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CHOICE OF HOST INSTAR IN *GONIOZUS THAILANDENSIS* GORDH & WITETHOM (HYMENOPTERA: BETHYLIDAE), A GREGARIOUS ECTOPARASITOID OF A SAPODILLA FRUIT BORER, *PSEUDOCEROPREPES* CF. *NAGA* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

Goniozus thailandensis *Gordh & Witethom is a gregarious larval ectoparasitoid of sapodilla fruit borer,* Pseudoceroprepes *cf.* naga, *in southern Thailand. The host instar preference and suitability for* G. thailandensis *oviposition was simultaneously tested in choice and no-choice situations. In the no-choice situation, 4th and 5th instars were 4.3 times more likely to be parasitized than 3rd instars. The differences, however, were not significant. The presence of alternative instars had no significant effect on parasitoid choice behavior. The overall parasitization rates observed (10%) were low but comparable to that in the field. The trends, however, suggested a preference towards later instars over earlier instars. Two, alternative, explanations for the negative test result for behavior choice in* G. thailandensis *are discussed. Firstly, the result could be dismissed because of low power. Secondly, the differences in probabilities of parasitization between 3rd, 4th and 5th instar hosts in no-choice experiment are not due to behavioral choice, but reflect differences in handling times or ease of oviposition among host instars. Larger, 5th instar hosts produced more cocoons and adult progeny than smaller, 3rd and 4th instar hosts. Development time, however, was, on average, shortest in 4th instar hosts. Slow development time (>20d) was more common in females than males. Developmental flexibility would allow* G. thailandensis *to survive in the field where host instar composition is seasonally variable.*

INTRODUCTION

The stage at which the host is parasitized has been reported to affect immature parasitoid survival, development time, and adult size[1,2,3,4,5]. Thus, to maximize parasitoid success, hosts should be at an age (or stage or instar) that is most suitable for parasitoid survival, growth, and development[6]. However, parasitoids may expand the suitable range of their hosts through adaptive responses such as host regulation[7,8,9] or development flexibility[2,10]. Mackauer[11] argued that the maintenance of a flexible host selection behavior, where the host acceptable range is broader than the host suitable range, should be a more effective long-term strategy by ensuring that the parasitoid would be able to respond effectively to minor phenotypic changes of the host.

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The selection of suitable hosts is performed by parasitoid females. If a female oviposits more frequently in one host stage than others, then oviposition preference is presumed[3,12,13]. However, the existence of preference requires that the parasitoid female make an active choice among various host stages available. To demonstrate behavioral choice is being made it must be shown that the presence of alternatives results in a change in behavior. Differences in host acceptance in a no-choice situation does not indicate choice as these differences may arise for other reasons including differences in searching or handling times.

Goniozus thailandensis Gordh & Witethom is a gregarious ectoparasitoid of a phycitine sapodilla fruit borer (SFB) attacking sapodilla fruit, *Manilkara achras* Fosberg (Sapotaceae), in southern Thailand[14]. The SFB host was recently named as *Pseudoceroprepes* cf. *naga* (M. Horak, personal communication). Approximately 13% of SFB larvae collected from Yo Island during 1989 to 1990 were parasitized by *G. thailandensis* (Vajarasathira, unpublished data). In spite of the low rate of parasitism, *G. thailandensis* might be a potential candidate for the biological control of the SFB due to its fossorial habit. This habit is desirable for the biological control of the SFB because the host larvae infest sapodilla fruit and a parasitoid which locates concealed host larvae is important in developing a biological control program for the larval stage of this pest[15].

The objective of our study was to investigate host instar preference and suitability for *G. thailandensis* oviposition. The choice experiment was conducted to test whether *G. thailandensis* has preference among 2 different host instars when they were offered simultaneously. The no-choice experiment was carried out to determine the pattern of resource (host) utilization of each host instar when available alone. The total number of parasitoid progeny produced, sex ratio, and development time in relation to host instars parasitized were also examined. Information on host instar preference for *G. thailandensis* oviposition is important to maximize mass rearing for classical and augmentative biological control programs, and for understanding how parasitoid populations might respond to changes in the life history stage structure of host populations.

MATERIALS AND METHODS

All experiments and cultures were kept at 26±1°C, 70-80% RH, and under a 12:12 (L:D) photocycle, unless stated otherwise.

Host culture

The SFB culture was initiated in 1993 with larvae collected from sapodilla orchards on Yo Island, Songkhla (6°17N, 7°56N, 101°30E, 106°20E)[16]. The SFB larvae were reared on unripe sapodilla fruit as described in Witethom and Silawatchananai[17], and Witethom and Gordh[15].

To prepare experimental larval hosts, instars were determined by comparison of cephalic width[17]. Third, 4th and 5th instars were tested for host instar preference and suitability since it was preliminary observed that 1st and 2nd instars were rarely parasitized (Vajarasathira, unpublished data). On the day before an experiment, larvae were individually transferred to each lidless container (5 cm in diameter, 6 cm high) with an unripe sapodilla fruit. The larvae were then left overnight to allow larval burrowing inside the fruit, thus resembling the natural infestation.

Parasitoid culture

G. thailandensis culture was begun with adults emerging from parasitized SFB larvae collected from sapodilla orchards. *G. thailandensis* was maintained on 5th instar SFB by the method of Witethom and Gordh [15].

Host instar preference and suitability

The host instar preference and suitability for *G. thailandensis* oviposition was simultaneously tested following procedure similar to those described by Liszka and Underwood[18].

To demonstrate that a behavior choice is being made it must be shown that the presence of alternative results in a change in behavior, otherwise it may be possible to explain the results as due to other factors, for example, differences in handling times.

The experimental design for the choice experiments is shown in Table 1. The note at the bottom of the table shows the comparisons used to test for choice. For example, to analyze the effects of alternative instar hosts on behavior with respect to 5th instar hosts, the chances of parasitization in treatment T3 was compared with that of 5th instar treatments T5 and T6.

The experiment was divided into 40 blocks to control for possible time effects. Each block included one replicate of each treatment. An experimental unit was a clear plastic cage (9.5 cm in diameter, 20 cm high) with two fruit each containing one host. It was observed that even when many hosts were given, rarely more than two hosts were ever used by *G. thailandensis* females during a 24-h period (Vajarasathira, unpublished data), thus the total number of host larvae in a cage was always two. When a cage had two host instars, there was one larva of each host instar.

Table 1. Experimental design to test for the presence of behavioral choice among host instars. The number in the table refer to host instar number. In the bottom half of the table which host is treated as the target depends on the comparison being made.

Treatment No.	Instar of Target Host	Instar of Alternative Host
T1	3	3
T2	4	4
T3	5	5
T4	3	4
	4	3
T5	3	5
	5	3
T6	4	5
	5	4

Note : Comparison T1 vs 3's in T4 and 3's in T5;
T2 vs 4's in T4 and 4's in T6;
T3 vs 5's in T5 and 5's in T6.

In each plastic cage, a sapodilla twig soaked in a bottle of water was provided as a cue for host searching. Honey was not supplied during the experiment.

The parasitoid females tested were presumably mated and aged 3-5 days; they have not been exposed previously to host larvae.

An individual female parasitoid was aspirated into a cage with prescribed host instar and number. After 24-h exposure, the host larvae were separated from a female parasitoid. They were reared and observed daily until parasitoid emergence, host pupation, or death. The host instar parasitized, the number and gender of parasitoid progeny emerged from each host stage were recorded. The development time for *G. thailandensis* emerging from each host instar was also noted.

Physical constraint

To examine whether parasitization was related to host tunnel opening, the head capsule width of 20 females of *G. thailandensis* and the diameter of larval holes, 20 for each instar, i.e., 3rd, 4th and 5th, were measured. The measurement was done under a stereomicroscope at 20-40X magnification with a micrometer.

Voucher specimens of SFB and *G. thailandensis* have been deposited in the insect collection of the Biology Department, Prince of Songkla University.

Data analysis

Choice experiments were analyzed using logistic regression. The control treatment, that is, two hosts of the same instar, was used as the reference group. A separate analysis was done for each instar. The strength of choice was conveniently expressed in terms of odds ratios estimated from the logistic regression. An odds ratio is the ratio of the odds of getting the outcome (parasitization) in one treatment divided by the odds of getting the outcome in another treatment. The individual odds are just the ratio of number of hosts parasitized:not parasitized.

RESULTS

No-choice experiment

In the absence of choice 4th and 5th instars were 4.3 times more likely to be parasitized than 3rd instars. However, overall parasitization rates in this experiment were low and the differences were not significant (Table 2).

Choice experiment

The probability of a 5th instar being parasitized was the same regardless of whether the alternative host present was a 3rd, 4th or of the same instar (Table 3, bottom 3 rows). That is, the odds ratios did not differ from 1. For 4th instar hosts, a trend towards lower odds of parasitization if the alternative host is a 5th instar (OR = 0.47) and a higher odds of parasitization if it is a 3rd instar (OR = 1.30), is the pattern that would be expected if behavioral choice in favor of larger hosts was occurring. The result, however, is not statistically significant (confidence intervals include 1). Thus, there was no evidence that the presence of alternative instars affected the probabilities of parasitization of a particular host instar. As in the no-choice experiment, 3rd instar hosts were almost never parasitized.

Table 2. Influence of host instar on parasitization in the absence of choice. Each instar presented separately. CI = Confidence interval for the odds ratio.

Host Instar	Host Parasitized	Host not Parasitized	Odds Ratio	95% CI
3	1	39	1.00	
4	4	36	4.33	(0.46-41.00)
5	4	36	4.33	(0.46-41.00)

Table 3. Influence of host instar on parasitization in the presence of alternative hosts. No odds ratio can be calculated in the third row because no 3rd instar hosts were parasitized.

Target Host Instar	Alternative Host Instar	Target Hosts Parasitized	Target Hosts Not Parasitized	Odds Ratio	95% CI
3	3	1	39	1.00	
	4	1	39	1.00	
	5	0	40	-	
4	3	5	35	1.29	0.31-5.19
	4	4	36	1.00	
	5	2	38	0.47	0.08-2.75
5	3	5	35	0.81	0.23-2.90
	4	5	35	0.81	0.23-2.90
	5	6	34	1.00	

Table 4. Physical constraint on parasitization from feeding hole size. Head widths of *G. thailandensis* and size of feeding hole of 2nd-5th instar SFB (mm).

	Range	Median
Head widths of *G. thailandensis*	0.78-0.88	0.83
2nd Instar Holes	0.75-1.26	0.93
3rd Instar Holes	1.52-2.26	1.65
4th Instar Holes	1.42-2.46	2.09
5th Instar Holes	2.25-3.25	2.65

Physical constraint

Access to host instars in the fruit might be physically constrained by the size of the feeding hole left by the larvae. Parasitoid head widths are similar in size to 2nd instar feeding holes (Table 4). There is no suggestion that physical size constraints are important for the other instars; hole sizes are all much larger than head widths.

Progeny and development time

Fifth-instar hosts yielded more cocoons and adult progeny than either 3rd or 4th instar hosts (Table 5). Some coccoons did not yield any progeny.

Development time of parasitoids differed significantly among host instar (ANOVA $F=5.54$ df=2, 217; P=0.004; Table 6). Fifth and 3rd instars took on average longer to develop than 4th instars (Bonferroni Comparisons $P<0.05$). Thirty four percent of 5th and 57% of 3rd instars took 20 or more days to develop, whereas this was only 18% for 4th instars. Slow development (20 days or more) was more common in females (38%) than males (25%).

This sex difference may be confounding the association between development time and instar. To adjust for sex differences and make a formal comparison of the proportions, a logistic regression analysis was done (Table 7). Parasitoids developing in 4th instar hosts were about half as likely to be slow developers as those in 5th instar hosts, even after adjustment for sex differences.

DISCUSSION

This is the first study known to the authors that has set out to explicitly test for behavioral choice in a parasitoid. The results of the test for *G. thailandensis* was negative. There was no evidence that the presence of alternative host instars affected the probabilities of parasitization of a particular host instar. That is, no evidence, of behavioral choice.

This result can be explained in two ways. Firstly, it could be dismissed as a consequence of inadequate power. The study was small (40 experimental units in all) and thus only had strong power (B=0.80, a=0.05) to detect 6-fold and larger preferences. Therefore, a much larger study would have to be conducted before it could be conclusively argued that preferences were unimportant. This is currently not feasible.

An alternative explanation for a negative test result is that differences in probabilities of parasitization between 3rd, 4th and 5th instar hosts when presented alone are not due to behavioral choice, but reflect differences in handling times or ease of oviposition among host instars.

For example, access to hosts in the fruit could be constrained by the physical size of the feeding hole on the surface of the fruit. Measurements of parasitoid head widths suggest that this could indeed explain why second instar hosts are rarely parasitized. Hole sizes made by 3rd, 4th and 5th instars, however, are all much larger than the parasitoid, and of 3rd and 4th instars largely overlap, thus differences in probabilities of parasitization among these instars cannot be explained by physical size constraints.

Either way, our study has demonstrated a useful design and analytical method for distinguishing behavioral choice from other causes of differences in resource utilization. As far as *Goniozus* is concerned, we can only argue that there is no evidence of a very large preference (OR>6) in favor of large vs. small instars.

Table 5. Influence of host instar on cocoon and progeny number and sex composition. Values in parenthesis are SDs.

Host Instar	Hosts Parasitized	Cocoons	Hosts Yielding Adults	Progeny[1]	% Males
3	2	2.5(0.7)	1	3.0(0.0)	33
4	8	2.9(1.4)	4	3.8(0.5)	40
5	8	11.4(3.5)	7	10.6(2.8)	16

[1] Mean based on cocoons yielding adults.

Table 6. Distribution of development times (days) of parasitoid in hosts of different instar.

Host Instar	16	17	19	20	21	22	Mean	% 20 or more days
3	0	0	3	2	2	0	19.9	57
4	14	2	20	4	4	0	18.9	18
5	28	0	84	43	12	2	19.3	34

Table 7. Multivariate logistic regression analysis of the association between slow development time (20 or more days) and host instar and sex.

Factor	Odds Ratio	95% CI
Instar		
3rd	2.37	(0.50-11.1)
4th	0.43	(0.19-1.00)
5th	1.00	
Sex = Male	0.55	(0.30-0.99)

As expected from consideration of amount of resources available, larger 5th instar hosts yielded more cocoons and progeny than smaller, 3rd and 4th instars. Development time, however, was, on average, shortest in 4th instar hosts. Slow development time (>20d) was more common in females than males, and because 4th instars had relatively more male offspring, sex could have been confounding the relationship between development time and host instar. A multivariate logistic regression analysis indicated that even after adjustment for sex, fast develompent time was still more common in 4th instar larvae than 5th or 3rd instars.

Development time can affect the fitness of an individual through its intrinsic rate of increase[19]. Fourth instar should be selected as a host stage for *G. thailandensis* because this stage facilitates the shortest parasitoid development time. There is, however, a trade-off between parasitizing 5th instars which yield more progeny and the faster development times if use 4th instars. On average, using a 5th instar yields 9.25 adult offspring per attempt (7*10.6/8) (Table 5), whereas a 4th instar only yields 1.90 (4*3.8/8) (Table 5). The ratio of these two figures is much larger than that for the mean development times (19.3 vs. 18.9) (Table 6). Thus, after any given amount of time a parasitoid using the 5th instar strategy rather than 4th instar will have produced many more offspring.

Developmental delay[2,10], rather than host regulation[7,8,9], may be strategy used by *G. thailandensis* to cope with suboptimal conditions in marginally suitable hosts. Thus, prolonged development time was observed in 3rd and 5th host instars. For *G. thailandensis*, there is no absolute preference for the most suitable host instar. Females parasitized less on nonsuitable hosts, thus supporting the hypothesis of Mackauer[11]. The acceptable range of SFB for female *G. thailandensis* is clearly broader (3rd to 5th instars) than its suitable range for the parasitoid' s progeny in terms of faster development and yielding more cocoons and adult progeny (4th and 5th instars, respectively). However, through developmental flexibility, *G. thailandensis* can use hosts that are less suitable at the time they are parasitized.

For a short-lived parasitoid, i.e., *G. thailandensis,* the probability of finding more than one suitable host at low host density is small, especially because SFB larvae usually are solitary; fruit normally contains only one larva per hole. Parasitoids searching for solitary, dispersed hosts rather than gregarious, aggregated hosts may not have multiple opportunities for parasitization. Parasitoid populations respond to changes in life history stage structure of host populations by being flexible in host instar selection. In the field, accepting and being able to use any host instars available would have a selective advantage because of the seasonal variation of host instar composition.

In order to maximize mass rearing of *G. thailandensis* for the biological control of SFB, 5th instar SFB should be used as a host since this instar produced more offspring than the smaller instars.

The low rate of parasitization suggests that *G. thailandensis* alone may not be capable of successfully controlling SFB. However, *G. thailandensis* may work complementarily with other natural enemies to control the SFB and other lepidopterous pests that inhabit in concealed places.

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บทคัดย่อ

Goniozus thailandensis Gordh & Witethom เป็นแตนเบียนภายนอกของหนอนเจาะผลละมุด, *Pseudoceroprepes* cf. *naga*, ที่พบทางภาคใต้ของประเทศไทย ในการศึกษาครั้งนี้ ทดสอบความชอบและความเหมาะสมของแมลงอาศัยที่มีต่อการวางไข่ของแตนเบียน *G. thailandensis* โดยให้แตนเบียนมีโอกาสและไม่มีโอกาสเลือกแมลงอาศัย ในสภาพที่แตนเบียนไม่มีโอกาสเลือกแมลงอาศัย แมลงอาศัยระยะที่ 4 และ 5 ถูกวางไข่มากกว่าแมลงอาศัยระยะที่ 3 4.3 เท่า แต่ความแตกต่างนี้ไม่มีนัยสำคัญ ส่วนในสภาพที่แตนเบียนมีโอกาสเลือกแมลงอาศัย การที่มีแมลงอาศัยต่างระยะอยู่ด้วยกันไม่มีผลต่อการเลือกแมลงอาศัยของแตนเบียน แต่มีแนวโน้มว่าแตนเบียนชอบแมลงอาศัยระยะหลังมากกว่าระยะต้นๆ ซึ่งผู้ทดลองได้อภิปรายถึงการที่แตนเบียน *G. thailandensis* ไม่แสดงพฤติกรรมการเลือกแมลงอาศัยไว้ 2 ประการคือ ประการแรกผลการวิจัยนี้ไม่สามารถนำมาอธิบายอะไรได้ เนื่องจากมีอำนาจจำแนกต่ำ ประการที่สอง ในสภาพที่แตนเบียนไม่มีโอกาสเลือกแมลงอาศัย ความแตกต่างของโอกาสในการถูกเบียนของแมลงอาศัยระยะที่ 3, 4 และ 5 ไม่ได้เป็นผลเนื่องมาจากพฤติกรรมการเลือกแมลงอาศัย แต่น่าจะเป็นผลเนื่องมาจากความแตกต่างในการจัดการกับแมลงอาศัย หรือขึ้นอยู่กับความยากง่ายในการวางไข่ในแมลงอาศัยแต่ละระยะ แมลงอาศัยระยะที่ 5 ซึ่งมีขนาดใหญ่จะผลิตดักแด้และตัวเต็มวัยของแตนเบียนมากกว่า แมลงอาศัยระยะที่ 3 และ 4 ซึ่งมีขนาดเล็กกว่า ส่วนระยะเวลาในการเจริญของแตนเบียนจะสั้นที่สุดในแมลงอาศัยระยะที่ 4 ระยะเวลาในการเจริญที่ช้ากว่าปกติ (>20 วัน) มักพบในแตนเบียนเพศเมียมากกว่าเพศผู้ คาดว่าความสามารถในการปรับระยะเวลาในการเจริญตามระยะของแมลงอาศัยเป็นวิธีการหนึ่งที่ทำให้แตนเบียน *G. thailandensis* มีชีวิตรอดอยู่ในธรรมชาติซึ่งมีการเปลี่ยนแปลงองค์ประกอบของแมลงอาศัยระยะต่างๆ ตามฤดูกาล