Journal of Insect Behavior, Vol. 13, No. 5, 2000

The Influence of Previous Experience and Starvation on Aphid Feeding Behavior

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Accepted February 21, 2000; revised April 4, 2000

It was hypothesized that (1) previous experience of aphids on a host plant leads to differences in their feeding behavior relative to aphids without previous experience on it and that (2) a change in the physiological state of the aphid modifies their experience-induced behavior. Using electronic recording, the feeding behavior of the aphid Sitobion fragariae *(Walker) on wheat* Triticum aestivum *L. and oat* Avena sativa *L. was examined, comparing aphids with or without previous experience on a given host and with or without a period of starvation before assessing probing behavior. All comparisons were performed within a single aphid clone to minimize the effect of genetic variation. Feeding behavior on wheat was significantly affected by previous experience and starvation. The effect of previous experience interacted with the host plant where feeding behavior was tested. Aphids feeding on wheat following previous experience on wheat showed a longer time and a higher number of pathway activities and less time in waveform F (i.e., mechanical stylet work and penetration difficulties) than did aphids feeding on wheat after a previous experience on oat. No differences in the time from the beginning of the recording until the first salivation into the sieve elements were found. When aphids were subjected to a period of starvation, the time devoted to xylem ingestion increased compared with that of nonconstrained aphids. These results are discussed in terms of factors affecting foraging decisions.*

KEY WORDS: feeding behavior; previous experience; starvation; stylet; xylem ingestion.

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0892-7553/00/0900-0699$18.00/0

INTRODUCTION

Foraging behavior is influenced by internal and environmental information (Stephens and Krebs, 1986; Mangel and Clark, 1986; Houston, 1993). Dynamic models of insect foraging behavior integrating both sources of information predict that, as internal physiological constraints increase, information-based abilities are reduced (Mangel, 1993). On the other hand, it is also predicted that, in the absence of concomitant changes in the physiological state (i.e., egg load, energy reserves, etc.), the acquisition of information about the environment which modifies the informational state of the individual (i.e., previous experience, conditioning, learning) may be adaptive. Behavioral decisions may also be affected by the combined variation of informational and physiological states (Mangel, 1993). Most studies addressing both components of behavior refer to oviposition behavior of parasitoids (Rosenheim and Rosen, 1991; Jaenike and Papaj, 1992; Grasswitz and Paine, 1993; Heimpel *et al.*, 1996; Pérez-Maluf and Kaiser, 1998; Ueno, 1999), while much less is known about their relationship in other behavioral activities such as feeding (Turelli and Hoffmann, 1988; Prokopy *et al.*, 1991).

Aphids are a group of specialized phloem-ingesting foragers which, during probing, insert their modified mouth parts, the stylets, into the plant tissues (Pollard, 1973). Inside the plant, the stylets follow mostly an intercellular path, with occasional punctures into cells of the epidermis, mesophyll, and vascular bundle (including the xylem, sieve elements, and their companion cells) (Pollard, 1973). Xylem penetration leads mostly to water ingestion and phloem ingestion implies mainly nutrient ingestion (Spiller *et al.*, 1990; Srivastava, 1987). Before committed ingestion in the sieve elements, aphids may spend several hours exploring the plant surface and internal tissues with their stylets. It is also known that aphids are able to use previous experience to obtain earlier access to phloem (Montllor *et al.*, 1983; Ramírez *et al.*, 1999). However, the extent to which feeding behavior is influenced by previous experience and by starvation remains unknown.

This paper considers the influence of informational and physiological states on the feeding behavior of the blackberry-grain aphid *Sitobion fragariae* (Walker) (Sternorrhyncha: Aphididae). Previous experience and starvation were chosen as parameters of informational state and physiological state, respectively. Thus, to test the effect of previous experience, aphids were subjected to a short period of experience on seedlings of a given host plant species and then the same insect's feeding behavior was evaluated in seedlings of the same host plant species or of a nonexperienced host plant species. To test the effect of starvation, the feeding behavior was evaluated after a period of plant deprivation which followed experience treatments. All comparisons were performed within a population of aphids belonging to a single clone to minimize a potential effect of genetic variation (Via, 1991; De Barro *et al.*, 1995; Mackenzie, 1996; Lushai *et al.*, 1997; Douglas, 1997). As shown for other nonparasitoid arthropods (Hileman *et al.*, 1995; Zhang and Sanderson, 1992), the qualitative predictions were that previous experience on a host would affect feeding behavior on that host relative to another host. It was also expected that a physiological constraint such as starvation would also affect feeding behavior, stressing experience-induced behavioral changes.

MATERIALS AND METHODS

Aphids. Individuals used were from a clone of *S. fragariae* derived from a single virginoparous apterous individual collected from a grass field in central Chile. The aphids were reared for about 10 to 12 generations on oat seedlings (*Avena sativa* L. cv. Nahuén) growing in plastic boxes in a room at $20 \pm 2°C$ and 16:8 (L:D).

Behavioral Monitoring of Feeding Behavior. The DC electropenetration graph technique (Tjallingii, 1978) was used to record aphid feeding behavior. A gold wire electrode (2 cm long $\times$ 25 μm in diameter) was fixed to the dorsum of the aphid with conductive silver paint and a copper electrode was inserted in the soil of a potted plant. Both electrodes were connected to a DC electrical circuit designed to monitor stylet incursions inside plant tissues (Tjallingii, 1978). When the aphid stylets penetrated into the plant tissues they closed the electrical circuit; the voltage changes produced were amplified and continuously monitored using real-time display WinEPG software (Flores *et al.*, unpublished). All signals were recorded on a PC hard disk for later analysis. Different stylet activities and the location of stylets can be inferred from specific patterns of voltage changes in the recorded signal (Tjallingii and Hogen Esch, 1993).

Effect of Previous Experience and Starvation on Feeding Behavior. To evaluate the effect of previous experience and starvation on feeding behavior, a three-way factor design was performed. Levels in factor "previous experience" were with and without previous experience on a given host; levels in factor "starvation" were with and without a period of starvation; levels in factor "test host" were wheat and oat, the hosts where EPGs were recorded. To test the effect of previous experience the focal host plant chosen was wheat (*Triticum aestivum* L. cv. Millaleu). Since aphids came from a cohort reared for many generations on oat, the effect on feeding behavior of a short period of experience on wheat was assessed on wheat and oat (Fig. 1, top). The effect of a period of experience on oat was also assessed by recording the feeding behavior on wheat and oat (Fig. 1, bottom). The period of experience

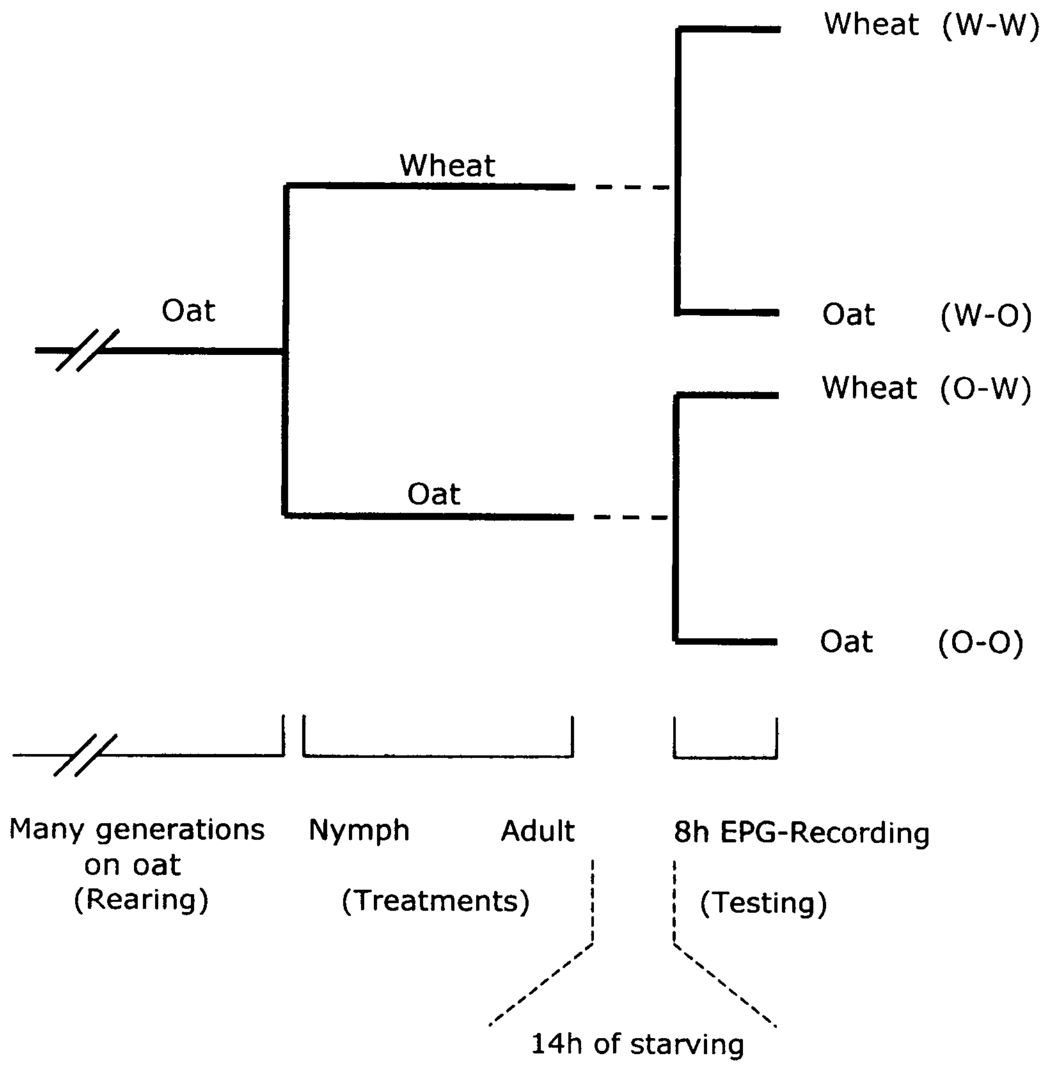

Fig. 1. Diagram showing the experimental design to test the effect of experience and starvation on probing behavior. Solid lines show aphids developing on a host plant. Dashed lines show the periods of starvation before assessing probing behavior on wheat (W) or oat (O).

on oat represented the "without previous experience" control treatment for the "experience on wheat" treatment. The effect of starvation was tested by subjecting aphids to a period of plant deprivation after both periods of experience (wheat or oat) before assessing feeding behavior on wheat and oat.

Apterous adult aphids (ca. 30) from the monoclonal colony maintained on oat were transferred to potted seedings of either wheat or oat in the two-leaf growth stage. After 24 h all adult aphids were removed and all new-born first instars were maintained in each host plant until they reached the reproductive stage. This sequence was performed several times to achieve all replications (n = 15 per treatment). Two groups of aphids were obtained: (1) with previous experience on wheat and (2) with previous experience on oat. Subsequently, electronic monitoring of the feeding behavior was performed on individuals from each group of aphids. Aphids were connected to the EPG electrode at about 1000 h and then kept for 1 h in a petri dish with a moist filter paper before being transferred to wheat or oat seedlings (two-leaf growth stage). This last transferal divided each group of aphids into two new groups, configuring a total of four experimental treatments: (1) experience on (1) wheat and assessment on wheat (W–W), (2) wheat and oat (W–O), (3) oat and wheat (O–W), and (4) oat and oat (O–O). Continuous monitoring of probing was performed for 8 h (Fig. 1). A multichannel amplifier was used which allowed a maximum of eight simultaneous recordings.

To evaluate the effect of starvation, two groups of aphids (experienced on wheat or oat) were obtained as described above and subjected to starvation in a petri dish with a moist filter paper for 14 h. At about 1000 h the next morning, they were connected to the EPG electrode, individually transferred to wheat or oat seedlings (two-leaf growth stage), and monitored for 8 h.

Behavioral Variables and Statistical Analysis. Each EPG graph obtained was analyzed with software designed *ad hoc* [WinEPG (Flores *et al.*, unpublished)]. Typical waveform patterns associated with nonpenetration (waveform usually designated by the letters NP), stylet pathway phase (waveforms A, B, and C combined, excluding waveform F), mechanical stylet work and difficulties during penetration (waveform F), xylem ingestion (waveform G), salivation into sieve elements (waveform E1), and phloem ingestion (waveform E2) were recognized (Tjallingii and Hogen Esch, 1993). Times allocated to each activity were dependent variables in a three-way multiple analysis of variance (MANOVA); a multivariate approach was chosen due to the interdependency of behavioral variables. As mentioned above, factors were "previous experience," "starvation," and "test host." The time from the beginning of the recording until the first salivation into sieve elements (waveform E1) and the number of stylet pathway phase (waveforms A, B, and C combined, excluding waveform F) were also compared among treatments. Data were log $(x + 1)$-transformed when ANOVA and MANOVA assumptions were violated.

RESULTS

Effect of Previous Experience on Feeding Behavior. Three-way MANOVA showed that feeding behavior was significantly affected by previous experience (Table I). Previous experience interacted significantly with test host, indicating that the effect of experience was modulated by the host plant where feeding behavior was tested. A posteriori comparisons revealed that aphids on wheat following previous experience on wheat (i.e., W–W) showed a longer time in waveform A + B + C (pathway activities) and less time in waveform F (i.e., mechanical stylet work and penetration difficulties)

Table I. Three-Way MANOVA Table for Results of the Experiment Involving the Effect of Previous Experience, Starvation, and Host Plant on the Feeding Behavior of the Aphid *Sitobion fragariae* on Wheat and Oat

Source	Wilks' λ[a]	df (PE)[b]	df (S)[b]	*P* level
Previous experience	0.861	6	107	0.0122
Starvation	0.509	6	107	0.0008
Test host	0.939	6	107	0.3433
Previous experience × Starvation	0.894	6	107	0.0593
Previous experience × Test host	0.802	6	107	0.0005
Starvation × Test host	0.930	6	107	0.2512
Previous experience × Starvation × Test host	0.925	6	107	0.2083

[a]Represents a multivariate *F* value based on a comparison of the error variance/covariance matrix and the effect variance/covariance matrix.
[b]PE, previous experience; S, starvation.

than did aphids feeding on wheat after a previous experience on oat (O–W). All aphids performed pathways activities, while 6 of 15 and 9 of 15 showed penetration difficulties after previous experience on wheat and oat, respectively ($\chi^2 = 0.40$, $P = 0.53$). Time from the beginning of the recording to the first salivation into sieve elements (waveform E1) was not significantly affected by experience or by test host ($F_{1,60} = 2.47$, $P = 0.12$, for previous experience factor; $F_{1,60} = 0.02$, $P = 0.88$, for test host factor; $F_{1,60} = 0.20$, $P = 0.65$, for the interaction).

Effect of Starvation on Feeding Behavior. The feeding behavior waveform was significantly affected by a period of starvation (Table I). On wheat, starvation reduced the time allocated to pathway activities of aphids with previous experience on wheat (C activity; Fig. 2A) and also significantly increased the time allocated to xylem ingestion by aphids with previous experience on wheat and oat (G activity; Fig. 2A). On oat, the period of starvation increased the time allocated to xylem ingestion by aphids with previous experience on wheat (G activity; Fig. 2B) and reduced nonpenetration activities by aphids with previous experience on wheat (NP activity; Fig. 2B). Starvation did not interact either with previous experience or with host plant.

Effect of Host Plant. The factor test host by itself did not significantly affect feeding behavior and did not interact significantly with starvation (Table I). As mentioned, test host interacted significantly only with previous experience (Table I).

DISCUSSION

The results show that previous experience and starvation of aphids significantly affected their feeding behavior. However, unlike the effect of

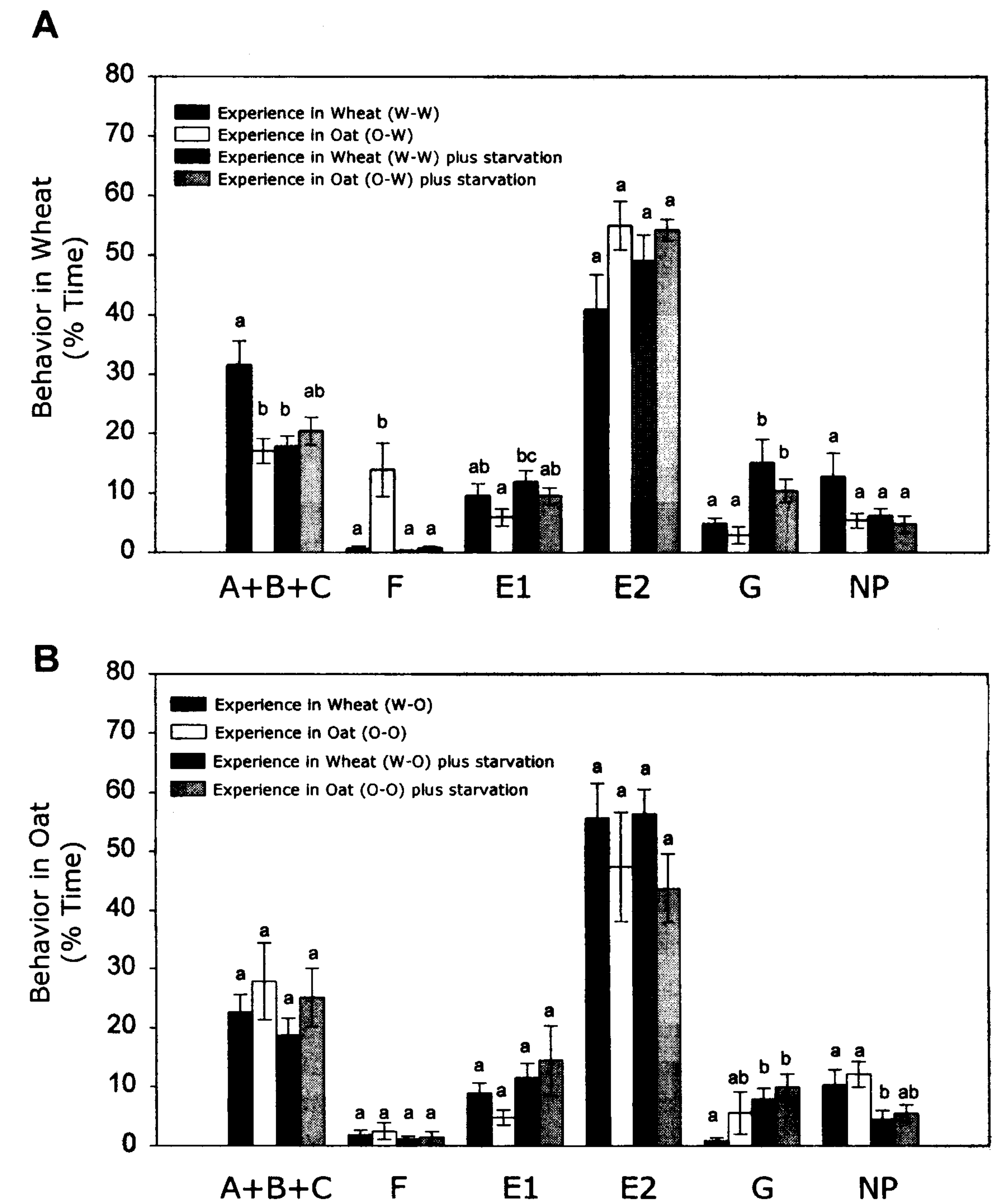

Fig. 2. Histograms showing the time allocated to each activity during 8 h of electronically recorded probing behavior on wheat (A) and oat (B). Bars represent standard errors for $n = 15$ in each case. Different letters within sets of bars mean that the differences between the values are significant at $P < 0.05$ (Tukey HSD multiple-comparison test).

starvation, the effect of previous experience depended on the host plant species where behavior was tested: previous experience on wheat significantly affected feeding behavior on wheat, but this was not true for behavior tested on oat. In particular, aphids with previous foraging experience on wheat and subsequently tested on wheat showed a longer time in pathway activities (waveform A + B + C) and a shorter time in mechanical stylet work and difficulties during penetration (waveform F) than aphids without previous experience on wheat. A more detailed analysis of the data revealed that this longer total time devoted to waveform A + B + C was due to a higher number of A + B + C events (140.2 ± 21 and 75.3 ± 7.7 for W–W and O–W treatments, respectively; $H = 4.83$, $P = 0.02$, Kruskall–Wallis test) rather than to a longer duration of these events (63.8 ± 8 and 58.4 ± 4.5 min for W–W and O–W treatments, respectively; $H = 0.36$, $P = 0.54$). Since during pathway activities the stylets actively explore inside plant tissues by penetrating different mesophyll and vascular cells, the longer time devoted to this activity and its high number may reflect a more selective behavior of aphids with previous experience on wheat.

In relation to waveform F, electron microscope techniques have shown that during the F pattern, the stylets are located along cell walls over a long distance (Tjallingii, 1987). Although the biological meaning of the F pattern in the EPG signal is not properly understood, it has been suggested that it may also represent part of a "grooming behavior" corresponding to an aphid attempting to clear its stylets from clumsy compounds (Caillaud *et al.*, 1995). Hence, the shorter time in mechanical stylet work and penetration difficulties may be attributed to a higher handling ability acquired after experience on wheat. In other words, during previous experience ("practice") aphids may acquire information that allows them to improve handling of the host plant, such as reducing mechanical difficulties while piercing plant tissues.

Differences in the effect of experience may be related to variations in the susceptibility of each host to aphid attack. Chemical properties of the host plant play an important role in insect behavioral plasticity (Jaenike and Papaj, 1992). Wheat and oat differ in their chemical constituents, particularly in the amount of hydroxamic acids, a family of compounds with deterrent properties toward aphids, which are present in wheat but not in oat (Niemeyer, 1988). Because phloem-related activities such as time to the first salivation into the sieve elements (waveform E1), total time devoted to E1, and phloem ingestion (waveform E2) did not differ between experience treatments on wheat, it is likely that experience of non-phloem-related activities (e.g., pathway through epidermis and mesophyll cells) played a major role in inducing aphids to reduced the time devoted to mechanical stylet work and difficulties during penetration and to more selective behavior during piercing cells inside the plant. Because experience on oat did not lead to these differences, this suggests that the effect of previous experience on behavior depends on plant quality, resistance of the host enhancing the role of previous experience on aphid behavior. The effect of the host could be stronger after experience on wheat cultivars with higher amounts of hydroxamic acids, i.e., cv. Naofén (Givovich and Niemeyer, 1991). On the other hand, although the assessment was not quantitative, aphids were smaller after experience on wheat than after experience on oat, a fact which could have also induced changes in feeding behavior. However, no significant increase in the time devoted to phloem ingestion was observed among experience treatments. In spite of this, the possibility that previous experience in a poor host could act as a source of motivation that affects decisions cannot be excluded (Mangel, 1993).

When starvation was included, behavior on both hosts was affected, producing an increase in the time devoted to xylem ingestion in both hosts. This finding is not surprising, since such a greater duration of xylem uptake of dehydrated aphids has been reported earlier (Spiller *et al.*, 1990), albeit not in relation to previous experience. On the other hand, since the time devoted to phloem ingestion did not change after the starvation period (waveform E2 in Figs. 2A and B), it seems that starvation affected water balance more critically than nutrient balance. It is possible that the rate of phloem ingestion may have changed after starvation; however, the experimental setup did not allow the comparison of this variable.

Although our design did not involve control experiments for the "tether effect," i.e., the effects associated with the wiring of the aphid to the EPG electrode (Prado and Tjallingii, 1999), control studies have shown previously that they do not significantly affect aphid stylet penetration behaviour or life-table parameters (Annan *et al.*, 1997). While significant behavioral differences have been reported between wired and free aphids during the first minutes of the aphid–plant interaction, when leaf surface factors are predominant (Powell *et al.*, 1993), the EPG technique provides reliable information about aphid–plant interaction when recordings, as in our case, comprise periods beyond 1 h and stylets reach nutritional tissues (Caillaud, 1999).

Our results show that non-physiologically-constrained aphids may be affected by previous experience. In fact, experience seems to benefit the handling abilities of a difficult host (wheat), but when aphids are physiologically constrained by a period of fasting, they reorient their behavior to reestablish their water balance, sacrificing potential handling advantages acquired during previous experience and eventually reducing acquired discriminative abilities. In terms of decision-making processes in insects, our results in aphids suggest that the benefits for foraging decisions obtained from previous experience are subordinate to decisions assuring the maintenance of a physiological balance. Physiological constraints in insects, such as a period of starvation as shown herein, may be critical in determining the pattern of foraging activities.

ACKNOWLEDGMENTS

We gratefully acknowledge funding from Universidad de Chile (Graduate Research Grant PG-047-96 to C.C.R.), FONDECYT (Grant 1961035 to

H.M.N.), and the International Program in the Chemical Sciences (IPICS). C.C.R. acknowledges CONICYT for a graduate fellowship during part of his Ph.D. studies. C.C.R. was supported during most of this work by the Presidential Chair in Science awarded to H.M.N.

REFERENCES

Annan, I. B., Schaefers, G. A., Tingey, W. M., and Tjallingii, W. F. (1997). Effects of treatments for electrical penetration graph recordings on behaviour and biology of *Aphis craccivora* (Aphididae). *Physiol. Entomol.* **22:** 95–101.

Caillaud, C. M. (1999). Behavioural correlates of genetic divergence due to host specialization in the pea aphid, *Acyrthosiphon pisum. Entomol. Exp. Appl.* **91:** 227–232.

Caillaud, C. M., Pierre, J. S., Chaubet, B., and Di Pietro, J. P. (1995). Analysis of wheat resistance to the cereal aphid *Sitobion avenae* using electrical penetration graphs and flow charts combined with correspondence analysis. *Entomol. Exp. Appl.* **75:** 9–18.

De Barro, P. J., Sherrat, T. N., David, O., and Maclean, N. (1995). An investigation of the differential performance of the clones of the aphid *Sitobion avenae* on two host species. *Oecologia* **104:** 379–385.

Douglas, A. E. (1997). Provenance, experience and plant utilisation by the polyphagous aphid, *Aphis fabae. Entomol. Exp. Appl.* **83:** 161–170.

Givovich, A., and Niemeyer, H. M. (1991). Hydroxamic acids affecting barley yellow dwarf virus transmission by the aphid *Rhopalosiphum padi. Entomol. Exp. Appl.* **59:** 79–85.

Grasswitz, T. R., and Paine, T. D. (1993). Influence of physiological state and experience on the responsiveness of *Lysiphlebus testaceipes* Cresson (Hymenoptera: Aphidiidae) to aphid honeydew and to host plants. *J. Insect Behav.* **6:** 511–528.

Heimpel, G. E., Rosenheim, J. A., and Mangel, M. (1996). Egg limitation, host quality, and dynamic behavior by a parasitoid in the field. *Ecology* **77:** 2410–2420.

Hileman, K. S., Brodie, E. D., Jr., and Formanowicz, D. R., Jr. (1995). Avoidance of unpalatable prey by predaceous diving beetle larvae: The role of hunger level and experience (Coleoptera: Dytiscidae). *J. Insect Behav.* **8:** 241–249.

Houston, A. I. (1993). The importance of the state. In Hughes, R. N. (ed.), *Diet Selection. An Interdisciplinary Approach to Foraging Behaviour*, Blackwell Scientific, Oxford, pp. 10–31.

Jaenike, J., and Papaj, D. R. (1992). Behavioural plasticity and pattern of host use by insect. In Roitberg, B. D., and Isman, M. B. (eds.), *Insect Chemical Ecology. An Evolutionary Approach*, Chapman and Hall, New York, pp. 245–264.

Lushai, G., Sherratt, T. N., David, O., De Barro, P. J., and MacLean, N. (1997). Host selection by winged summer females of the aphid *Sitobion avenae. Entomol. Exp. Appl.* **85:** 199–209.

Mackenzie, A. (1996). A trade-off for host plant utilization in the black bean aphid, *Aphis fabae. Evolution* **50:** 155–162.

Mangel, M. (1993). Motivation, learning and motivated learning. In Papaj, D. R., and Lewis, A. C. (eds.), *Insect Learning: Ecological and Evolutionary Perspectives*, Chapman and Hall, New York, pp. 158–173.

Mangel, M., and Clark, C. W. (1986). Towards a unified foraging theory. *Ecology* **67:** 1127–1138.

Montllor, C. B., Campbell, B. C., and Mittler, T. E. (1983). Behaviour of two biotypes of the greenbug, *Schizaphis graminum*, in relation to resistance in sorghum. *Entomol. Exp. Appl.* **34:** 99–106.

Niemeyer, H. M. (1988). Hydroxamic acid (4-hydroxy-1,4-benzoxazin-3-ones), defence chemicals in the Gramineae. *Phytochemistry* **27:** 3349–3358.

Pérez-Maluf, R., and Kaiser, L. (1998). Mating and oviposition experience influence odor learning in *Leptopilina boulardi* (Hymenoptera: Eucoilidae), a parasitoid of *Drosophila. Biol. Control* **11:** 154–159.

Pollard, D. G. (1973). Plant penetration by feeding aphids (Hemiptera: Aphidoidea): A review. *Bull. Entomol. Res.* **62:** 631–714.

Powell, G., Hardie, J., and Pickett, J. A. (1993). Effects of the antifeedant polygodial on plant penetration by aphids, assessed by video and electrical recording. *Entomol. Exp. Appl.* **68:** 93–200.

Prado, E., and Tjallingii, W. F. (1999). Effects of experimental stress factors on probing behaviour by aphids. *Entomol. Exp. Appl.* **90:** 289–300.

Prokopy, R. J., Drew, R. A. I., Sabine, B. N. E., Lloyd, A. C., and Hamacek, E. (1991). Effect of physiological and experiential state of *Bactrocera tyroni* flies on intra-tree foraging behavior for food (bacteria) and host fruit. *Oecologia* **87:** 394–400.

Ramírez, C. C., Caballero, P. P., and Niemeyer, H. M. (1999). The effect of the previous exposure to hydroxamic acid in the probing behavior of the aphid *Sitobion fragariae* on wheat seedlings. *J. Chem. Ecol.* **25:** 771–779.

Rosenheim, J. A., and Rosen, D. (1991). Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: Distinguishing the influences of egg load and experience. *J. Anim. Ecol.* **60:** 873–894.

Spiller, N. J., Koenders, L., and Tjallingii, W. F. (1990). Xylem ingestion by aphids—A strategy for maintaining water balance. *Entomol. Exp. Appl.* **55:** 101–104.

Srivastava, P. N. (1987). Nutritional physiology. In Minks, A. A., and Harrewijn, P. (eds.), *Aphids. Their Biology, Natural Enemies and Control*, Elsevier, Amsterdam, pp. 99–121.

Stephens, D. W., and Krebs, J. R. (1986). *Foraging Theory*, Princeton University Press, Princeton, NJ.

Tjallingii, W. F. (1978). Electronic recording of penetration behaviour by aphids. *Entomol. Exp. Appl.* **24:** 721–730.

Tjallingii, W. F. (1987). Stylet penetration activities by aphids: New correlations with electrical penetration graphs. In Labeyrie, V., Febres, G., and Lachaise, D. (eds.), *Proceedings of the 6th International Symposium on Insect–Plant Relationships*, W. Junk, The Hague, pp. 301–306.

Tjallingii, W. F., and Hogen Esch, T. (1993). Fine structure of aphid stylet routes in plant tissues in correlation with EPG signals. *Physiol. Entomol.* **18:** 317–328.

Turelli, M., and Hoffmann, A. A. (1988). Effects of starvation and experience on the response of *Drosophila* to alternative resources. *Oecologia* **77:** 497–505.

Ueno, T. (1999). Host-feeding and acceptance by a parasitic wasp (Hymenoptera: Ichneumonidae) as influenced by egg load and experience in a patch. *Evol. Ecol.* **13:** 33–44.

Via, S. (1991). Specialized host plant performance of pea aphid clones is not altered by experience. *Ecology* **72:** 1420–1427.

Zhang, Z. Q., and Sanderson, J. P. (1992). Effects of host plant experience on foraging behavior of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Ann. Entomol. Soc. Am.* **85:** 775–783.