

# Host-Handling Behavior: An Innate Component of Foraging Behavior in the Parasitoid Wasp *Ampulex compressa*

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## Abstract

The reproductive success of parasitoids depends on their ability to locate, select, and handle hosts quickly and efficiently. Learning has been shown to play a role in host finding and host choice, but the role of learning in the handling of hosts has received little attention. We tested whether the speed and accuracy of host handling improve with experience in the wasp *Ampulex compressa*. This parasitoid performs an elaborate behavioral sequence when parasitizing its host, the cockroach *Periplaneta americana*. We provide a quantitative description of the behavioral sequence, and show that: (a) the duration of the whole sequence, (b) the number of completed stages, and (c) the precision of an important stage in the handling sequence, host antennal cutting, are similar in inexperienced and experienced individuals. We discuss features of *A. compressa*'s life history that may select for innate host handling.

## Introduction

Learning, defined as any adaptive experience-induced change in behavior (Thorpe 1956), is well documented in insects (Papaj 1993). Some of the best-known cases of insect learning concern foraging behavior. Insects learn to navigate to their food sources (Collett 1996); to associate chemical, visual or mechanical cues with the presence of attractive or repulsive foods (Hammer & Menzel 1995; Dukas & Bernays 2000); to adjust their diet selection, and time in feeding patches, to prey availability (Papaj & Prokopy 1989); and to handle their prey more efficiently as they gain experience (Chittka & Thomson 1997).

Much of the research on insect learning deals with pollinating insects, in particular with honeybees and bumblebees. A wide array of choice tests has focused on associative learning in bees, i.e. learning to respond to a sensory cue that signals a food reward (Seeley 1995). A second direction of study concerns the operant learning capabilities of bees, namely learning to perform a behavioral sequence quickly and accurately to obtain a food reward. Pollinators

improve in speed and accuracy of flower handling with repeated trials in field and laboratory tests, and retain their flower-handling skills overnight (Lavery 1994; Keasar et al. 1996). Flowers that are morphologically complex require a longer learning period than structurally simple flowers. Individuals that forage on two flower types at the same time require a longer learning period (Chittka & Thomson 1997; Gegear & Lavery 1998).

Parasitoids resemble pollinators in that they need to find, evaluate, and handle their prey (hosts), although most host tissue is consumed by the parasitoid's offspring, rather than by the foraging individual (Quicke 1997; O'Neill 2001). Associative learning is clearly involved in the host-searching behavior of parasitoids. Adult and larval parasitoids learn to respond to kairomones or visual cues associated with the substrate of their prey (Vet & Groenewold 1990; Kerguelen & Cardé 1998; Steidle 1998; Dukas & Duan 2000; Gandolfi et al. 2003). Generalist eucoilid parasitoids were shown to respond to these cues more than related specialist species (Poolman Simons et al. 1992). Associative learning is also

implicated in the host-evaluation process, as parasitoids reject fewer potential hosts after experiencing a poor environment, and in some cases learn to discriminate hosts that are already parasitized (Roitberg et al. 1992, 1993a, b; van Baaren & Boivin 1998). The role of operant learning in host handling, however, has received little attention, possibly because host handling is frequently a complex and prolonged behavioral sequence.

The selective advantage of learned, rather than innate, patterns of prey handling is expected to depend on the lifestyle of the foraging animal. Learning is expected to evolve when foraging conditions are variable, so that no single innate handling technique is adequate under all conditions (Stephens 1993). The benefit of learning should also increase when a learned pattern is applied many times during the forager's lifetime, while rare behaviors are expected to be genetically preprogrammed (Roitberg et al. 1993b; Manning & Dawkins 1998). Learning may be further favored if the forager obtains information about the likely influence of the decision on its fitness. If no information is obtained, learning is of no value (Parmesan et al. 1995). Flower handling by generalist nectarivores, a technique that varies among flower species, is practiced hundreds of times within each foraging bout, and yields immediate feedback on success (amount of food reward obtained). These factors provide a clear selective advantage for learning (Dukas 1998; McNeely & Singer 2001). A similar reasoning can be applied to predict the role of learning for prey handling by parasitoids: life-history features such as a wide host range, or high fertility, may favor learning because they require repeated handling of hosts using a variety of techniques. A narrow host range and a small egg complement, on the other hand, may select for innate host-handling behavior.

In the present study, we consider the role of learning in the host-handling behavior of the solitary sphecid wasp *Ampulex compressa*, a parasitoid of the cockroach *Periplaneta americana*. This parasitoid specializes on a single host genus, and parasitizes a single host every other day for about 2 mo under insectary conditions (G. Haspel, pers. comm.). Various parasites alter the behavior of their hosts (Moore 2002) and the way *A. compressa* controls the behavior of its host is almost certainly one of the most sophisticated alterations of behavior ever attributed to an insect parasitoid. Wasps oviposit on the cuticle of adult cockroaches, following a complex behavioral sequence of host handling (Veltman & Wilhelm 1990; Fouad et al. 1994). A complete handling sequence includes two consecutive stings, applied

directly into the central nervous system of the host (Haspel et al. 2003). The injected venom cocktail induces a sustained lethargic state in the prey (Piek et al. 1984). After stinging, the wasp often cuts the cockroach's antennae with its mandibles, and feeds on the hemolymph from the cut end. It then grasps one of the cockroach's antennae, leads the host to a suitable cavity for oviposition (such as a hollow log), and lays an egg on its cuticle. Finally, the wasp frequently blocks the entrance to the oviposition site with small pebbles collected nearby (Libersat 2003). This elaborate behavior provides much potential for variation, both among *A. compressa* individuals, and among different oviposition events of the same individual. For example, the time required to complete the handling sequence, and the order of activities within a sequence, may vary substantially. Moreover, not all handling sequences are carried out to completion, providing an additional source of variability among sequences. This begs the question whether *A. compressa* individuals improve in their host-handling skills with experience, i.e. whether learning contributes to the variability in host handling.

We tested two competing hypotheses regarding the importance of learning for host handling in this species. According to the first hypothesis, *A. compressa*'s host-handling sequences are innate. This hypothesis predicts that the order of activities within this sequence, the time needed to complete them, and their accuracy, will remain constant over successive ovipositions. According to the alternative hypothesis, learning plays a key role in host-handling behavior of *A. compressa*. The predictions arising from this hypothesis are that, as the foraging experience of the parasitoids increases: (a) host-handling durations will decrease, (b) a larger part of the host-handling sequence will be performed, and (c) the variation in the order of behaviors within the host handling will sequence will decrease. We tested these predictions by comparing the duration and organization of the host-handling sequence in naïve and experienced females.

Before ovipositing, the wasps always cut their host's antennae. Prior to cutting, they slide their mandibles several times over each antenna, seemingly trying to locate a suitable cutting point. We assessed whether the parasitoids respond to cues associated with antennal geometry (such as some change in the shape of the segments that form the antenna) when deciding on the cutting point. If learning is important for accurate host handling in *Ampulex* (our alternative hypothesis), the wasps' response to such geometrical cues is predicted to

change with experience. For example, naïve wasps may cut their hosts' antennae at random locations, while experienced individuals may be more responsive to the antennal geometry. These considerations led us to look for geometrical features that characterize antennal cutting points, for naïve and experienced *Ampulex* females.

## Methods

Observations were made under controlled laboratory conditions (31°C, 60% relative humidity, 12 :12 h light : dark cycle), in 40 × 40 × 40 cm plexiglass observation cages, and were conducted during the light cycle, between Sep. 2003 and Mar. 2004. The parasitoid stock has been maintained in the laboratory since 1992, with no selection for any particular behavioral trait. Parasitoid pupae obtained from laboratory stock were allowed to hatch singly. Each of 10 adult females was allowed to mate with two males for at least 3 d. During this period, the females acclimated to the observation cage. After male removal, the females, presumed mated, were presented with a female cockroach host, randomly selected from laboratory stock. We used *P. americana* cockroaches as hosts, because they are part of *A. compressa*'s natural host range (Williams 1942). Pilot observations revealed that *A. compressa* parasitizes female hosts more readily than males. We provided the wasps with a test tube to imitate an oviposition nest, and with small aquarium pebbles to block the entrance to the oviposition tube.

Each of the 10 wasps was observed four times, with 3-d intervals between successive observation sessions. All observations were performed by the same observer. We supplied each parasitoid with one host per observation session. No hosts were available to the wasps between observation sessions, but they were fed with honey during this period.

We defined the following stages in the host-handling sequence: (1) host targeting, (2) thorax sting, (3) head sting, (4) host probing, (5) antennal cutting, (6) host feeding, (7) nest exploration, (8) host insertion into the nest, (9) oviposition, and (10) collection of pebbles. We numbered the stages according to this sequence. We recorded the number of stages completed in each observation, their order and the time required to complete them. Observation sessions lasted 2 h, or until the wasp started collecting pebbles after oviposition. The mean (SD) duration to the pebble collection stage was 52:11 (26:22) min.

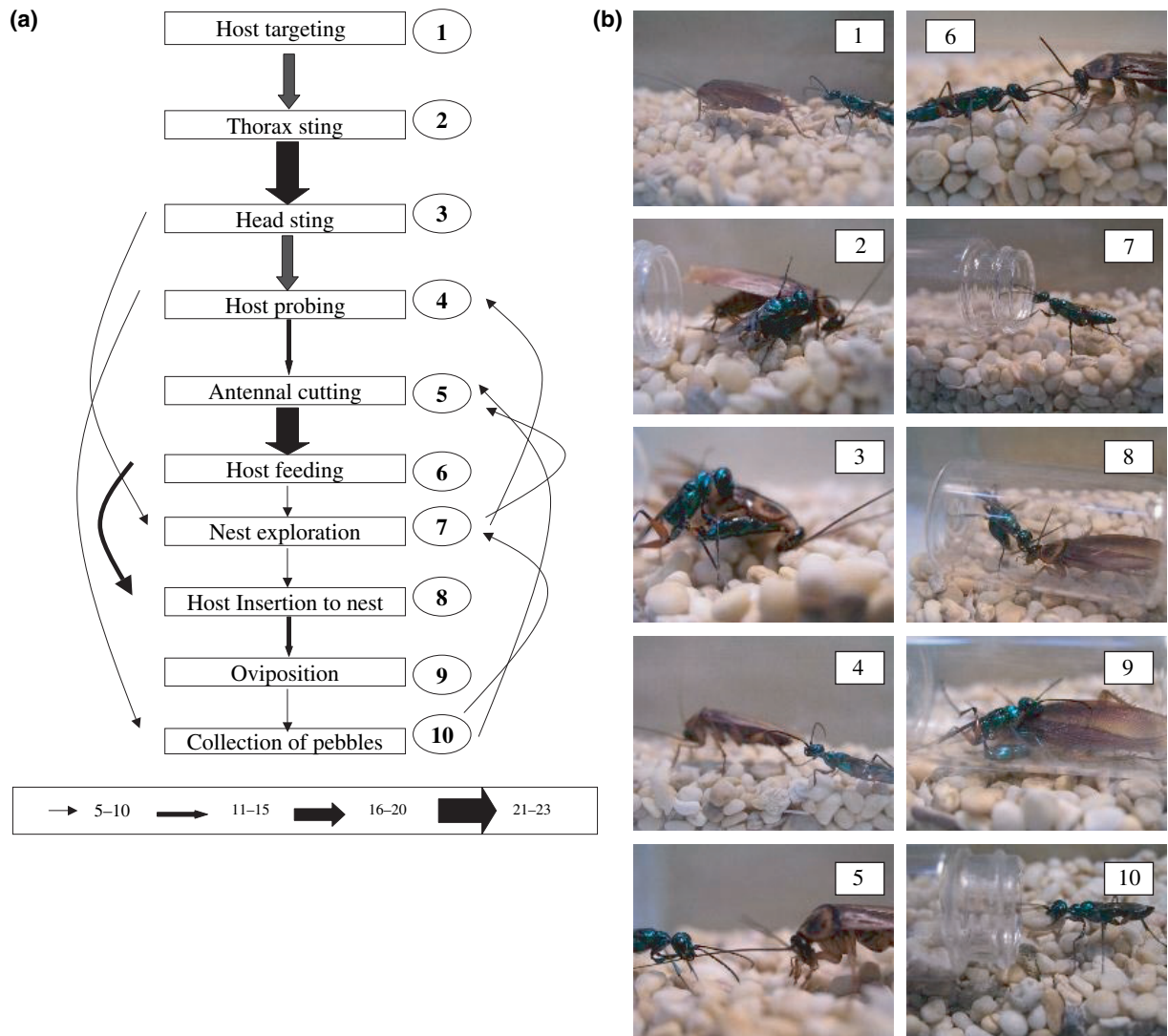
The wasps were returned to the laboratory culture at the end of the observations. We used repeated-

measures ANOVA to test for the effect of wasp experience on the number of completed stages, and the duration of host handling. We tested the effect of individual (independent variable,  $n = 10$ ) on the number of completed stages and the duration of host handling (dependent variables), treating the four observations of each individual as the within-subject repeated measure.

To identify potential geometrical cues that may guide wasps when deciding on the antennal cutting point, we collected 30 host antennae cut by six parasitoid individuals during observations. We glued them with Permout medium onto microscope slides. Under a compound microscope, we counted the number of antennal segments proximally and distally to the wasps' cutting point, and measured their lengths and diameters using the Analysis<sup>TM</sup> software package (Soft Imaging System, Münster, Germany). We used a stepwise regression analysis to determine the contribution of the following variables to the variance in the location of the cutting point among antennae: (1) total antennal length; (2) segment length; (3) segment diameter; (4) rate of change in segment length; and (5) rate of change in segment diameter. We determined the rates of change in length and diameter by calculating the differences in length and diameter between each two neighboring antennal segments. Then, we averaged these differences over a sliding window of 11 segments. Analyses were performed with STATISTICA 6.0 (StatSoft, Tulsa, OK, USA).

## Results

All host-handling sequences started with host-targeting (stage 1), and most proceeded to stages 2, 3, etc., until the wasp either completed the sequence or abandoned the host. Nevertheless, some deviations from this pattern occurred, such as skipping of stages or reversal of their order (Fig. 1). All 10 stages were completed in only 15 of 40 observations. We found no significant difference in the number of completed stages among the four observations of each individual [ $F_{(3,27)} = 0.263$ ,  $p = 0.85$ ; Fig. 2]. We defined a complete host-handling sequence as 'success', and counted the number of successes per individual (this number can range from 0 to 4). Two of the 10 wasps did not oviposit into any of the four hosts presented to them (0 successes). The remaining individuals had one success ( $n = 3$ ), two successes ( $n = 3$ ), three successes ( $n = 1$ ) or four successes ( $n = 1$ ). The number of successes in a series of random binary trials (when each trial either 'succeeds' with probability  $p$

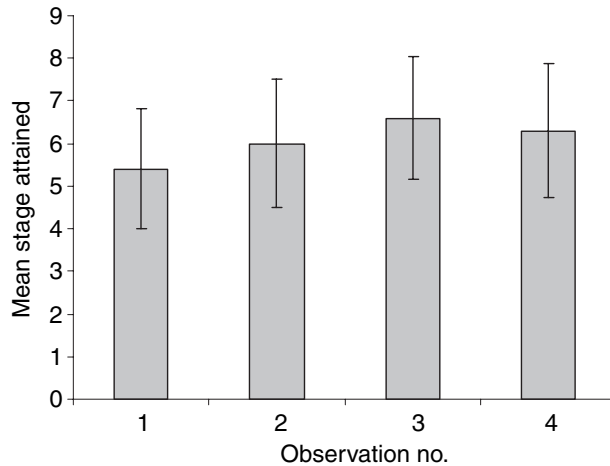


**Fig. 1:** (a) An ethogram that demonstrates the behavioral sequence involved in parasitization. The ethogram comprises 10 main stages, which were performed in the same sequence in most observations. Transitions that are labeled with arrows occurred five times or more. Arrow thickness correlates with transition frequencies, as detailed in the legend. (b) Illustration of the host-handling stages

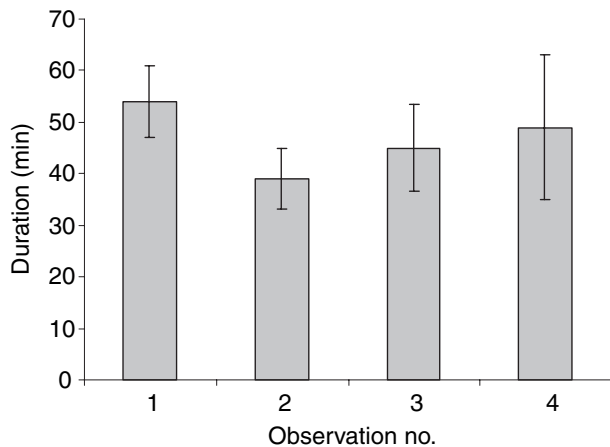
or ‘fails’ with probability  $1 - p$ ) is distributed geometrically. The distribution of the number of successes in our observations did not differ significantly from a geometric distribution with the same  $p$ -value (Kolmogorov–Smirnov test,  $d = 0.185$ ,  $p = 0.385$ ), as expected for a randomly generated distribution. This suggests that the variability in the number of successes arises from chance events, rather than from between-wasp differences in handling skills. Neither did the wasps complete fewer stages on their first exposure to a host (observation 1) when compared with their second exposure (repeated-measures ANOVA, post hoc test for planned comparisons,

$F = 0.358$ ,  $p = 0.564$ ). A complete host-handling sequence, which included all 10 stages, was followed by another complete sequence in the next observation in eight cases, and by an incomplete host-handling sequence in two cases.

We considered 25 observations during which the parasitoids ( $n = 10$ ) performed the handling sequence at least to stage 5 (probing of host antennae). The duration of the first five stages did not differ significantly among consecutive observations [Fig. 3, repeated-measures ANOVA,  $F_{(3,9)} = 0.985$ ,  $p = 0.44$ ]. For each observed handling sequence, we determined whether the order of stages conformed



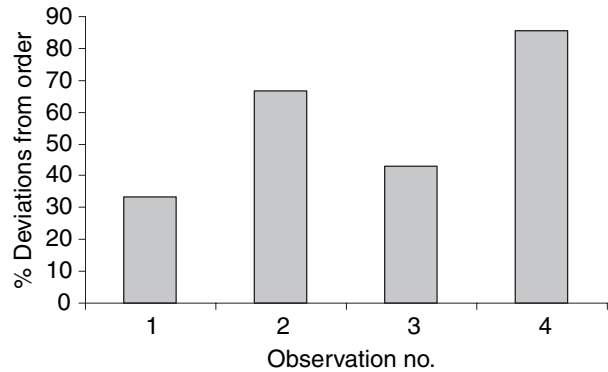
**Fig. 2:** Number of completed stages in the ethogram as a function of wasp experience. Mean values are shown with their 95% confidence intervals



**Fig. 3:** Time to completion of the first five stages of host handling as a function of wasp experience. Mean values are shown with their 95% confidence intervals

to the order depicted in Fig. 1. The proportion of sequences that deviated from this order of stages did not change over consecutive observations (Fig. 4).

Antennal length and number of segments varied between antennae in our sample. Mean (SD) antennal length was  $20.83 \pm 2.93$  cm, and the total number of segments was  $96.0 \pm 11.9$ . The parasitoids cut their hosts' antennae at  $48.6 \pm 9.01$  (mean  $\pm$  SD) segments from their base, that is, at  $51 \pm 8\%$  of the total number of segments. The variance in antennal length and diameter at the cutting points across hosts of each wasp was as large as among hosts of different parasitoids (ANOVA,  $F_6 = 1.156$ ,  $p = 0.363$  for segment length,  $F_6 = 1.023$ ,



**Fig. 4:** Percentage of host-handling sequences that deviated from the 'correct' order of stages

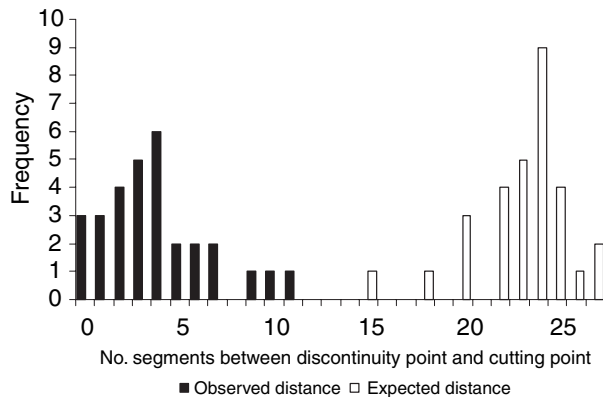
$p = 0.436$  for segment diameter). Eighty-three percent of the variance in the location of the cutting point among antennae can be explained using parameters of antennal geometry. The only significant explanatory variable was the rate of increase in antennal length, which accounted for 76% of the variance (Table 1). Wasps typically cut the cockroaches' antennae at or near the point of maximal increase in length between consecutive segments, which can be considered a point of discontinuity. This suggests that the parasitoids may cut their hosts' antennae when they perceive a rapid increase in the length of antennal segments. The mean distance between the discontinuity point and the cutting point was  $3.87 \pm 2.83$  segments. We calculated the frequency distribution of the distance (measured in number of segments) between the antennal cutting point and the point of discontinuity. This distribution differs significantly from an expected frequency distribution for the same sample, constructed on the assumption that cutting points are determined at random ( $\chi^2 = 150$ ,  $df = 3$ ,  $p < 0.001$ ; Fig. 5).

We tested whether the wasps' responses become more accurate with experience as an additional parameter of learning. We scored the distance (in number of segments) between the cutting point and the point of maximal change in segmental length for each of the mounted antennae. The mean values of this deviation were  $5.00 \pm 1.02$  (SEM) segments for naïve wasps ( $n = 7$  hosts), and  $3.78 \pm 0.72$  segments for experienced wasps ( $n = 18$  hosts handled by a wasp with prior host-handling experience). The decrease in the deviation with experience was not statistically significant (repeated-measures ANOVA on square-root-transformed data,  $F_{3,21} = 0.987$ ,  $p = 0.432$ ).

**Table 1:** Output of stepwise regression analysis, aimed to evaluate the effects of host antennal geometry on the segment selected for cutting by the parasitoid

Variable	Sample size	Mean	SEM	Multiple R <sup>2</sup>	R <sup>2</sup> change	F	p-value
Fastest increase in segment length ( $\mu\text{m}/\text{segment}$ )	30	46.87	1.62	0.760	0.760	89.027	0.000
Fastest increase in segment diameter ( $\mu\text{m}/\text{segment}$ )	30	32.10	3.47	0.779	0.018	2.278	0.142
Total length of antenna ( $\mu\text{m}$ )	30	20834.28	535.63	0.809	0.030	4.172	0.051
Segment length ( $\mu\text{m}$ )	30	213.88	5.75	0.817	0.007	1.018	0.322
Segment diameter ( $\mu\text{m}$ )	30	223.48	5.80	0.831	0.014	2.062	0.163

Partial regression coefficients are reported, because some explanatory variables are correlated.



**Fig. 5:** Frequency distribution of the distance (measured in number of segments) between the antennal cutting point and the point of discontinuity. The discontinuity point is defined at the maximal rate of change in segment length of the host antenna. The expected frequency distribution is constructed on the assumption that cutting points in the sample are determined at random

## Discussion

Our observations support the hypothesis that *A. compressa*'s handling behavior is primarily genetically programmed, rather than learned, because of the following evidence: (a) host handling generally follows an ordered sequence of stages; and (b) *A. compressa* females do not perform the host-handling sequence faster, or manage to complete it more frequently, as they gain experience. Yet, some variability in host-handling behavior prevails, as parts of the sequence are sometimes deleted, or performed at a different order (Fig. 1). Thus, the host-handling behavior is not rigid enough to be considered a fixed action pattern.

An important source of behavioral variability in our study arose from handling sequences that were aborted before completion. The wasps oviposited into only 15 of 40 hosts during observations. They went through parts of the host-handling sequence with the remaining hosts, but did not complete these

sequences. This suggests that some hosts are rejected during handling, at least under laboratory conditions. This variability may reflect quality differences among hosts, or between-wasp differences in the motivation to oviposit. Motivation to oviposit may, in turn, be affected by prior experience. Some parasitoids increase host acceptance after a successful oviposition (Kerguelen & Cardé 1996). This may also be the case for *A. compressa*, because a fully completed host-handling sequence was directly followed by a second fully completed sequence in eight of 10 observations.

Our observations thus suggest that host handling in *A. compressa* involves little learning. While lack of learning may reflect constraints of the wasps' data processing abilities, it may also constitute an adaptive behavioral pattern. Can this parasitoid's lifestyle provide a selective advantage to such stereotyped behavior? We propose that the following life-history characteristics may favor innate host-handling behavior in this species.

### Narrow host range

*Ampulex compressa* specializes on adult cockroaches of the genus *Periplaneta*. Unlike generalist parasitoids, one innately determined handling pattern may be sufficient to allow appropriate handling of many hosts.

### Low fecundity

Mated *A. compressa* females oviposit once every other day, for about 2 mo, under laboratory conditions. Thus, lifetime fecundity in the laboratory is approx. 30 ovipositions. Virgin females do not search for hosts in the laboratory (N. Sheffer, pers. obs.). Fecundity in nature is probably lower, because the availability of mates, hosts and nest sites may be limited. Predation and parasitism likely further reduce *A. compressa*'s lifespan and reproductive prospects in

their natural habitat. Low fecundity, a general feature of large, long-lived parasitoids (Jervis & Ferns 2004), does not favor the evolution of learned host-handling behavior. This is because the benefits of learning (efficient host handling) are expected to compensate for the costs (poor initial performance) only when the behavior is practiced frequently.

#### No parental care

Females do not remain near their developing offspring, and therefore cannot use their own reproductive success as a reinforcement cue in a learning process.

The large variability in the dimensions of cutting points of antennae handled by individual wasps implies that the antennal cutting point is not constrained by the size of the wasps' mandibles. Rather, our results show that *A. compressa* typically cuts the cockroach's antennae at or near the point of maximal increase in length between consecutive segments. This indicates that the wasp may cut its host's antennae when it perceives a rapid increase in the length of antennal segments. Antennal measurements indirectly suggest that the precision of antennal cutting does not improve with experience. What is the possible significance of the location of cutting for the parasitoid's foraging success?

Many parasitoids obtain proteins and other nutrients from the host hemolymph (Quicke 1997). Wasps may select a cutting point on the cockroach's antennae that is optimal for easy hemolymph flow during antennal feeding. Such host feeding may be required for egg maturation (Jervis & Kidd 1986; Collier 1995). It may also provide a way for the parasitoid to assess the quality of its hosts. Possible cues that may be used by the parasitoid are the rate of hemolymph flow (as an indicator of host size), and hemolymph chemistry (as an indicator of the host's sex, developmental stage, or nutritional status). This assessment could affect the parasitoid's subsequent behavior: after feeding on a low-quality host, a wasp could, for example, reject it and hunt for another cockroach. Indeed, hosts were rejected after the host-feeding stage in 10 of 40 observations in our study. In hosts that are accepted, host quality cues could affect the sex of the egg laid by the parasitoid (Ueno 1999). These possibilities require further study in the *Ampulex-Periplaneta* system.

The present study focused on the role of host-handling in a highly host-specific parasitoid. Generalizing from information on flower handling by insect pollinators, we speculate that host-handling

may be even more important in the foraging behavior of generalist parasitoids. Pollinators are limited in their ability to efficiently handle, and feed on, several flower types of different morphologies. This learning constraint was suggested to select for flower-constant foraging, i.e. specialization on a single flower species, in bees (Darwin 1876). Applying similar reasoning to host-parasitoid interactions, we predict that 'host-constant' foraging may be advantageous for parasitoids that had learned a particular host-handling technique. This prediction provides interesting prospects for further study.

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