae: observations on *A. trifida*

Six experiments were carried out in a greenhouse unit where temperature fluctuated daily between 20 and 28 °C. Each was initiated between 09.00 and 11.00, and completed within 6 h. Each of five experiments treated apterae collected from (a different) one of the five aphid-collecting localities; the sixth experiment tested Minnesota aphids a second time. Aphids used in this assay had just completed the host-settling assays described in §2e below and were thereafter kept on plant material until 0.5–1.5 h before testing.

In each experiment, each of 16 aphids participated in a separate continuous observation trial on each of four potted *A. trifida* plants. A trial was initiated with the placement of an aphid onto the meristematic tissues of a test plant (where it would ordinarily feed) by means of a camel-hair

brush. Aphid probing behaviours were then continuously observed and recorded for 15 min with The Observer program on a laptop computer (Noldus 1991). Latencies until probing (identified by the placement of the rostrum onto the plant surface, at an angle perpendicular to the body), distributions of probing events (bouts) and gaps between probing events (interbouts) were calculated.

(d) Host-feeding by apterae: electrical penetration graph (EPG) analyses

To investigate searching efficiency of aphid mouthparts after initial host-acceptance and probing, we applied direct current electrical penetration graph (EPG) techniques (Tjallingii 1990) to a number of eastern and south-western apterae on potted *Ambrosia trifida* plants. Each aphid was attached to a gold wire (20 µm diameter) with silver paint and allowed to acclimatize on a plant overnight. The next day, the gold wire was connected to an amplifier to which the plant was also connected via a metal probe in the soil. When the rostrum (enclosing the elongate mouthparts) was lowered to the plant surface, cuticle penetration usually occurred within a few seconds, completing an electrical circuit. Subsequent probing produced diagnostic electrical waveforms that were recorded by using the computer program Stylet 2.0 (Tjallingii & Hogan Esch 1993). These were used to assess mouthpart activities within plant tissues, including feeding. We analysed the time from cuticle penetration to the first potential drop (indicating cell penetration and sampling), the time to reach the feeding site in the phloem, the number of phloem-feeding bouts and the proportion of time spent feeding on phloem in the first 12 h on the plant.

(e) Host-finding and settling by apterae in the presence of additional species of Asteraceae

Six experiments were performed in a greenhouse unit where temperature fluctuated daily between 20 and 28 °C, in four cylindrical clear Plexiglass arenas (60 cm high × 46 cm in diameter). Each arena contained individual potted plants of *Ambrosia trifida* (sole host of eastern aphids and principal host of south-western aphids), *Viguiera dentata* and *Heterotheca subaxillaris* (species in the family Asteraceae that are non-hosts for eastern aphids and additional hosts for south-western aphids), and *Solidago wrightii* (an asteraceous non-host for all aphids). Plant heights within arenas were adjusted so that a roughly equal biomass of each poked through and extended above a false floor of brown cardboard. Plants within each arena were arranged equidistant from each other in a square, as were the arenas themselves.

Each of five experiments treated apterae collected from (a different) one of the five aphid-collecting localities; the sixth experiment tested Minnesota aphids a second time. In each experiment, equal numbers of test aphids were placed in the centre of each arena before covering the arena with mesh. Approximately 24 h after the 09.00 starting time, we scored the number of aphids on each test plant.

3. RESULTS**(a) Host-finding**

Alates took off and flew but usually did not make directed flights to the host plant, so that orientation responses could not be scored. However, a significantly higher proportion of eastern aphids ultimately found the host during the test period (sign test, $p < 0.01$) (figure 1).

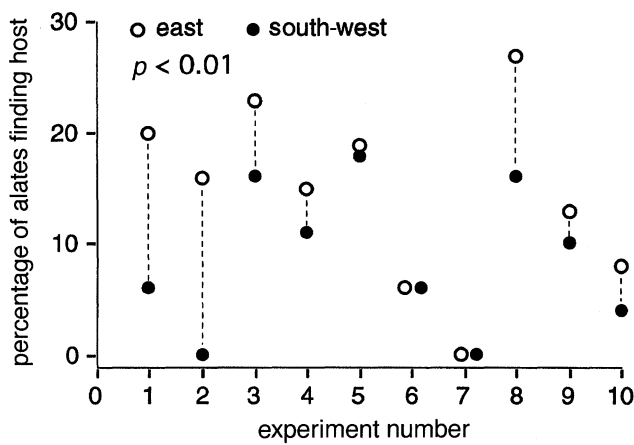


Figure 1. Percentages of alate aphids finding the *Ambrosia trifida* host plant in each of ten five-hour windtunnel experiments. Eastern aphids found the host more readily than south-western aphids.

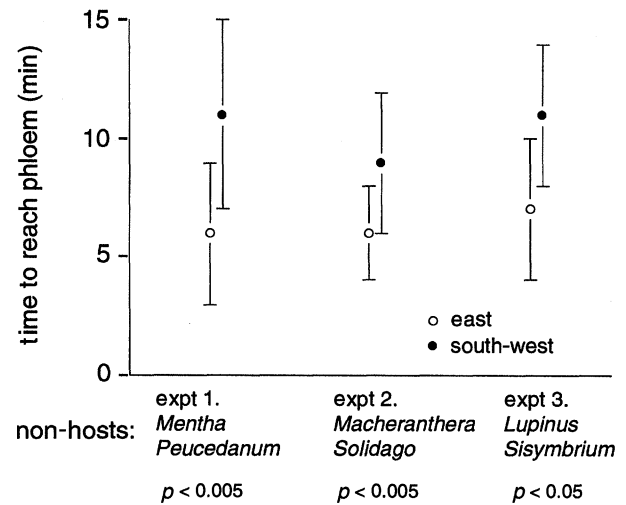


Figure 2. Time taken by aphids to reach the *Ambrosia trifida* host cuttings in bouquets of host and non-host plants in each of three experiments. Medians with MAD (median absolute deviation) error bars are shown. Eastern aphids reached the host sooner than south-western aphids.

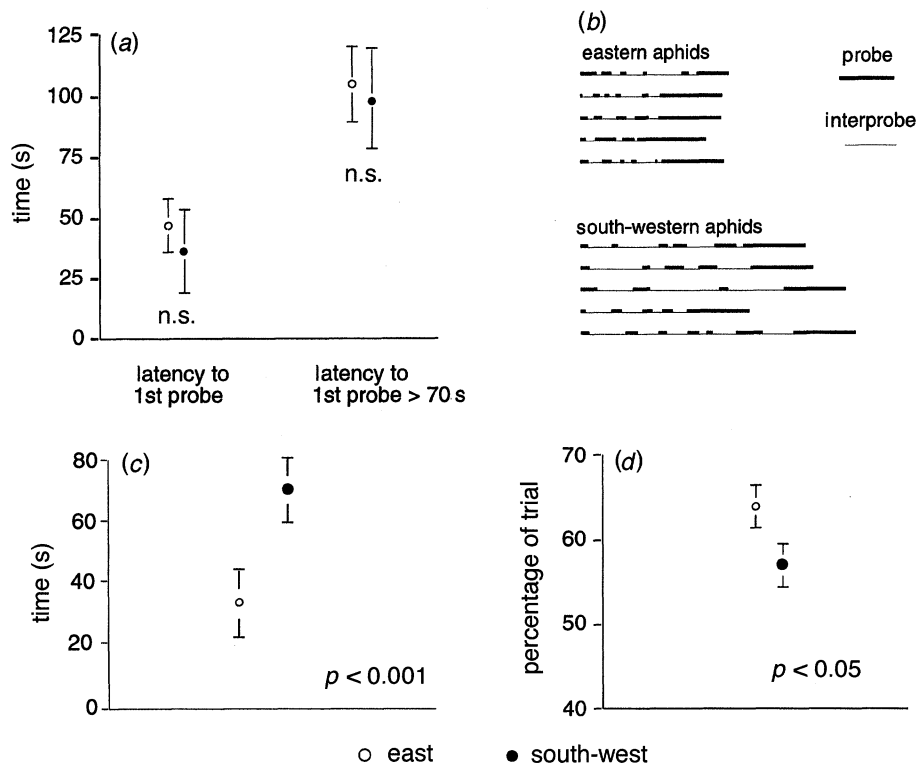


Figure 3. (a) Latency to probing after placement on plants. Eastern and south-western aphids did not differ. (b) Examples of probing patterns preceding the first persistent probe by five eastern and five south-western aphids. (c) Length of the first interbout. Eastern aphids initiated a second bout of probing faster than south-western aphids. (d) Percentage of time spent probing during the 15-min trial. All data are from aphids on *Ambrosia trifida*. Values in (a), (c) and (d) are given as median values with MAD error bars.

(b) Host-selection

Eastern aphids reached *A. trifida* significantly sooner than south-western aphids in all three experiments with bouquets of mixed plants (Wilcoxon's signed-rank tests: experiment 1, $p < 0.005$; experiment 2, $p < 0.005$; experiment 3, $p < 0.05$) (figure 2).

(c) Host-acceptance

Initial probing attempts during the continuous observation trials were often very short and belonged to a separate population of behaviours from more persistent probes of over 70 s (D. J. Funk and E. A. Bernays, unpublished data) (figure 3b gives some examples). Eastern and south-western aphids did not differ in the median times to

either initial probing (Mann-Whitney U -test, $p > 0.05$) or first 'persistent probes' (Mann-Whitney U -test, $p > 0.5$) (figure 3a). However, interbouts occurring before the first persistent probe tended to be shorter (figure 3b), and the first interbout length was significantly shorter in eastern aphids (figure 3c) (Mann-Whitney U -test, $p < 0.01$). Overall eastern aphids also probed for a greater fraction of the trial than did south-western aphids (Mann-Whitney U -test, $p < 0.05$) (figure 3d).

(d) Host-feeding

Electrical recordings showed that *U. ambrosiae* behave similarly to other aphids once their mouthparts have penetrated the plant cuticle. Major potential drops indicated

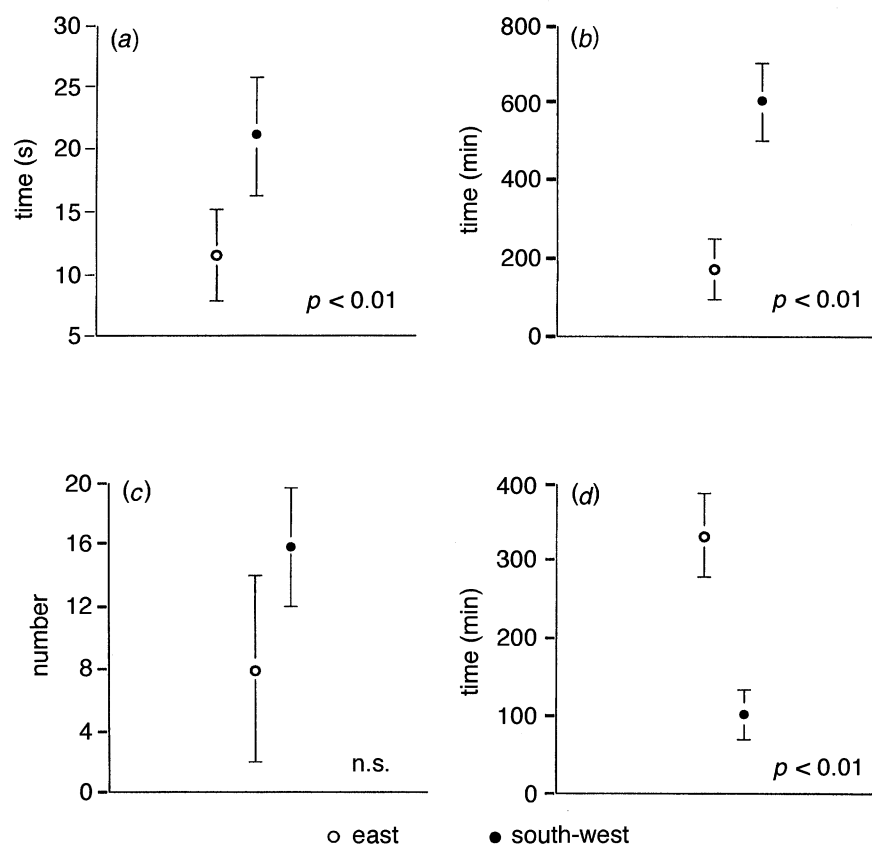


Figure 4. (a) Latency from cuticle penetration and electrical contact to first potential drop, indicating intracellular sampling of sap. Eastern aphids sampled sooner than did south-western aphids. (b) Latency from electrical contact to first waveform characteristic of phloem feeding. Eastern aphids fed from phloem sooner than south-western aphids. (c) Number of separate phloem-feeding events in 12-h test period. Eastern and south-western aphids did not differ. (d) Time spent phloem-feeding during the 12-h test period. Eastern aphids fed more than south-western aphids. In all cases the values represent medians with MAD error bars.

penetration into, and sampling of, cells (Martin *et al.* 1997), whereas prolonged potential drops with characteristic rhythmic changes in potential indicated phloem feeding (Tjallingii 1990). The time between first electrical contact and the first potential drop was significantly shorter for eastern aphids (Mann–Whitney *U*-test, $p < 0.01$) (figure 4a), as was the time required to reach and feed from phloem tissue (Mann–Whitney *U*-test, $p < 0.05$) (figure 4b). Eastern aphids tended to have fewer separate phloem-feeding events, although the differences were not significant (Mann–Whitney *U*-test, $p > 0.05$) (figure 4c), and they settled into prolonged phloem-feeding bouts more readily than south-western aphids, leading to a significantly greater proportion of the 12 h trials spent feeding (Mann–Whitney *U*-test, $p < 0.01$) (figure 4d).

(e) *Host-settling*

After being allowed to find and evaluate plants from four genera of Asteraceae for 24 h, a significantly higher fraction of eastern aphids had settled on *A. trifida*, the preferred host plant (Funk & Bernays 1999), whereas more south-western aphids were found on suboptimal plants (figure 5). Successful settling on the *A. trifida* plants was also significantly different (χ^2 -test, $p < 0.05$).

4. DISCUSSION

The idea that neural limitations constrain the efficiency of generalists more than that of specialists is not new. (Since Levins & Courtney 1983; Lewis 1986; Papaj 1990). More recently, a number of authors have suggested that constraints on information processing might help explain the general tendency of herbivorous insects to specialize on relatively few host plants (see, for example, Dukas &

Real 1991, 1993; Fox & Lalonde 1993; Bernays & Wcislo 1994; Kotler & Mitchell 1995; Larsson & Ekbom 1995; Bernays 1996; Dall & Cuthill 1997). Empirical investigations of this hypothesis have, however, only recently been initiated.

For the multiple aspects of host-related behaviour tested here, specialist *Uroleucon ambrosiae* from the eastern USA made faster, more efficient decisions than did their more generalized south-western counterparts, and they did so with striking consistency. These results, demonstrating a relation between restricted diet breadth and efficiency of host-plant selection, support the neural-constraints hypothesis. These findings are particularly compelling because they were observed in natural and closely related populations within a single herbivore species.

The two previous experimental tests of neural constraints in insect herbivores also found specialists to be better decision-makers. Janz & Nylin (1997) showed that specialist butterflies chose to oviposit on individual nettle plants that yielded higher offspring survival, whereas generalist butterflies failed to discriminate in favour of these higher-quality plants. Bernays (1998) reared a species of generalist grasshopper on either a single food or a mixed diet and found that grasshoppers reared as specialists initiated feeding sooner after contact with food than those reared as generalists, and also exhibited fewer and shorter pauses while feeding. Similarly, tests on bees with different diet breadths have demonstrated greater behavioural efficiency of relative specialists (Dukas & Real 1993).

Because nervous systems have limited capacity to process multiple sensory inputs (Dusenbery 1992), identifying, discriminating, and choosing among potential host

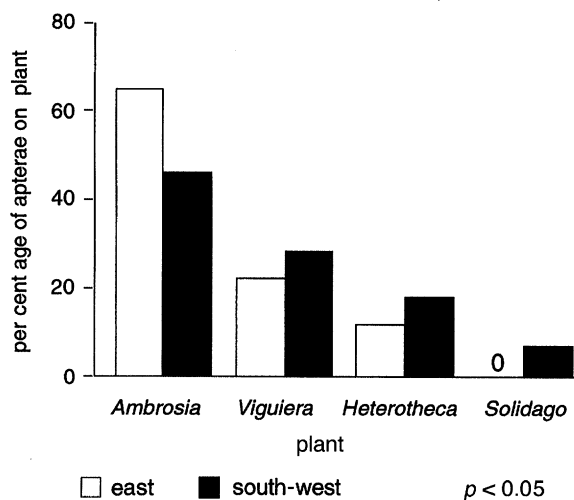


Figure 5. Percentage of aphids settling on plants from four Asteraceae genera during 24 h choice tests. Eastern aphids settled more on the principal host plant, *Ambrosia trifida*, and less on the alternative plant species, than south-western aphids. The probability value refers to the difference between proportions of eastern and south-western aphids on *A. trifida*.

plants presents a challenge to insect herbivores. The same challenge is encountered by any animal engaging in any behaviour; experimental demonstrations of these constraints have mostly focused on vision in mammals. Such work has shown that simultaneous computations across the entire field of vision are impossible so that attentiveness to different parts of the visual field must occur over time (see, for example, Maunsell 1995).

The ability to focus on particularly important stimuli while ignoring others provides an important means of avoiding the time-absorbing indecision that would otherwise result from these constraints on information processing (LaBerge 1995; Dukas 1998). Such 'selective attention' is more feasible when the stimulus is conspicuous. This principle is assumed to explain the value of 'sign stimuli' to animals in many different contexts, especially intra- and interspecific communication (see, for example, Tinbergen 1948; Endler 1988). It may further explain the extreme sensitivity of many specialist insect herbivores to one or a few of the myriad plant compounds that characterize their extraordinarily complex chemical environment (see, for example, Bernays & Chapman 1994).

If selective attention increases the accuracy with which a herbivore evaluates the quality of a host for larval development (as in Janz & Nylin 1997), the fitness advantages of specialization are obvious. Less clear is whether faster decision-making also enhances fitness. Does it really matter if a choice takes one minute or three minutes? In some birds, developing a search image (selective attention to a few visual cues) has been shown to increase feeding rate and improve competitive ability (see, for example, Reid & Shettleworth 1992), demonstrating a functional advantage of behavioural efficiency. Although such interference competition is probably rare in herbivorous insects (Strong *et al.* 1984), a more general consequence of increased decisiveness may be decreased vulnerability to

predators. An animal that is engaged in food-associated decision-making may be less attentive to the risk of predation. This has been shown for birds (see, for example, Lima & Dill 1990; Sih 1993) and fish (see, for example, Milinski 1990), and feeding-related activities in caterpillars can increase predation rate 100-fold (Bernays 1997). We suggest that the lower decisiveness of generalist herbivores shown here and by Bernays (1998) constitutes a selective disadvantage in natural systems that favours the evolution of specialization. The notion that a genetically based increase in selective attention to particular plant chemicals promotes specialization complements the roles for allelochemicals suggested by earlier authors (e.g. Feeny 1992). The need for enhanced selective attention in the face of neural constraints is consistent with theories implicating plant species abundance (Futuyma 1983) and predation risk (Bernays & Graham 1988; Bernays 1989) in the evolution of herbivore specialization.

In *Uroleucon ambrosiae*, any mechanistic differences underlying the divergent efficiencies of eastern and south-western aphids are unlikely to involve major differences in neural machinery, although this has not been investigated. Eastern clones could perceive a greater sensory contrast between *A. trifida* and other potential hosts than do south-western clones, owing to increased sensitivity to host-specific or non-host signals. In our host-finding and host-acceptance assays, however, east-south-west differences were observed although no choice of plants was offered. This result suggests that increased sensitivity to, or arousal by, the principal host itself contributes to faster decisions and motor output by the eastern aphids.

In future work, the investigation of additional herbivore taxa and the examination of alternative bases for behavioural efficiency (such as divergent adaptations to climate) will help determine just how significant neural constraints may be in the evolution of host-specialization.

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REFERENCES

- Bernays, E. A. 1989 Host range in phytophagous insects: the potential role of generalist predators. *Evol. Ecol.* **3**, 299–311.
- Bernays, E. A. 1996 Selective attention and host-plant specialization. *Entomol. Exp. Appl.* **80**, 125–131.
- Bernays, E. A. 1997 Feeding by caterpillars is dangerous. *Ecol. Entomol.* **22**, 121–123.
- Bernays, E. A. 1998 The value of being a resource specialist: behavioural support for a neural hypothesis. *Am. Nat.* **151**, 451–464.
- Bernays, E. A. & Chapman, R. F. 1994 *Host plant selection by phytophagous insects*. New York: Chapman & Hall.
- Bernays, E. A. & Graham, M. 1988 On the evolution of host specificity in phytophagous arthropods. *Ecology* **69**, 886–892.
- Bernays, E. A. & Wcislo, W. 1994 Sensory capabilities, information processing and resource specialization. *Q. Rev. Biol.* **69**, 187–204.

- Carvalho, R. C. Z., Blackman, R. L. & Spence, J. M. 1998 The genus *Uroleucon* Mordvilko (Insecta, Aphidoidea) in South America, with a key and descriptions of four new species. *Zool. J. Linn. Soc.* **123**, 117–141.
- Courtney, S. 1983 Models of host-plant location by butterflies: the effect of search images and searching efficiency. *Oecologia* **59**, 317–321.
- Dall, S. R. X. & Cuthill, I. C. 1997 The information costs of generalism. *Oikos* **80**, 197–202.
- Dukas, R. 1998 Constraints on information processing and their effects on behaviour. In *Cognitive ecology: the evolutionary ecology of information processing and decision making* (ed. R. Dukas), pp. 89–128. Chicago University Press.
- Dukas, R. & Real, L. 1991 Learning foraging tasks by bees: a comparison between social and solitary species. *Anim. Behav.* **42**, 269–276.
- Dukas, R. & Real, L. 1993 Cognition in bees: from stimulus reception to behavioral change. In *Insect learning* (ed. D. R. Papaj & A. C. Lewis), pp. 343–373. New York: Chapman & Hall.
- Dusenbery, D. B. 1992 *Sensory ecology*. New York: W. H. Freeman & Co.
- Endler, J. A. 1988 Frequency-dependent predation, crypsis and aposematic coloration. *Phil. Trans. R. Soc. Lond.* **B 319**, 505–523.
- Feeny, P. 1992 The evolution of chemical ecology. In *Herbivores: their interactions with secondary plant metabolites* (ed. G. A. Rosenthal & M. R. Berenbaum), pp. 1–44. New York: Academic Press.
- Fox, C. W. & Lalonde, R. G. 1993 Host confusion and the evolution of insect diet breadths. *Oikos* **67**, 577–581.
- Futuyma, D. J. 1983 Evolutionary interactions among herbivorous insects and plants. In *Coevolution* (ed. D. J. Futuyma), pp. 207–231. Sunderland, MA: Sinauer Associates.
- Futuyma, D. J. & Moreno, G. 1988 The evolution of ecological specialization. *A. Rev. Ecol. Syst.* **19**, 207–233.
- Jaenike, J. 1990 Host specialization in phytophagous insects. *A. Rev. Ecol. Syst.* **21**, 243–273.
- Janz, N. & Nylin, S. 1997 The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. *Proc. R. Soc. Lond.* **B 264**, 701–707.
- Knowlton, G. F. 1983 *Aphids of Utah*. Utah State Agricultural Experiment Station Research Bulletin 509: December.
- Kotler, B. P. & Mitchell, W. A. 1995 The effect of costly information in diet choice. *Evol. Ecol.* **9**, 18–29.
- LaBerge, D. 1995 *Attentional processing*. Cambridge, MA: Harvard University Press.
- Larsson, S. & Ekbom, B. 1995 Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos* **72**, 155–160.
- Levins, R. & MacArthur, R. 1969 An hypothesis to explain the incidence of monophagy. *Ecology* **50**, 910–911.
- Lewis, A. C. 1986 Memory constraints and flower choice in *Pieris rapae*. *Science* **232**, 863–865.
- Lima, S. L. & Dill, L. M. 1990 Behavioural decisions made under risk of predation: review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Martin, B., Collar, J. L., Tjallingii, W. F. & Fereres, A. 1997 Intracellular ingestion and salivation by aphids may cause the acquisition and inoculation of non-persistently transmitted plant viruses. *J. Gen. Virol.* **78**, 2701–2705.
- Maunsell, J. H. R. 1995 The brain's visual world: representation of visual targets in the cerebral cortex. *Science* **270**, 764–769.
- Milinski, M. 1990 Information overload and food selection. In *Behavioural mechanisms of food selection* (ed. R. N. Hughes), pp. 721–737. Berlin: Springer.
- Moran, N. 1985 The genus *Uroleucon* (Homoptera: Aphididae) in Michigan: key, host records, biological notes, and descriptions of three new species. *J. Kansas Entomol. Soc.* **57**, 596–616.
- Moran, N. 1986 Benefits of host plant specificity in *Uroleucon* (Homoptera: Aphididae). *Ecology* **67**, 108–115.
- Noldus, L. P. J. J. 1991 The Observer: a software system for collection and analysis of observational data. *Behav. Res. Methods Instr.* **23**, 415–429.
- Papaj, D. 1990 Interference with learning in pipevine swallowtail butterflies: behavioral constraint or possible adaptation. *Symp. Biol. Hung.* **39**, 89–101.
- Rausher, M. D. 1978 Search image for leaf shape in a butterfly. *Science* **200**, 1071–1073.
- Reid, P. J. & Shettleworth, S. J. 1992 Detection of cryptic prey: search image or search rate? *J. Exp. Psychol.: Anim. Behav. Proc.* **18**, 273–286.
- Sih, A. 1993 Effects of ecological interactions of forager diets: competition, predation risk, parasitism and prey behaviour. In *Diet selection: an interdisciplinary approach to foraging behaviour* (ed. R. N. Hughes), pp. 182–212. Oxford: Blackwell.
- Strong, D. R., Lawton, J. H. & Southwood, R. 1984 *Insects on plants*. Cambridge, MA: Harvard University Press.
- Tinbergen, N. 1948 Social releasers and the experimental methods required for their study. *Wilson Bull.* **60**, 6–51.
- Tjallingii, F. W. 1990 Continuous recording of stylet penetration activity by aphids. In *Aphid-plant genotype interactions* (ed. R. K. Campbell & R. D. Eikenbary), pp. 89–99. New York: Elsevier.
- Tjallingii, F. W. & Hogan Esch, Th. 1993 Fine structure of aphid stylet routes in plant tissues in correlation with EPG signals. *Physiol. Entomol.* **18**, 317–328.