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How do female parasitoid wasps assess host size during sex-ratio manipulation?

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Running headline: King: Sex ratios and host size assessment

Abstract. As in many parasitoid wasps, *Spalangia cameroni* females oviposit a greater proportion of daughters in large than in small hosts. How females assess host size for this sex-ratio manipulation was examined: do females require visual cues and do they use exposed surface area or volume or duration required to drill into a host prior to oviposition? Visual cues are not necessary; in the dark, females still produced a greater proportion of daughters in large hosts than in small hosts. To examine whether females use exposed surface area or volume to estimate host size, proportion of daughters was compared among unburied hosts and hosts that had been half-buried either horizontally or vertically. Burying hosts did not interfere with host size assessment for sex-ratio response; sex ratios did not differ between partially-buried hosts and unburied hosts of the same size. Females do not appear to use duration required to drill into a host prior to oviposition to assess a host's resources. Drill duration was not consistently greater or lesser in the types of hosts in which daughters versus sons tend to be oviposited. Specifically, a greater proportion of daughters are oviposited in large hosts than in small hosts and in young hosts than in old hosts. Drill duration was greater in large hosts than small hosts but was less in young hosts than old hosts. The greater average drill duration observed for daughters than for sons suggests that daughters may be more costly to produce than sons.

The study of sex ratios and sex allocation has received considerable attention (for reviews see e.g. Charnov 1982; Clutton-Brock & Iason 1986; Waage 1986; King 1987). The sex ratios of parasitoid wasps have been well-studied in part because they have a known mechanism for maternal manipulation of sex: unfertilized eggs develop into sons, and fertilized eggs develop into daughters. Thus, mothers can potentially control offspring sex ratio by adjusting the ratio of unfertilized to fertilized eggs at oviposition. In fact, there is evidence that females in some parasitoid wasp species do adjust sex ratio in response to certain environmental conditions, including host characteristics (King 1987, 1993). How females assess these environmental conditions has not been well-studied and is addressed here for the parasitoid wasp *Spalangia cameroni*'s sex-ratio response to host size.

Spalangia cameroni (Hymenoptera: Pteromalidae) parasitize fly pupae found in livestock manure. Females crawl as deep as 5 cm below the surface of the manure in search of hosts (Rueda & Axtell 1985). Upon encountering a host, a female walks over it several times, tapping it with her antennae. To oviposit, she drills through the puparium (the hard shell around a fly pupa) with her ovipositor and lays an egg on the pupa within. Generally only one *S. cameroni* offspring develops on each host. *Spalangia cameroni* females oviposit a greater proportion of daughters in large hosts than in small hosts (King 1988, 1990), a pattern seen in most, but not all, parasitoid wasps (King 1987, 1993).

It is not known how females measure the size of a host. Here, using sex-ratio response as an assay, I examine 1) whether females need visual cues in order to measure host size, 2) whether females use exposed surface area or volume to estimate host size, and 3) whether females use the duration of oviposition behaviour patterns, particularly duration to drill into a host, to assess host size. To test the last hypothesis, I compare drill duration in small versus large hosts and then in old versus young hosts. Females might be expected to take less time to drill into smaller hosts because the puparia (shells) of smaller hosts appear to be thinner (personal observation). Thus, females might use a simple rule of ovipositing male eggs when drill duration is short. If females use this rule, they would also be predicted to have shorter drill durations in old than in young hosts because, in addition to producing a greater proportion of sons from small hosts than from large hosts, females also produce a greater proportion of sons from old hosts than from young hosts (King 1990).

METHODS

General Methods

The *Spalangia cameroni* used in this study were from a colony established in 1985 with wasps that emerged from *Musca domestica* and *Stomoxys calcitrans* pupae collected in Indiana, U.S.A (King 1991). The wasp colony was maintained at 23-28°C continuous light, using *M. domestica* as hosts (King 1988). I produced large and small hosts for the experiments by manipulating the volume of host eggs per volume of host media: 800 mm³ of eggs were reared in 1030 ml of larval medium to produce large hosts of about 24 mm³; 350 mm³ of eggs were reared in 130 ml of larval medium to produce small hosts of about 15 mm³ (King 1988; Seidl and King in press). Females

used in experiments had emerged within 1 d prior to use, and each female had been paired with a virgin male and observed to mate. Unless specified otherwise, hosts less than 1-day-old were presented to females in small plastic vials (40 mm high by 36 mm top diameter by 27 mm bottom diameter) with a drop of honey on the vial wall or lid for food. In the videotape experiments, young hosts were 0-day-old and old hosts were 3-days-old. When presented to the wasps, 0-day-old hosts were less than 24 h old (timed from the initiation of pupal tanning).

Role of Visual Cues

To test whether females require visual cues to assess host size, I gave each female seven large hosts and seven small hosts in the dark. The large and small hosts were distributed haphazardly in the bottom of a vial. After 24 h, I removed the female and placed the large and small hosts in separate vials. Offspring were sexed and counted after they reached the adult stage. I compared the sex ratio and the number of offspring between treatments, using one-tailed paired t-tests, with mother as the sampling unit. If females produce a greater proportion of sons in small hosts than in large hosts even in the dark, then visual cues are not necessary for host size assessment.

Response to Partially-Buried Hosts

To determine whether females use exposed surface area or volume to estimate host size, I compared sex ratio responses among unburied hosts and hosts that have been half-buried either horizontally or vertically. I presented each female with 12 large hosts for each of 2 successive days. The hosts were presented in vials three-fourths full of sand. The 12 hosts each day consisted of four unburied hosts, four hosts half-buried vertically (the long axis of the host perpendicular to the surface of the sand), and four hosts half-buried horizontally (the short axis of the host perpendicular to the surface of the sand). After the hosts were placed on, or buried in, the sand, the surface of the sand was wetted; this prevented females from burrowing to reach unexposed parts of the hosts. After being with a female for 24 h, the three types of hosts were removed from the sand and isolated in small plastic vials where development was completed. I analyzed the effect of burying on sex ratio and on number of offspring by multivariate analyses of variance (MANOVA), with mother as the sampling unit (Norusis 1988).

Duration of Oviposition Behaviour Patterns in Different-sized Hosts

To examine the effect of host size on oviposition behaviour patterns, I videotaped ovipositing females. I introduced each female ($N > 70$) into a petri dish (35 mm diameter X 10 mm deep) containing a young host (of variable size) which had been 'cemented' to the dish with a small drop of water. Each female was videotaped from the time she was introduced into the petri dish until after she had drilled into the host at least once. The female was removed after she left the host (i.e. when all limbs ceased contact with the host) or if she had not begun drilling into a host within 2 h. Each female had received 14 large young hosts for the 24 h before testing because preliminary tests suggested that females with prior host experience initiate drilling more quickly than females that have not previously been exposed to hosts.

Videotaping was with a Javelin colour video camera through a Wild dissecting microscope using a JVC s-VHS digital recorder with s-VHS tapes on extended play. Illumination was from fiber-optic gooseneck lights which gave off no noticeable heat.

The following data on oviposition behaviour patterns were collected for each female from these videotapes by observing the tapes on a 19" color monitor and calculating the duration of each behaviour pattern to the nearest second from the video-recorder.

(1) Start-to-exploration duration: time at which the female was put in with the host until she began pulling her abdomen forward and touching the puparium repeatedly in a small area with the tip of her abdomen.

(2) Exploration-to-departure duration: time at which the female began probing the host puparium with the tip of her abdomen until she stepped off the host and all of her limbs ceased contact with the host (includes the following time intervals).

(3) Drill duration: time at which a particular drilling was initiated until the ovipositor was completely inserted into the host, as indicated by the middle of the abdomen contacting the host and the angle between the ovipositor and abdomen tip going from v-shaped to nearly straight.

(4) Within-puparium duration: time at which the ovipositor was completely inserted into the host at the end of drilling until it was withdrawn completely from the host.

Not all females provided data on all events, as when the orientation of the female obscured the view of her ovipositor.

The sex of the wasp offspring emerging from each host was determined. Host width and length were measured to the nearest 0.05 mm, using a micrometer on a dissecting microscope. Host volume was calculated using the equation for a prolate spheroid, $\frac{2}{3}\pi(\text{host width}/2)^2(\text{host length})$ (Holdaway & Smith 1932).

The effects of host volume on durations of oviposition behaviour patterns were examined by regression analyses, with durations log-transformed prior to analyses when it improved normality without decreasing linearity. Analyses of effects of host volume on durations were restricted to females that were successful in drilling their hosts (i.e. whose ovipositors went all the way into the host). I excluded females whose hosts moved (N = 6), because in their natural habitat, manure and adjacent hosts would probably prevent hosts from moving as females began drilling. I also excluded females that drilled all the way into hosts multiple times (N = 12), because I could not be sure which drilling event resulted in the offspring that subsequently emerged. In addition, I excluded females that did not produce emerging offspring, i.e. a fly or nothing emerged from the host (N = 16).

For comparisons of durations, between hosts from which males versus females subsequently emerged, and between hosts from which wasps versus no wasps emerged, I used t-tests when assumptions of normality were met; otherwise, I used Mann-Whitney U tests.

Duration of Oviposition Behaviour Patterns in Old versus Young Hosts

To examine the effect of host age on oviposition behaviour patterns, females were videotaped ovipositing in large young and old hosts. Each female was given both

host ages; the order in which the two ages were presented was alternated from female to female.

In addition to the four oviposition behaviour durations collected in the previous experiment, the following were also collected:

(5) Start-to-antennae-tap duration: time at which the female was put in with the host until she began tapping the puparium with her antennae.

(6) Drill location: where on the surface of the host the female drilled -- the head end, the abdomen end, or the middle; a female was defined as drilling at one of the ends if she was no farther from it than the length from her head to her thorax (about one-fifth the length of the host).

(7) Number of unsuccessful drills: the number of times in which the female attempted to drill the host for at least one minute but the ovipositor never completely inserted into the host.

In contrast to the previous videotape experiment, to keep sample sizes reasonably large, analyses included females that attempted to drill but were never successful, females that drilled all the way into hosts multiple times, and females that did not produce emerging offspring. Females with a host that moved were excluded. Data on drill duration and location and within-puparium duration were collected on each female's first successful drill. The effects of host age on oviposition behaviour patterns were examined by paired t-tests when assumptions of normality were met; otherwise, by sign tests. Thus, mother was the sampling unit.

RESULTS

Role of Visual Cues

In the absence of visual cues, females produced a greater proportion of sons from small hosts than from large hosts (0.30 ± 0.042 versus 0.16 ± 0.040 ; $t = 2.61$, $df = 15$, $P = 0.01$). There was no significant difference between the number of offspring produced from small and large hosts (4.9 ± 0.63 versus 6.0 ± 0.70 ; $t = 1.40$, $df = 15$, $P = 0.09$).

Response to Partially-buried Hosts

The proportion of sons emerging from hosts that were unburied, half-vertically buried, and half-horizontally buried did not differ significantly (Table I; MANOVA Pillais approximate $F = 0.09$, $df = 2, 40$, $P = 0.92$). Number of offspring did differ significantly among the three types of hosts (Table I; MANOVA Pillais approximate $F = 5.00$, $df = 2, 41$, $P = 0.01$). Fewer offspring were produced from vertically-buried than from unburied hosts ($t = 3.08$, $df = 42$, $P = 0.002$, $a = 0.02$ when adjusted for multiple comparisons (Rice 1989)). The number of offspring produced from horizontally-buried hosts was not significantly less than from unburied hosts ($t = 1.42$, $df = 42$, $P = 0.08$, adjusted $a = 0.05$) nor significantly greater than from vertically-buried hosts ($t = 1.43$, $df = 42$, $P = 0.08$, adjusted $a = 0.03$).

Duration of Oviposition Behaviour Patterns in Different-sized Hosts

Of 49 females that produced emerging offspring in this videotape experiment, 37

inserted once, nine inserted twice, one inserted three times and two inserted four times into a single host. Only three of the females that inserted multiply subsequently inserted in the same location as the first.

The size of the host in which a female oviposited affected the duration of two of the five behaviour patterns considered. Females with larger hosts began exploring their hosts with the tips of their abdomens sooner (Fig. 1) and took significantly longer to drill (Fig. 2). There was no significant effect of host volume on exploration-to-departure duration (log transformed duration: $R^2 = 0.01$, $df = 29$, $P = 0.69$) or within-puparium duration ($R^2 = 0.03$, $df = 25$, $P = 0.38$).

Because drill duration in larger hosts was greater (Fig. 2) and because on average daughters emerged from larger hosts than sons ($t = 1.88$, $df = 33$, $P = 0.03$), drill duration was greater for hosts that subsequently produced daughters than for hosts that produced sons (Fig. 2; mean \pm SE duration 4.88 min \pm 0.45, range = 2.05-9.40 min versus 3.74 min \pm 0.46, range = 1.55-6.48 min, $t = 1.70$, $df = 26$, $P = 0.05$). When the effect of host volume on drill duration was controlled, there was no additional effect of offspring sex on drill duration (partial correlation coefficient = 0.19, $P = 0.35$). Controlling for offspring sex, the effect of host volume was still significant (partial correlation coefficient = 0.37, $P = 0.03$).

Other than for drill duration, there were no significant differences in durations of oviposition behaviour patterns between hosts from which males versus females subsequently emerged: start-to-exploration duration ($t = 0.05$, $df = 34$, $P = 0.96$), exploration-to-departure duration ($U = 111.0$, $N_1 = 13$, $N_2 = 19$, $P = 0.63$), or within-puparium duration ($t = 0.57$, $df = 26$, $P = 0.57$).

There were no significant differences in durations of oviposition behaviour patterns between females that produced emerging offspring and females that drilled through their host but produced no emerging offspring, i.e. a fly or nothing emerged from the host (start-to-exploration duration, $U = 241.0$, $N_1 = 36$, $N_2 = 16$, $P = 0.35$; exploration-to-departure duration, $U = 193.0$, $N_1 = 32$, $N_2 = 14$, $P = 0.46$; drill duration, $t = 1.32$, $df = 39$, $P = 0.19$; within-puparium duration, $t = 0.76$, $df = 38$, $P = 0.45$). The hosts from which no wasp offspring emerged also were not significantly smaller than the hosts from which wasps emerged ($t = 0.94$, $df = 51$, $P = 0.18$).

Duration of Oviposition Behaviour Patterns in Old versus Young Hosts

There was considerable variation among females in the duration of oviposition behaviour patterns (Table II), with some differences between young and old hosts. Females probed old hosts with the tips of their abdomens sooner than young hosts. Successful drills took longer in old hosts than in young hosts; and once females had drilled into their hosts, they spent more time with their ovipositors in old hosts than in new hosts. (These effects of host age on drill duration and within-puparium duration were significant even when the analyses were restricted to females that produced emerging offspring from both the young and the old hosts ($t = 4.32$, $df = 9$, $P = 0.002$)). There was no significant difference between old and young hosts in how soon females began tapping the hosts with their antennae. Females made more unsuccessful drill attempts on old hosts than on young hosts (mean \pm SE 1.04 \pm 0.15 versus 0.25 \pm 0.098; $t = 4.03$, $df = 27$, $P = 0.001$). I did not compare durations of oviposition behaviour

patterns between hosts from which males versus females subsequently emerged, because no males emerged from old hosts, and only two males emerged from young hosts.

Among drills that were at the end of a host, most of the drills in old hosts were at the abdomen end (67%, 12 of 18); most of the drills in young hosts were at the head end (65%, 15 of 23) ($G = 4.18$, $df = 1$, $P < 0.05$).

DISCUSSION

Female *S. cameroni* do not require visual cues to measure host size for offspring sex-ratio manipulation: a greater proportion of sons were produced from small hosts than from large hosts in the dark, and sex ratios in the dark did not differ from those in the light (King 1988; for large hosts $t = 0.71$, $df = 41$, $P > 0.40$; for small hosts $t = 0.35$, $df = 41$, $P > 0.50$). That visual cues are not necessary is not surprising given that females sometimes burrow as deep as 5 cm below the surface of the manure (Rueda & Axtell 1985), where light probably does not reach. The use of non-visual cues by *S. cameroni* is also consistent with the non-visual nature of the cues that a confamilial, *Nasonia vitripennis*, uses during sex-ratio manipulation to assess whether a host is parasitized (King & Skinner 1991).

The sex-ratio responses of female *S. cameroni* to host size and to host age appear to be based on females assessing something other than external puparial dimensions. Firstly, if females were using external dimensions to assess host size, partially-buried hosts might seem smaller, yet females did not produce a greater proportion of sons in such hosts. Secondly, old hosts are of the same external width as young hosts, yet females produce a greater proportion of sons from old hosts than from young hosts (King 1990).

External host dimensions seem to be important in some parasitoid wasps, affecting the sex-ratio response of *Coccygomimus turionellae* and the clutch size responses of *Trichogramma minutum* and *Pteromalus puparum* (Sandlan 1979; Schmidt & Smith 1985; Takagi 1986). *Trichogramma minutum*'s clutch-size response to host size appears to be based on the duration between a female's first contact with a host and her first subsequent contact with the substrate, i.e. her initial transit time (Schmidt & Smith 1987). In contrast to *T. minutum* and *P. puparum*, the clutch size of females of the pupal parasitoid *Nasonia vitripennis* are similar in hosts that are buried three-fourths of their length versus one-third (Wylie 1967).

Initial transit time does not seem to be the mechanism of host size measurement for sex-ratio manipulation in *S. cameroni*. If initial transit time were important, I would have expected burying hosts to affect sex-ratio response, and it did not. Females gave the same sex-ratio response to unburied hosts as to half-buried hosts. Time or distance to walk across a host may be unreliable indicators of host size for *S. cameroni* in nature. The hosts of *S. cameroni* are frequently clumped and completely or partially buried in manure (personal observation), which may affect the time or distance to walk across a host. In contrast, in natural conditions *T. minutum*'s hosts are not buried.

Spalangia cameroni females exhibit some responses to host size prior to drilling and oviposition. Females that were presented with larger hosts explored their hosts

with the tips of their abdomens sooner (Fig. 1). Also, fewer offspring were produced from vertically-buried hosts than from unburied hosts, suggesting that amount of exposed surface area or exposed volume affects whether a female oviposits in a host. Early effects of host size on whether a female explores a host and whether or not she oviposits in it may not affect subsequent decisions of what sex of offspring to oviposit.

Another mechanism by which some parasitoids may assess host size is by measuring host curvature, e.g. by antennae-to-head angle (Schmidt & Smith 1986). *Spalangia cameroni* females do not appear to use host curvature alone to assess size: the sex-ratio from vertically-buried and horizontally-buried hosts did not differ. These two types of buried hosts are the same in exposed volume and surface area but differ in exposed curvature.

The buried host experiment indicates that females do not use curvature alone to assess host size. However, the experiment does not eliminate the possibility that females use a combination of information on curvature and their location on the host. For parasitoids such as *S. cameroni* whose hosts are ellipsoidal, not spherical, host curvature will provide a reliable indicator of host size only if a female recognizes where on the host she is measuring curvature (e.g., by detecting host spiracles), if she measures curvature at a consistent site (which *S. cameroni* does not do), or if she measures minimum or maximum curvature.

Drill duration was affected by host size and age, but females do not appear to use drill duration to assess host resources for sex-ratio manipulation. Although *S. cameroni* produces a greater proportion of sons both from smaller hosts and from older hosts (King 1988, 1990), drill duration was shorter for smaller hosts but longer for older hosts. Furthermore, there was considerable overlap in drill duration between hosts from which sons subsequently emerged and hosts from which daughters subsequently emerged (Fig. 1). Further evidence that old hosts may be more difficult to drill than young hosts comes from the greater number of unsuccessful drills in old than in young hosts. Old hosts may be harder due to greater sclerotization.

Drill duration may be important in understanding selection pressures on overall population sex ratio. The greater drill duration for daughters than for sons will translate into greater costs of producing a daughter than a son if energy is a limiting resource for wasps and drilling is energetically expensive. Such an energy cost difference may select for an increased production of sons (Fisher 1930). *Spalangia cameroni*'s sex ratio in both the laboratory and field is female-biased (Table 1; King 1991). However, the female bias may result from local mate competition (Hamilton 1967) creating an opposing selective force (King 1989). Time costs of daughters and sons appear to be equivalent given that total time spent on the host (exploration-to-departure duration) did not differ with offspring sex.

The possibility that *S. cameroni* females use the amount of chemicals given off by hosts (e.g. carbon dioxide) to assess host size during offspring sex decisions remains to be examined. Females might detect chemicals once they have drilled into a host by using sensory organs on their ovipositors (van Lenteren 1981).

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Table I. Sex ratio (proportion of sons) and clutch size of females given unburied, horizontally-buried, and vertically-buried hosts

	Sex ratio		Clutch size	
	X ± SE	N	X ± SE	N
Unburied	0.24 ± 0.037	42	5.1 ± 0.31	43
Horizontally-buried	0.22 ± 0.037	42	4.6 ± 0.28	43
Vertically-buried	0.23 ± 0.038	42	4.2 ± 0.25	43

Table II. $X \pm SE$ (Range) duration (min) of oviposition behaviour patterns of videotaped females in host age experiment (See text for description of behaviours)

	N	Young hosts	Old hosts	Paired tests
		$X \pm SE$	$X \pm SE$	
		(Range)	(Range)	
Start-to-antennae-tap	27	9.84 \pm 4.44 (0.57 - 108.03)	3.51 \pm 1.02 (0.03 - 23.98)	Sign Test, P = 0.25
Start-to-exploration	25	18.46 \pm 5.40 (1.48 - 110.73)	8.26 \pm 2.56 (1.43 - 59.58)	Sign Test, P = 0.01
Exploration-to-departure	14	19.02 \pm 3.59 (8.72 - 59.93)	43.83 \pm 6.74 (22.32 - 122.55)	Sign Test, P = 0.01
Drilling	14	6.70 \pm 0.89 (3.05 - 13.60)	22.58 \pm 2.81 (7.20 - 40.22)	t = 5.96, P < 0.001
Within-puparium	14	5.24 \pm 0.96 (1.98 - 13.60)	6.93 \pm 0.86 (3.03 - 15.13)	Sign Test, P = 0.01

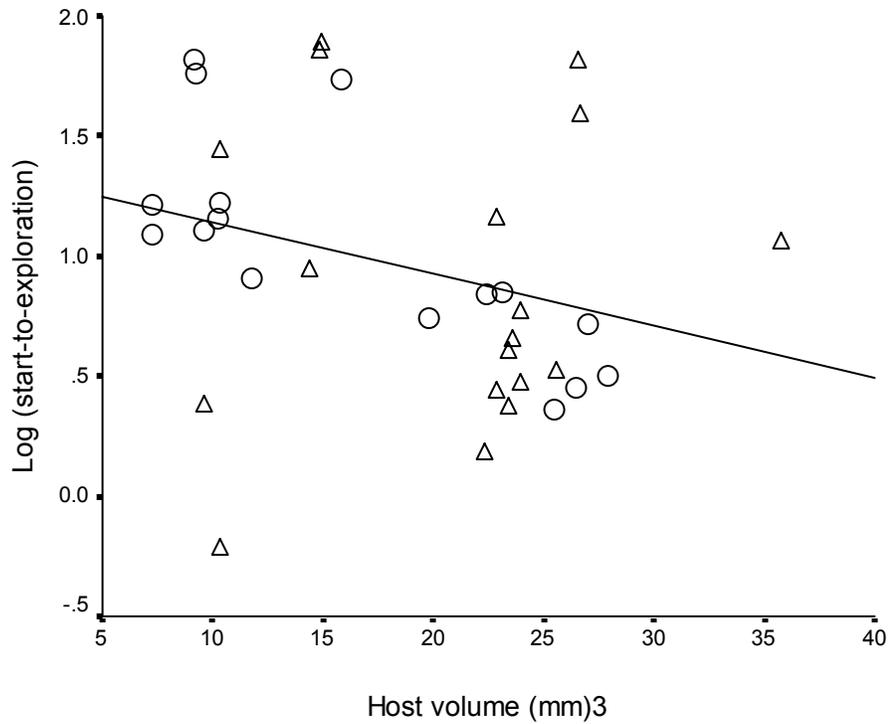


Figure 1. Log_{10} (start-to-exploration duration in minutes) in hosts of different volumes from which a male (o) or a female (Δ) wasp subsequently emerged ($Y = 1.359 - 0.022X$, $R^2 = 0.09$, $N = 34$, $P = 0.04$).

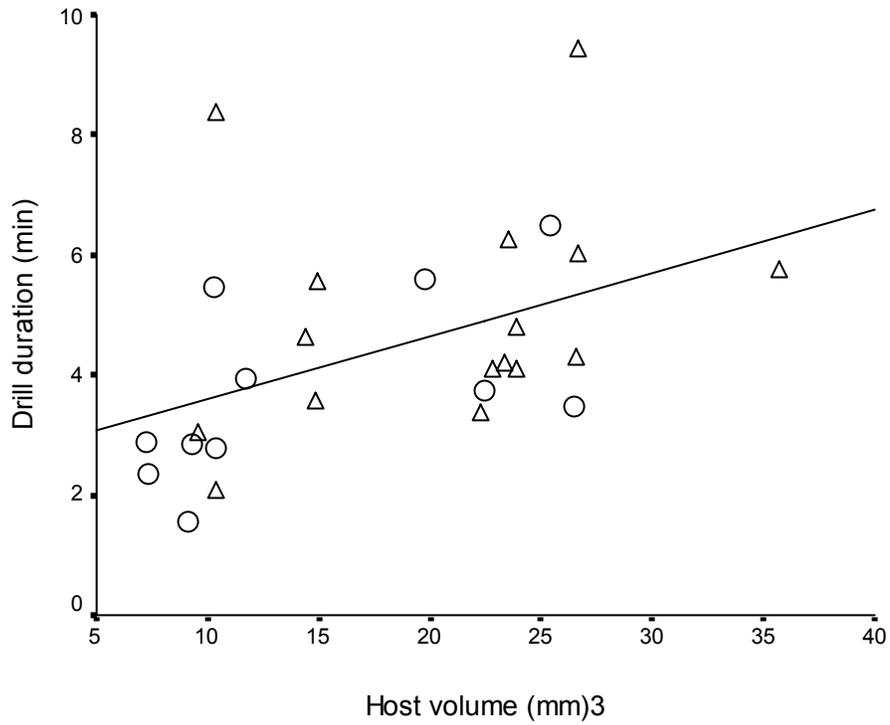


Figure 2. Drill duration (min) in hosts of different volumes from which a male (o) or a female (Δ) wasp subsequently emerged ($Y = 0.105X + 2.544$, $R^2 = 0.21$, $N = 27$, $P = 0.01$).