

MEASUREMENT OF HOST CURVATURE BY THE PARASITOID WASP *TRICHOGRAMMA MINUTUM*, AND ITS EFFECT ON HOST EXAMINATION AND PROGENY ALLOCATION

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SUMMARY

The parasitoid wasp *Trichogramma minutum* Riley (Hymenoptera: Chalcidoidea: Trichogrammatidae) adjusts its progeny allocation and host examining behaviour to the exposed volume of its host – an insect egg. The female wasp examines a potential host by walking over its surface while drumming its antennae against it, spending a longer time examining larger hosts. If wasps of different sizes are presented with glass beads of the same diameter, examining time increases significantly the larger the bead is relative to the wasp. Since the wasps' velocities do not differ with wasp size, the total distance travelled during host examination also increases with relative host diameter.

When large and small wasps are placed on large and small hosts such that the relative curvature is constant, examining time and total path length are the same. Smaller wasps take more steps to travel the same distance, therefore the duration of the examination walk, rather than step number or relative distance, is adjusted to host curvature. This adjustment of examination time may ensure that the surface of hosts of different sizes are examined adequately, despite differences in total area.

Progeny allocation, usually dependent only on exposed host surface area, can be affected by the wasps' measure of curvature. When hosts are mounted on the tips of thin wires rather than on the substrate, no finite cues dependent on surface area are available to the wasps. Such hosts receive only 25 % more progeny, either in the light or in total darkness, than hosts which are resting on the substrate, demonstrating that an upper limit to clutch size is set by cues dependent on curvature. The structure of the compound eyes suggests that the visual acuity of *Trichogramma* is insufficient to account for their ability to discriminate between small differences in host curvature. By placing large and small wasps on point-mounted hosts of fixed diameter, we show that the clutch size limit is set according to the relative size of the host.

These observations are discussed in terms of a mechanosensory mechanism of curvature measurement.

Key words: *Trichogramma*, parasitoid, oviposition, host examination, host measurement, compound eye.

INTRODUCTION

The minute (0.4–0.6 mm in length) wasps of the genus *Trichogramma* (Hymenoptera: Chalcidoidea: Trichogrammatidae) are parasitoids of a wide variety of insects' eggs, and are able to measure the size of potential host eggs in order to allocate the appropriate number of their own progeny (Salt, 1935; Klomp & Teerink, 1962, 1967; Schmidt & Smith, 1985*a,b*). The determination of host volume is made during the wasp's examination walk over the host surface (Klomp & Teerink, 1962, 1967), and depends upon external cues rather than information about the internal contents of the host (Schmidt & Smith, 1985*a*).

In previous experiments we have shown that *Trichogramma* allocate fewer progeny to hosts partially embedded in the substrate than to hosts resting on the substrate, demonstrating that the wasp responds to factors dependent upon the surface area independently of host diameter (Schmidt & Smith, 1985*a*). However, the duration of the wasp's examination walk on the host surface depends only upon host diameter and not surface area; when the surface area of a host is changed, but curvature remains constant, host examining time does not change. In contrast, when curvature is changed, examination time does change, indicating that the wasps can measure some curvature-dependent parameter (Klomp & Teerink, 1962; Schmidt & Smith, 1985*a*). Host diameter also appears to play an important role in host recognition, since only objects within a limited range of cross-sectional diameters are accepted as potential hosts (Salt, 1935; Taylor & Stern, 1971; de Jong & Pak, 1984).

On the basis of these earlier observations, we have suggested that the wasps must make measurements related to both surface area and diameter, and may use both to estimate exposed host volume (Schmidt & Smith, 1985*a*). According to this model, the wasp would use its measure of host diameter to set the duration of the examination walk and an upper limit on the number of eggs laid. The measure of host diameter would thus serve as an estimate of the maximum potential volume of the host, an estimate which is then corrected in response to surface-area-dependent cues to set the actual number of eggs laid.

During the examination walk the wasp drums the surface continuously with its antennae, apparently inspecting the surface for chemical cues (Salt, 1935, 1937; Quednau, 1960; Klomp & Teerink, 1962; Klomp, Teerink & Ma, 1980). By measuring changes in the relative positions of the wasp's body parts during this examination walk, we have shown that *Trichogramma* females could respond to host diameter by determining the scapal-head angle of the antennae during drumming, since this angle shows the most significant change with host curvature (Schmidt & Smith, 1986). In this way, the wasps would be responding to the curvature of the surface directly, rather than to the diameter of the object itself. An important feature of this mechanism is that it would only allow the wasps to measure curvature relative to their own size; an absolute measure would not be available. To investigate further the mechanism of curvature measurement by *Trichogramma*, and the details of its response to host diameter, this paper addresses the following questions.

1. Does the wasp use relative or absolute curvature to set the duration of its examination walk?
2. Is the absolute or relative length of the examination walk set in response to curvature?
3. Is an upper limit to clutch size set according to absolute or relative host curvature?

MATERIALS AND METHODS

Field-collected strains of *Trichogramma minutum* were obtained from the University of Guelph, Canada. The field host was spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae). The wasps were initially maintained on *Sitotroga cerealella* (Oliver) (Gelechiidae) before being transferred to *Manduca sexta* (L.) (Sphingidae). Cultures were maintained on *M. sexta* through more than 65 generations, in the laboratory, at 24–27°C, 30–40% relative humidity, with 10-day generations (Schmidt & Smith, 1985a). In all experiments, each wasp was used only once. In the rearing colony, where hosts are presented as irregular clumps, the mean number of larvae per parasitized host was 11.9 ± 4.9 ($N = 163$), and the rate of parasitization was 42% ($N = 370$).

Wasps were measured with an ocular micrometer. Head length was defined as the distance between the medial ocellus and the tips of the closed mandibles in profile. We have shown previously that head length is linearly allometric with the lengths of other body parts over the size range of wasps used (Schmidt & Smith, 1986).

Hosts used were eggs of *M. sexta*, obtained from Carolina Biological Supply Co. (Burlington, NC 27215, USA). The hosts were killed by freezing at -12°C before shipment, stored at -4°C and used 5–6 days after oviposition. All hosts used were measured individually with an ocular micrometer after exposure to the wasps.

In the experiments in which clutch size was determined, the number of final instar larvae, rather than the actual number of eggs laid, was used to estimate the clutch size of the wasp. The larvae were dissected from the host using an electrolytically sharpened tungsten needle. Since the internal volume of all the hosts used in these experiments was the same, any larval mortality due to crowding would probably have been greatest for those hosts containing the most eggs initially. As a result, the differences in progeny allocation reported here may be conservative. However, the differences observed between hosts were clearly not produced by differential mortality. Under similar conditions, using hosts of comparable diameter, Suzuki, Tsuji & Sasakawa (1984) showed only insignificant larval mortality. To prevent repeated parasitization (superparasitism) of the same host, each wasp was watched and removed as soon as it had withdrawn its ovipositor. Each host was presented to a single wasp only once; if the host was not accepted, it was replaced.

All experiments were conducted in the open laboratory at room temperatures of 24–27°C, relative humidity 30–40%, under diffuse daylight or fluorescent lighting of similar intensity. For microscope observations of examination behaviour, a heat-filtered tungsten light was used.

The statistical significance of the differences in the observed means was determined using a two-tailed *t*-test. The significance of differences in variance was tested with the *F*-distribution. Where the variance differed significantly, a weighted version of the *t*-test was used, according to the method of Ostle & Mensing (1975). The significance of the correlation coefficients was tested using the method of Beyer, Hackel, Pieper & Tiedge (1982). All means are quoted \pm standard deviation.

Experiment 1. Examination walk

Spherical glass beads were used as model hosts. They were cleaned by washing in acetone, ethanol and distilled water, and were mounted individually on 2×2 cm white cards with a minimal amount of gum arabic. Bead diameters differed significantly between small (0.946 ± 0.062 mm) and large beads (1.37 ± 0.17 mm) ($P \ll 0.001$) (Table 1).

Wasps used in the experiment were 24–36 h post-emergence and isolated 1–2 h from old host material before use. The head lengths differed significantly between the large and small wasps selected from the colony ($P \ll 0.001$) (Table 1). The mean head lengths of the large wasps were 0.243 ± 0.015 mm, and of the small wasps 0.172 ± 0.017 mm. Differences in wasp size are phenotypic variations arising from different numbers of larvae developing within a single host (Flanders, 1935; Klomp & Teerink, 1967); smaller wasps are produced under conditions of larval crowding and competition for limited nutrient.

Three treatment groups were formed by combining wasps and beads of different sizes. In group A, small wasps were presented with large beads; in group B, large wasps were presented with large beads; and in group C, small wasps were presented with small beads (see Table 1). Wasp and bead sizes were chosen so that the proportional difference between large and small wasps (1.41) was similar to that between bead diameters (1.43). For each individual wasp, size and bead diameter were measured, and relative bead size (bead diameter/wasp head length) was calculated.

The examination walk and the wasp's initial transit across the bead were timed with a specially designed event recorder program using a TRS-Model 100 (Radio Shack) portable computer (J. M. Schmidt & J. J. B. Smith, in preparation), the timing loop of which has an accuracy of ± 0.05 s. This program allowed the entry of observations as they occurred in real time. Timing of both initial transit and the examination walk was begun when the wasp first contacted the bead with its antennae. The wasp's next contact with the junction between the bead and the substrate was taken as the end of the initial transit. Timing of the examination walk was completed as soon as the wasp stopped drumming and began to drill its ovipositor into the surface of the bead. Only wasps which attempted to oviposit were included in the data set.

Experiment 2. Point- vs surface-mounted hosts

Trichogramma females used for this experiment were 18–24 h old, mated and unfed, with a mean head length of 0.22 mm. No difference in mean wasp size was

found between treatment groups. Two treatment groups were prepared. For the point-mounted group (D), individual *M. sexta* hosts were mounted on the ends of 0.114 mm tungsten wires by touching the tip of the wire to a droplet of gum arabic and then to the host surface. The wires were then mounted in surgical wax so that the hosts did not contact the substrate. For the surface-mounted group (E), the hosts were individually mounted on 2×2 cm squares of white plastic with a minimal amount of gum arabic. For the point-mounted hosts, a single wasp was placed directly onto each host surface using a sharpened tungsten needle. Wasps walked onto the surface-mounted hosts directly from the substrate. Trials in which the wasps left the host, or contacted the wire on which the host was mounted, were rejected. Wasps were also observed examining point-mounted glass beads, which had a mean diameter of 1.36 ± 0.06 mm.

After the wasps had completed ovipositing, the hosts were removed. The parasitized hosts were incubated at 26°C for 6 days, then dissected open to determine the number of last instar larvae contained in each.

To determine the mean fecundity of the population of wasps used in experiment 2, 37 wasps were selected from the colony, each placed in a container with more than 30 hosts, and allowed to oviposit freely.

Experiment 3. Point-mounted hosts: light vs dark

Wasps and point-mounted hosts were as described for experiment 2. In the 'light' group (F), a wasp was placed on each host as in experiment 2, and allowed to examine it and oviposit in diffuse daylight. In the 'dark' treatment group (G), a wasp was placed on a host, and the arena was immediately covered with a light-proof box. The wasp completed its examination in the dark. After 2–3 min [a period much greater than the mean examination time (Table 1)], the container was removed, and the wasp completed ovipositing in daylight. Both groups were observed until the wasps had completed ovipositing, at which time they were removed and the hosts treated as in experiment 2.

Experiment 4. Point-mounted hosts: variable wasp size

Trichogramma females were as in experiment 1. Point-mounted hosts were prepared as in experiments 2 and 3. Each host was exposed to a single wasp placed directly onto the host surface. Two treatment groups were prepared on the basis of wasp size. In group H the head lengths of the wasps averaged 0.186 ± 0.010 mm (range 0.16–0.20 mm), and in group J they averaged 0.230 ± 0.011 mm (range 0.22–0.25 mm) (Table 2). The mean diameters of the hosts used did not differ significantly between treatment groups, whereas relative diameters (host diameter/wasp head length) did differ ($P < 0.001$, Table 2). Numbers of resultant progeny were determined as described previously.

Morphological investigations

The size and number of ommatidia composing the compound eyes of *Trichogramma* were established using scanning electron microscopy as described by

Schmidt & Smith (1985c). All measurements were taken from specimens ranging in total body length between 0.45 and 0.55 mm.

RESULTS AND DISCUSSION

In experiment 1, the small wasps (group A) examined large hosts for a significantly longer time than did the large wasps (group B) ($P \ll 0.001$) (Table 1). There was no significant difference in examination time between small wasps on small hosts (group C) and large wasps on large hosts (group B) where the beads were the same relative size ($P > 0.10$) (Table 1). Although the wasps differed in size, there was no significant difference in the initial transit time between groups A and B ($P > 0.10$) where the beads were the same absolute size; however, transit time for wasps of group C (on the small beads) was significantly reduced ($P < 0.01$) (Table 1).

The correspondence between relative bead diameter and examination time, and the difference in the examining times of large and small wasps on beads of the same diameter, indicate that the duration of the examination walk depends upon the relative proportions of the wasp and bead, and not upon the absolute curvature of the surface. However, this observation alone does not establish that the wasps are only able to measure relative curvature. While the examination times differ significantly, the total distance travelled by both large and small wasps could remain constant for a given absolute host curvature if smaller wasps travelled more slowly than larger ones. In these experiments, the smaller wasps would have had to travel at half the speed of the larger wasps to account for the time differences, even though they were only 30% smaller in head length. However, the absence of a significant difference in initial transit times for large (group B) and small (group A) wasps on beads of the same diameter shows that their velocity is similar and independent of their body size (Table 1). Elsewhere, we have described the initial transit as a nearly straight path extending from the point of first contact to the opposite side of the host (J. M. Schmidt & J. J. B. Smith, in preparation). The length of this path, following a great circle over the host surface, is dependent only on host size, and not upon wasp size; thus with similar initial transit times for large and small wasps, it is clear that their velocities cannot differ significantly. Using the calculated values of initial transit length and the observed transit times, the mean velocity of the wasps is about 0.70 mm s^{-1} for all three groups (Table 1), a result similar to that obtained when *M. sexta* hosts were used instead of beads (J. M. Schmidt & J. J. B. Smith, in preparation).

Since the examination time for small wasps is about twice that for large wasps on similar hosts, and they walk at the same velocity, small wasps must travel about twice as far as large wasps during their examination walk, and an even greater distance relative to their body size. In order to compare quantitatively the relative distance travelled by the wasps, a 'relative length factor' was calculated by dividing the examining time (at constant velocity, an absolute measure of total path length) by the head length of the wasps to obtain a measure of relative path length (Table 1). Since the distance travelled with each step is likely to be directly proportional to the size

Table 1. *The effects of relative wasp size on host examination time, wasp velocity and step number*

Treatment group	N	Wasp head length (mm \pm S.D.)	Glass bead diameter (mm \pm S.D.)	Relative bead size	Examining time (s \pm S.D.)	Initial transit time (s \pm S.D.)	Initial transit length (mm)	Estimated mean velocity (mm s ⁻¹)	Relative length factor (s mm ⁻¹)
A Small wasp Large host	27	0.172 \pm 0.017 ^a	1.37 \pm 0.17 ^c	8.0	81.4 \pm 22.6 ^e	5.7 \pm 3.5 ^g	3.85	0.68	473 \pm 175 ⁱ
B Large wasp Large host	28	0.243 \pm 0.015 ^b	1.36 \pm 0.15 ^c	5.6	41.5 \pm 17.2 ^f	5.7 \pm 3.4 ^g	3.85	0.68	171 \pm 81 ^j
C Small wasp Small host	23	0.173 \pm 0.017 ^a	0.946 \pm 0.062 ^d	5.5	44.7 \pm 15.2 ^f	3.4 \pm 2.2 ^h	2.39	0.70	258 \pm 113 ^k

Relative bead size = bead diameter/head length.
Relative length factor = examining time/head length.
Significant differences within columns between means with different superscripts ($P < 0.01$).

of the wasp, the relative length factor is also an index of the number of steps taken by the wasp: the greater the distance travelled relative to the size of the wasp, the greater the number of steps taken. Accordingly, the smaller wasps (group A) must take about 2.75 times as many steps as larger wasps (group B) on the same-sized hosts (difference significant, $P < 0.005$). Since examination time, absolute distance travelled, relative distance travelled and number of steps do not correspond to absolute curvature, we conclude that the wasps are responding only to relative curvature. In effect, the smaller wasps respond to the hosts of the same absolute diameter as if they were larger hosts. This conclusion is in agreement with the model proposed earlier in which antennal angle measurements are used by the wasp to measure relative curvature (Schmidt & Smith, 1986), and also accounts for the observation by Flanders (1935) that small wasps accept small hosts more frequently than large wasps accept small hosts.

The wasps could adjust their examination time in response to their measure of relative curvature either by setting the absolute time during which they will walk on the host surface, or by setting the number of steps they will take. Which mechanism is used is revealed by the results for groups B and C. Here the relative bead size was the same, and no significant difference was observed in the examination times (Table 1). In addition, the calculated mean velocities of the wasps were again constant, regardless of the wasp size (Table 1). Since the wasps of both groups travelled at the same speed for approximately the same period, they must have travelled a similar total distance during host examination. However, a comparison of the relative length factors (examining time/head length) for groups B and C shows that the smaller wasps must have taken 1.6 times as many steps as the larger wasps to traverse this distance (difference significant, $P < 0.005$). Since it is unlikely that the wasps would have any measure of their absolute size upon which to adjust the number of steps needed, this suggests that *Trichogramma* sets the duration of its examination walk, rather than the number of steps taken. The result is to set the absolute distance to be travelled, rather than the distance relative to body size.

A similar setting of host examination time has been shown in other parasitoid wasps, including *Telenomus heliothidis* Ashmead (Scelionidae) (Strand & Vinson, 1983) and *Aphytis* spp. (Aphelinidae) (van Lenteren & DeBach, 1981). Which parameter of the walk is fixed in these species is not established. Another example is the adjustment of distance between turns in the chemotactic responses of many insect species (Bell, 1984). Some short-distance orientation responses also appear to require the setting of a particular path length, for example the navigation of ants and bees described by Jander (1957, 1963) and maze learning by ants (Schneirla, 1933, 1943).

The examination walk of *Trichogramma* is an important aspect of its host selection behaviour. During the walk, the wasp slows its walking speed by a factor of 10 or more, from 8–12 mm s⁻¹ on a level surface to 0.4–0.7 mm s⁻¹ (J. M. Schmidt & J. J. B. Smith, in preparation) while drumming the host surface continuously with its antennae. As a result, many more closely spaced regions of the host surface are sampled for chemosensory and tactile stimuli than during the more general walking behaviour of the wasp on a level substrate. Contact chemosensory cues, especially

those associated with the marking of hosts by the wasp itself or by other conspecifics, are detected during the examination walk (Salt, 1937; Klomp *et al.* 1980; de Jong & Pak, 1984) and mediate host acceptance or rejection during this stage of parasitization (Vinson, 1985). By linking the duration of the examination walk to its measure of host diameter, the wasp would ensure that large hosts will be examined as thoroughly as small hosts, while at the same time minimizing the handling time invested in small hosts. In essence, the examining walk may be fitted to the maximum potential surface area of the host to ensure adequate coverage to detect possible chemical cues. The relationship of *Trichogramma*'s examining behaviour to the detection of olfactory markers that indicate previous parasitizations has been described by Klomp *et al.* (1980).

Experiments 2, 3 and 4 show that host diameter, in addition to setting examination time and mediating host recognition (Salt, 1935; Klomp & Teerink, 1962; Schmidt & Smith, 1985*a,b*), also plays a part in the adjustment of clutch size in response to host size. We have previously shown that reduction of the exposed surface area of a host results in a reduction in the number of progeny allocated to the apparently smaller hosts (Schmidt & Smith, 1985*a,b*), indicating that the wasps use a parameter dependent on surface area to set clutch size. We have suggested that, in the absence of cues dependent on surface area, the wasp might use curvature to set an upper limit to clutch size. By using point-mounted hosts in which the wasps do not encounter any junction between host and substrate, cues dependent upon exposed surface area are effectively eliminated. In particular, the initial transit, the principal indicator of exposed surface area (J. M. Schmidt & J. J. B. Smith, in preparation), is undefined or infinite. In experiment 2, the wasps laid only about 25 % more progeny in point-mounted, as opposed to substrate-mounted, hosts (Table 2). If they depended only upon initial transit, or any other such indirect measure of surface area, to set clutch size, they should have laid many more eggs into the point-mounted hosts than into hosts resting on the substrate. The 25 % increase is consistent with the supposition that the wasp is still able to make a 'correct' estimate of exposed volume in the point-mounted hosts, since about 25 % more surface area is available than for the hosts resting on the substrate. Thus our two-parameter model, in which curvature can replace surface area cues to set an upper limit to clutch size, is supported (Schmidt & Smith, 1985*a*).

That this upper limit is not simply a limit to the number of eggs available to the female wasp is shown by comparing the mean total number of eggs produced by each wasp (67.3 ± 30.8 , $N = 37$) with the clutch size (15.2 ± 6.1 , $N = 22$), which we identify as the upper limit in experiment 2. Neither does it represent an upper limit for larval survival, since well over 30 final instar larvae are often found in the colony hosts, and up to 47 have been observed to develop normally to the pupal stage.

Although we have shown earlier that progeny adjustment to exposed volume proceeds normally in total darkness (Schmidt & Smith, 1985*a*), it can still be argued that visual cues, rather than mechanosensory information, might be relevant to a wasp in the point-mounted experiment. In experiment 3, no significant difference in

Table 2. *Progeny allocation to point-mounted hosts compared for light, dark, and different wasp size treatments*

Treatment group	N	Wasp head length (mm)	Host diameter (mm)	Host volume (mm ³)	Relative diameter	Progeny/host
Experiment 2						
D: Point-mounted host	22	0.22 ± 0.05	1.36 ± 0.06			15.2 ± 6.1
E: Surface-mounted host	100	0.23 ± 0.05	1.35 ± 0.05			11.9 ± 5.2
Experiment 3: point-mounted hosts						
F: Light	28	0.21 ± 0.04	1.36 ± 0.07			10.9 ± 4.3
G: Dark	39	0.21 ± 0.05	1.37 ± 0.06			11.3 ± 4.9
Experiment 4: point-mounted hosts						
H: Small wasp	11	0.186 ± 0.010	1.54 ± 0.05	1.91	8.28 ± 0.61	20.5 ± 4.9
J: Large wasp	17	0.230 ± 0.011	1.54 ± 0.05	1.91	6.7 ± 0.36	15.0 ± 5.4
Relative diameter = host diameter/wasp length. All means ± S.D.						

clutch size was found for point-mounted hosts examined in the light (group F) and in the dark (group G) ($P > 0.10$) (Table 2). Since all examination activity apart from the initial mounting of the host took place in darkness, most visual cues were eliminated. The remaining possibility that the wasps 'saw' the curvature of the host horizon as they were placed on its surface is rendered unlikely by consideration of the visual acuity of the *Trichogramma* eye. *Trichogramma* have apposition compound eyes, like those of other Hymenoptera (Land, 1985). Each compound eye consists of 170 nearly equal ommatidia, arranged in a hemiellipsoid 15 ommatidia wide and 17 from top to bottom. The diameter of the ommatidial corneas is between 7 and 9 μm . The total vertical angle subtended by the ommatidia is 160–180°, each single ommatidium subtending a visual angle of 9–11° [angle of anatomical resolution (Land, 1985)]. In contrast, the compound eye of *Apis* consists of 3000–4000 ommatidia (Snodgrass, 1956), which each subtend an angle of 1–4° (Dethier, 1953; Kaestner, 1972). Behavioural experiments have shown that bees can only distinguish between points subtending 1° of the visual field (Lindauer, 1957). In other insects with apposition eyes, the angle between neighbouring ommatidia also corresponds closely to the observed limits of behavioural discrimination (Land, 1985) and to the electrophysiologically measured angular sensitivities (Devoe, 1985). On this basis, the visual acuity of *Trichogramma* would appear to be approximately 9°. The visual resolution must also be limited by diffraction [Rayleigh limit (Land, 1985)] caused by the small size of the lens (Barlow, 1952), which will result in considerable blurring of the image. This corresponds to available data on visual orientation by *Trichogramma*: the wasps usually first orient towards 0.3 mm high hosts at a distance of 1–2 mm (Laing, 1938), when the host extends more than 8° above the horizon.

Previous experiments have shown that wasps can distinguish between hosts of 1.09 mm and 1.29 mm in diameter, as measured by examination time (Schmidt & Smith, 1985a). The difference in the curvature of the horizon for *Trichogramma* standing on hosts of these diameters would not exceed 3–5°, an angular separation therefore too small to be resolved by its eye. In addition, with such a small change in the angle of the horizon, the area of the visual field occupied by these two host diameters would not differ greatly. Since differences in proportional surface area between regions of the visual image would also be small, effects dependent upon light intensity, for example the darkening of the edge region as it curves away from the wasp, would probably not be large enough to be resolved by eyes of such limited acuity and high diffraction. Most importantly, such intensity effects depend not only on the size of the host, but also on the direction and magnitude of external illumination, factors which would not necessarily be consistent between hosts.

In experiment 3, progeny were allocated to hosts in darkness with similar accuracy as in daylight conditions, indicating that the wasps are using a measure more accurate and more generally applicable than would be possible with vision. Thus we must conclude that the wasps were indeed using a mechanical measure to assess host volume.

The apparent discrepancy between clutch sizes obtained for point-mounted hosts in experiments 2 and 3 was due to the use of different host egg batches for these separate trials. Size is only one of several parameters which control progeny allocation by *Trichogramma*. Chemical cues, especially those relating to host age, also significantly affect clutch size (Marston & Ertle, 1969). As a result, comparisons can only be made between treatment groups in which the hosts are drawn from the same batch at the same time. Chemical variations in egg composition are probably also responsible for much of the variation observed within treatment groups, although natural variation between wasps is also reported to be high (Walter, 1983).

In experiment 4, point-mounted hosts of the same diameter were allocated significantly more progeny by small wasps than by larger wasps ($P < 0.02$) (Table 2). Smaller wasps laid an average of 1.4 times as many eggs into each host. The corresponding ratio of relative host diameters was 1.24 (Table 2). These results demonstrate that, as for examination time, the wasps set an upper limit to clutch size in response to a measure of *relative* surface curvature rather than to the absolute curvature of the host, since only this variable differed significantly between treatment groups (Table 2). The difference in clutch size also demonstrates that its upper limit is dependent upon a measure of host dimension and is not simply some general limit. It shows again that the upper limit is not just dependent on larval survival in hosts of limited nutrient content, since hosts in both treatment groups contained the same volume. Furthermore, it confirms that the limit is independent of the fecundity or total ovariole production of the wasp. Fecundity, as measured by eggs laid or ovarioles available at emergence, is directly dependent upon wasp size; smaller wasps produce fewer eggs (Klomp & Teerink, 1967). However, in experiment 4, the smaller wasps laid more eggs into each host than the larger wasps (Table 2), despite their proportionately lower total ovariole number.

Experiment 4 also reveals a problem in using relative curvature as a measure of host volume. Here smaller wasps produced more progeny per host, each of which was therefore allocated proportionately less host volume (Table 2). As a direct result, the emerging offspring of the small wasps would themselves be smaller and less fit than those produced by the larger wasps, since the larvae would have less nutrient and developmental space available (Flanders, 1935; Klomp & Teerink, 1967). Thus a mechanism by which the ovipositing female could assess absolute host volume independently of her own size should be favoured. Such a mechanism is in fact used by the wasps where the hosts are resting directly on the substrate, either singly or in clumps; we show elsewhere the importance under these conditions of the initial transit, an absolute measure (J. M. Schmidt & J. J. B. Smith, in preparation). Nevertheless, the ability to estimate volume in the absence of host-substrate discontinuities may be important, for example in the parasitization of stalked eggs.

The wasp's measure of surface curvature not only mediates the setting of a maximum volume estimate, but also appears to be a sufficient cue for initiating host examination. Since the wasps were allowed to mount the host from a surface held tangential to the host's surface, there was no large, acute discontinuity in the substrate which could have been used as a cue to begin examining. Fifteen of twenty wasps tested also examined and attempted to oviposit into suspended glass bead models, demonstrating that the wasps do not require olfactory cues from the substrate to mediate attempts at oviposition. If examining is initiated by appropriate changes in surface curvature, this factor must play a critical role in the process of host recognition. Objects with very small or large curvatures may not initiate host examining behaviour and may be ignored by the wasp during host searching. Salt (1935) found that cylindrical pieces of glass are accepted as potential hosts only when the cross-sectional diameter is above a certain minimal dimension, suggesting that there is a range of surface curvatures outside which an object is rejected by the wasp or simply not detected as distinct from the substrate.

The finding that these wasps use relative curvature measurements also has practical implications for the use of *Trichogramma* as a biological control agent. Flanders (1935) found that the acceptance range for host sizes varied between wasps of different sizes; smaller wasps accepted smaller hosts, larger wasps accepted larger hosts. Since the wasps apparently only measure relative curvature, the host ranges of different sizes of *Trichogramma* may differ somewhat, so that smaller target host species may require the application of smaller wasps to ensure host recognition and acceptance. Complementary considerations arise in the mass rearing of *Trichogramma* in terms of selecting appropriate rearing hosts to obtain wasps of the required size.

We have proposed, on the basis of morphological investigations and studies of the relative positions of body parts during host examination, that the wasp's response to surface curvature is mediated by detecting changes in the scapal-head angle of the antennae (Schmidt & Smith, 1986). Hairplates located in this joint region could provide the required sensory information about angular displacement of the antennae (J. M. Schmidt and J. J. B. Smith, in preparation). It is particularly significant that

this mechanism depends upon the size of the wasp and its appendages relative to the curvature of the host surface (Schmidt & Smith, 1986); it cannot provide information about the absolute curvature or diameter of a host. The present results provide further evidence that this mechanism is indeed used by *Trichogramma*.

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REFERENCES

- BARLOW, H. B. (1952). The size of ommatidia in apposition eyes. *J. exp. Biol.* **29**, 667–674.
- BELL, W. J. (1984). Chemo-orientation in walking insects. In *Chemical Ecology of Insects* (ed. W. J. Bell & R. T. Cardé), pp. 93–109. Sunderland, MA: Chapman & Hall.
- BEYER, O., HACKEL, H., PIEPER, V. & TIEDGE, J. (1982). *Mathematik für Ingenieure, Naturwissenschaftler, Ökonomen und Landwirte*, vol. 17, *Wahrscheinlichkeitsrechnung und mathematische Statistik*. Leipzig: B. G. Teubner Verlag.
- DE JONG, E. J. & PAK, G. A. (1984). Factors determining differential host–egg recognition of two host species by different *Trichogramma* spp. *Meded. Fac. Landbouww. Rijksuniv. Gent.* **49**, 815–825.
- DETHIER, V. G. (1953). Vision. In *Insect Physiology* (ed. K. D. Roeder), pp. 488–522. New York: John Wiley & Sons, Inc.
- DEVOE, R. D. (1985). The eye: electrical activity. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 6, *Nervous System: Sensory* (ed. G. A. Kerkut & L. I. Gilbert), pp. 277–354. Oxford: Pergamon Press.
- FLANDERS, S. E. (1935). Host influence on the prolificacy and size of *Trichogramma*. *Pan-Pacif. Ent.* **11**, 175–177.
- JANDER, R. (1957). Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa*) L. *Z. vergl. Physiol.* **40**, 162–238.
- JANDER, R. (1963). Insect orientation. *A. Rev. Ent.* **8**, 95–114.
- KAESTNER, A. (1972). *Lehrbuch der speziellen Zoologie*, vol. 1, part IIIA. Jena: Gustav Fischer Verlag.
- KLOMP, H. & TEERINK, B. J. (1962). Host selection and number of eggs per oviposition in the egg parasite *Trichogramma embryophagum* Htg. *Nature, Lond.* **195**, 1020–1021.
- KLOMP, H. & TEERINK, B. J. (1967). The significance of oviposition rates in the egg parasite, *Trichogramma embryophagum* Htg. *Archs néerl. Zool.* **17**, 350–375.
- KLOMP, H., TEERINK, B. J. & MA, W.-C. (1980). Discrimination between parasitized and unparasitized hosts in the egg parasite *Trichogramma embryophagum* (Hym., Trichogrammatidae): a matter of learning and forgetting. *Neth. J. Zool.* **30**, 254–277.
- LAING, J. (1938). Host-finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts. *J. exp. Biol.* **15**, 281–302.
- LAND, M. F. (1985). The eye: optics. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 6, *Nervous System: Sensory* (ed. G. A. Kerkut & L. I. Gilbert), pp. 225–275. Oxford: Pergamon Press.
- LINDAUER, M. (1957). Sonnenorientierung der Bienen unter der Äquatorsonne und zur Nachtzeit. *Naturwissenschaften* **44**, 1–6.
- MARSTON, N. & ERTLE, L. R. (1969). Host age and parasitism by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *Ann. ent. Soc. Am.* **62**, 1476–1482.
- OSTLE, B. & MENSING, R. W. (1975). *Statistics in Research*. Third edition. Ames: Iowa State University Press.
- QUEDNAU, W. (1960). Über die Identität der *Trichogramma*-Arten und einiger ihrer Ökotypen (Hymenoptera, Chalcidoidea, Trichogrammatidae). *Mitt. biol. Reichsanst Ld-u Forstw.* **100**, 11–50.
- SALT, G. (1935). Experimental studies in insect parasitism. III. Host selection. *Proc. R. Soc. Ser. B* **117**, 413–435.

- SALT, G. (1937). The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts. *Proc. R. Soc. Ser. B* **122**, 57–75.
- SCHMIDT, J. M. & SMITH, J. J. B. (1985a). Host volume measurement by the parasitoid wasp *Trichogramma minutum*: The roles of curvature and surface area. *Ent. exp. appl.* **39**, 213–221.
- SCHMIDT, J. M. & SMITH, J. J. B. (1985b). The mechanism by which the parasitoid wasp *Trichogramma minutum* responds to host clusters. *Ent. exp. appl.* **39**, 287–294.
- SCHMIDT, J. M. & SMITH, J. J. B. (1985c). The ultrastructure of the wings and the external sensory morphology of the thorax in female *Trichogramma minutum* Riley (Hymenoptera: Chalcidoidea: Trichogrammatidae). *Proc. R. Soc. Ser. B* **224**, 287–313.
- SCHMIDT, J. M. & SMITH, J. J. B. (1986). Correlations between body angles and substrate curvature in the parasitoid wasp *Trichogramma minutum*: possible mechanism of host radius measurement. *J. exp. Biol.* **125**, 271–285.
- SCHNEIRLA, T. C. (1933). Some important features of ant learning. *Z. vergl. Physiol.* **19**, 439–452.
- SCHNEIRLA, T. C. (1943). The nature of ant learning. II. The intermediate stage of segmental maze adjustment. *J. comp. Psychol.* **34**, 149–176.
- SNODGRASS, R. E. (1956). *Anatomy of the Honey Bee*. Ithaca: Comstock Publishing Associates.
- STRAND, M. R. & VINSON, S. B. (1983). Host acceptance behaviour of *Telenomus heliothidis* (Hymenoptera: Scelionidae) toward *Heliothis virescens* (Lepidoptera: Noctuidae). *Ann. ent. Soc. Am.* **76**, 781–785.
- SUZUKI, Y., TSUJI, H. & SASAKAWA, M. (1984). Sex allocation and effects of superparasitism on secondary sex ratios in the gregarious parasitoid, *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). *Anim. Behav.* **32**, 478–484.
- TAYLOR, T. A. & STERN, V. M. (1971). Host preference studies with the egg parasite *Trichogramma semifumatum* (Hymenoptera: Trichogrammatidae). *Ann. ent. Soc. Am.* **64**, 1381–1390.
- VINSON, S. B. (1985). The behaviour of parasitoids. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 9 (ed. G. A. Kerkut & L. I. Gilbert), pp. 417–469. Oxford: Pergamon Press.
- VAN LENTEREN, J. C. & DEBACH, P. (1981). Host discrimination in three ectoparasites (*Aphytis coheni*, *A. lingnanensis*, and *A. melinus*) of the oleander scale (*Aspidiotus nerii*). *Neth. J. Zool.* **31**, 504–532.
- WALTER, S. (1983). Zur Biologie und Ökologie von Eiparasiten aus der Gattung *Trichogramma* Westwood (Hym., Chalc.). Part 2. Untersuchungen unter Laborbedingungen. *Zool. Jb. (Syst.)* **110**, 419–441.