Diel Activity Patterns of the Squash Bug Egg Parasitoid *Gryon pennsylvanicum* (Hymenoptera: Scelionidae)

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ABSTRACT Mated, 1-d-old female *Gryon pennsylvanicum* (Ashmead) exhibit a diel pattern of activity and rest. Daily activity (e.g., oviposition, walking, grooming, flying, feeding) is greatest during morning hours (0815–1215 hours CST). Two forms of resting behavior occur. "Motionless" is a temporary state occurring mostly during afternoon hours. The more pronounced resting phase, "tucking," occurs in aggregated individuals of both sexes and is a form of rest previously undescribed in the parasitic Hymenoptera. The period of tucking persists from before lights go off to about 1 h after the lights go on. In individual wasps, activity resumes abruptly at about 0830 hours; by 0930 hours, all adults become active. Observations of a field population show a similar pattern of diel activity. The significance of these data for biological control programs is discussed.

KEY WORDS Insecta, *Gryon pennsylvanicum*, diurnal behavior, biological control

ALTERNATING CYCLES OF activity and rest are common among invertebrates (see Brady 1981 for review). Within the Insecta, quantitative studies of this type of behavioral periodicity have been made for a wide range of taxa (Lewis & Taylor 1964; Barbosa & Frongillo 1977; Cerna 1978; Ekbom 1982; Tobler 1983; Lockwood & Story 1984, 1986; Hu et al. 1986; Chadee et al. 1987; Walter 1988; Chadee et al. 1989). However, there are few investigations of diel activity–resting patterns in parasitic hymenopterans (but see Barbosa & Frongillo 1977, Ekbom 1982, Hu et al. 1986, Walter 1988).

Gryon pennsylvanicum (Ashmead) is an indigenous egg parasitoid of the squash bug, *Anasa tristis* (DeGeer), and very little is known about its behavior. Furthermore, diel activity has not been reported for any scelionid despite the family's importance in biological control (Orr 1989). Therefore, our objectives were to describe and quantify aspects of *G. pennsylvanicum*'s diel behavior in the laboratory and field.

Materials and Methods

Insect Cultures. Our squash bug colonies originated from eggs, nymphs, and adults from squash and pumpkin fields outside Manhattan, Kans., in July 1988. Cultures were maintained in large, mesh-covered cages at a 16:8 (L:D) photoperiod (Cool White and Grow Lux fluorescent lamps), 27 ± 2°C, and RH about 75%, on potted *Cucurbita pepo* L. squash, cultivar Early Prolific Straightneck (Wilhitte Seed Company, Poolville, Tex.).

Parasitoid colonies were initiated in August 1988 with field-collected adults. They were maintained in Plexiglas boxes in growth chambers at 26.7 ± 0.5°C, about 75% RH, and 16:8 (L:D). Every other day, 12–16 squash bug egg masses of 10–20 eggs each (<1 d old) were glued with honey to strips of index cards and added to the colony together with free water and honey for food.

Description and Quantification of Diel Behavior. We observed male and female adult *G. pennsylvanicum* of mixed ages in colony boxes throughout five mornings over a 2-wk period in July 1989. Also, each afternoon, we observed colonies once an hour for 5 min, beginning at 1600 hours and ending at 2200 hours (CST). These observations were aided by the use of a hand-held 10× magnifier. Adults also were inspected in glass shell vials with a 10–70× binocular microscope at the same times.

To quantify diel behavior in *G. pennsylvanicum* in the laboratory, pairs of newly emerged male and female wasps were placed in 15 cotton-plugged, 14.8 cc (4 dram) shell vials with honey streaks at 1000 hours. The vials were illuminated by fluorescent lamps suspended about 0.5 m above the vials. To diffuse the light, a sheet of corrugated plastic was placed just under the lamps. Light intensity was 600 lux, temperature was 26–27°C, and the ambient relative humidity about 20%. Photoperiod was 16:8 (L:D) with lights on between 0700 and 2300 hours. At 2100 hours, when mating was assumed to have occurred, females were transferred individually to clean shell vials. Each female then received a squash bug egg mass (18 eggs <1 d old). Vials within the arena were given a number randomly from 1 through 15 and arranged in a row. This arrangement permitted a rapid scan sample of all vials in numerical order. Scan sampling enables data to be taken on a relatively large group of individuals (Martin & Bateson 1986). Females were chosen for tests because preliminary data revealed that wasps of both sexes exhibited very similar resting behavior, and because we planned to relate diel periodicity to daily oviposition.

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Two tests were run on consecutive days. In each test, a different group of 15 females of the same age and condition was used. The first observations were made at 0400 hours and continued every 15 min until 0100 hours of the following day. Observations were aided by a 10× hand-held magnifier. During the dark cycle, a red light (40 watts) also was used to make observations. Behaviors were recorded on a check sheet. Categories included "tucking" (see Results for description); "motionless" (wasp standing but not moving and clearly not in a tucking posture); "antennating" (antennae drumming rapidly on substrate but otherwise motionless); "walking"; "grooming" (legs rubbing any part of the body surface, but most commonly the antennae, other legs, or dorsal segments of thorax and abdomen); "feeding" (on honey streaks); "flying"; and "probing–ovipositing" (combined because oviposition is not easily distinguishable from probing, and probing may occur without the release of an egg). The location and orientation of the female also was recorded (i.e., on or off the egg mass; in the top, middle, or bottom third of the vial; and head oriented toward the top, middle, or bottom of the vial).

Test day had no significant effect on the category of behavior observed at each sample (test of partial independence; $P \geq 0.05$; Zar 1984). Therefore, data from both days were pooled ($n = 30$ females). For statistical analysis, all behavioral categories except "tucking" and "motionless" were combined and designated as "active." In addition, the sample periods represent pooled data from all 15-min intervals within a 4-h period. A χ^2 test was run to compare the total number of occurrences of three behavioral categories (active, motionless, and tucking) for five 4-h sample periods. These were: 0400–0800, 0815–1215, 1230–1630, 1645–2045 and 2100–0100 hours.

To observe *G. pennsylvanicum*'s behavior in the field, we established a field population at Keats, Kans. (approximately 8 mi west of Manhattan), in the summer of 1990 by releasing laboratory-reared wasps onto ten 6-wk-old transplanted squash of the previously described cultivar. Squash bugs had been released earlier onto plants to provide a supply of host eggs. Wasps then underwent approximately three generations in the field based on thermal accumulation data (Nechols et al. 1989) before experiments began. Observations were made at 3-h intervals and were aided by a 10× hand-held magnifier. During dark hours, a flashlight with a red filter also was used. Samples consisted of systematically searching the leaves, petioles, and stems of 10 squash plants, each for 5 min. The behavior of every *G. pennsylvanicum* adult found during that interval was recorded on a check sheet using the same categories described above. The location and orientation of each wasp also was recorded. A subsample indicated that the population consisted of a mixture of female and male wasps (approximately 8:1 ratio). Two tests were run, 1 wk apart, during late August (see results for specific dates). In the first test, observations began at 0600 and ended at 2400 hours; the second test ran from 0300 through 1200 hours, with one additional sample taken at 2100 hours. Field temperatures ranged from a low of 25°C in the early morning to a high of 40°C in the afternoon.

Oviposition Pattern. To determine *G. pennsylvanicum*'s pattern of daily oviposition, tests were conducted in the laboratory as described previously except for the following differences. Females were given their first egg mass at 2400 hours. Egg masses then were removed and replaced every 4 h throughout a 24-h cycle. To determine the number of eggs laid within each period, squash bug egg masses were held for 48 h and dissected for the presence of parasitoid larvae. This procedure was used because *G. pennsylvanicum* eggs are difficult to find within host eggs, and because a very high percentage (>95%) of *G. pennsylvanicum* eggs hatch (unpublished observations). We examined *G. pennsylvanicum*'s periodicity of oviposition early in the adult female's life, when the majority of eggs is laid (Nechols et al. 1989). Studies of other parasitic hymenopterans have shown that ovipositional periodicities generally do not shift over the lifetime of the adult (Barbosa & Frongillo 1977, Hu et al. 1986). Test day was shown to have no significant effect (test of partial independence, $P \geq 0.05$) on number of eggs laid and number of females ovipositing for each sample period. Therefore, data were pooled for both test days. A χ^2 test was run to compare the total number of eggs laid and the number of females ovipositing at each 4-h period. Voucher specimens are located in the Kansas State University Entomological Museum (Voucher no. 022).

Results

Description and Quantification of Diel Behavior. Adult *G. pennsylvanicum* have a cyclic pattern of daily activity. During prolonged resting periods, adults of both sexes maintained a distinct posture which, hereafter, we refer to as "tucking." This behavior occurred both in the field and in the laboratory. Tucking was observed in year-old and recently established *G. pennsylvanicum* colonies. Parasitoids were observed tucking on substrates that ranged from Petri dishes and shell vials to whole plants.

In the morning, adults were distributed throughout the rearing boxes and were engaged in various activities (e.g., walking, feeding, flying). When active, heads and antennae were held out in front of the body and legs were extended in a standing or semistanding posture (Fig. 1A). In contrast, during late afternoons and evenings, the wasps aggregated in groups of 5–30 tucking individuals (mixed sexes) in the upper corners and along the top edges of the boxes. Most parasitoids oriented their heads toward the bottom of the box. Similarly, wasps in

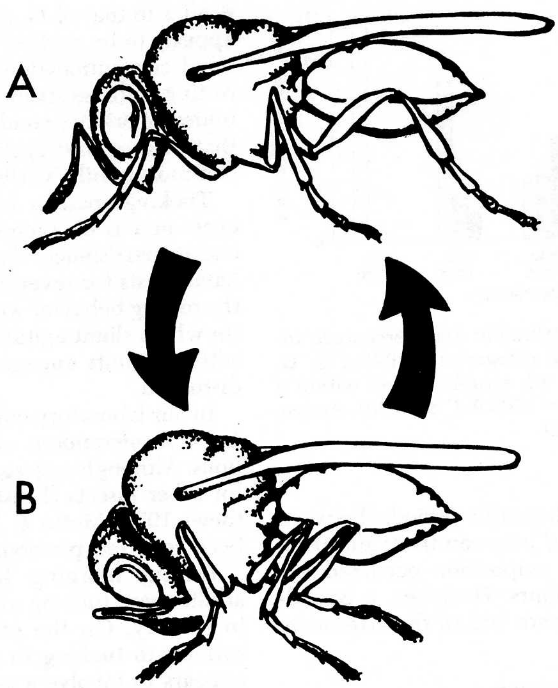

Fig. 1. Schematic diagram of adult *G. pennsylvanicum* female. (A) Active posture; note the antennae are held out in front of the head. (B) Tucking posture; note the head is facing the ventral surface of the thorax, the antennae are pulled in close to the head, and the legs are bent.

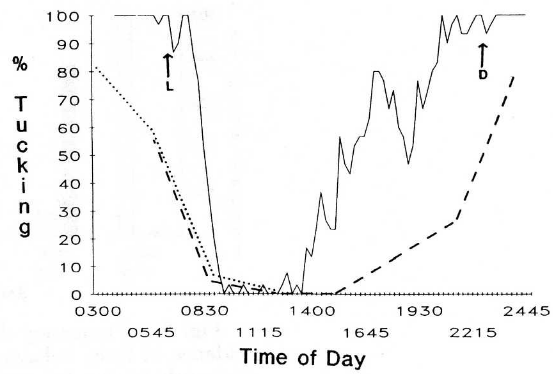

Fig. 2. Diel tucking profile of adult *G. pennsylvanicum* in the laboratory and field. Laboratory observations (——) were made over a 21-h period (n = 30 females). L, lights on; D, lights off. In the field study, sunrise and sunset occurred at 0542 and 1917 hours (19 August 1990; - - -) and 0548 and 1906 hours (26 August 1990; ·····). The number of wasps observed at each sample interval ranged from 47 to 58 on 19 August and from 45 to 54 on 26 August.

glass vials aggregated near the top in the tucking posture with their heads facing the bottom of the vial.

During tucking, a typical *G. pennsylvanicum* adult held its head in a lowered position, nearly touching the ventral surface of the thorax (Fig. 1B). The elbowed antennae were held very close to the head, almost flat against the frons. The tibial segment of each leg was folded beneath the femur so that the wasp appeared to be squatting. All wasps observed in the laboratory were in a tucking posture at 0400 hours (Fig. 2). A high percentage of the adults remained in the tucking posture until 0800 hours (1 h after lights had come on). Within the next 45 min, activity increased greatly, and by 0930 hours, most wasps had become active (e.g., were walking, grooming, flying, and probing–ovipositing). Some activity was observed at all sample times throughout the light cycle, but very little occurred during the dark cycle. After 1300 hours, the frequency of adults in the tucking posture increased in a fluctuating pattern. By 2100 hours, 90% of the wasps had returned to the tucking posture. A high percentage of tucking (93.3–100%) continued from 2115 hours until the last reading at 0100 hours.

Field observations showed a similar pattern; the percentage of wasps tucking was highest during hours of darkness (82.2% at 0300 and 78.7% at 2400 hours) (Fig. 2). In contrast, only 5–6% of the wasps were tucking at 0900 hours, and little tucking was observed at 1200 hours. Thereafter, no tucking was observed until 1800 hours. The percentage of *G. pennsylvanicum* observed tucking was consistently lower at all times in the field than in the laboratory.

Fig. 3 shows the frequency distribution and percentage incidence of three major behavioral categories (active, motionless, and tucking) at 4-h intervals in the laboratory. Chi-square analysis indicates that the category of behavior exhibited was significantly ($P \leq 0.0001$) related to the time of day. A high percentage (86.7–100%) of tucking occurred between 0400 and 0800 hours and between 2045 and 0100 hours. In contrast, between 0815 and 1215 hours, wasps were engaged in predominantly (78%) active behavior. Between 1230 and 1630 hours, about half of the wasps remained active, whereas the percentage of wasps in the motionless (36%) and tucking (28%) categories increased. Between 1645 and 2045 hours, the percentage of active and motionless wasps decreased from the previous sample period; those in the tucking posture increased to 70%.

Females spent most of their active time probing–ovipositing (Fig. 4). This behavior occurred mainly between 0815 and 1630 hours, although some probing–ovipositing was observed between 1645 and 2045 hours. During the most active interval (0815–1215 hours), walking, grooming, and feeding occurred approximately 6 times less frequently than probing–ovipositing. Other active behaviors were infrequent.

Oviposition Pattern. Time of day had a significant effect on oviposition by *G. pennsylvanicum* (χ^2 test, $P \leq 0.05$). Very little oviposition occurred

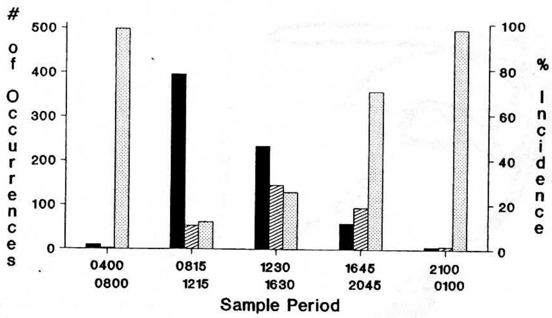

Fig. 3. Frequency distribution and percentage incidence of three behavioral categories exhibited by *G. pennsylvanicum* for each 4-h sample period within a 21-h observation period. $\chi^2 = 1608.9$; $P \leq 0.0001$. Active, ■; motionless, ▨; tucking, ▩.

during the initial two 4-h sample periods (between 2400 and 0400 hours and between 0400 and 0800 hours) (Table 1). Peak oviposition occurred between 0800 and 1200 hours. However, a considerable number of eggs were laid in the afternoon.

Discussion

A pattern of cyclical rest similar to what we observed in adult *G. pennsylvanicum* has been published for only one other hymenopteran, the honeybee *Apis mellifera* L. In this social species, diel resting is associated with a posture in which the antennae are held close to the head (Kaiser 1984). In addition, resting in honeybees is governed by a circadian rhythm, which may be correlated physiologically with a state that approximates sleep in mammals (Kaiser & Steiner-Kaiser 1983; Kaiser 1984, 1988). Thus, the tucking posture and persistent form of rest we quantified for *G. pennsylvanicum* represent the first published account of this type of periodic behavior in the parasitic Hymenoptera. However, other scelionids in the genera *Telenomus* and *Trissolcus* maintain a posture

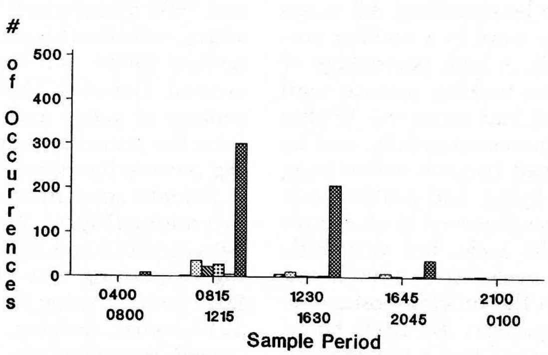

Fig. 4. Frequency distribution of each category of all active behavior of adult female *G. pennsylvanicum* for each 4-h sample period within a 21-h observation period. ▨, antennate; ▩, walk; ▧, groom; ⊞, feed; □, fly; ▩, prob/ovi.

similar to that of *G. pennsylvanicum* during what appears to be cyclical periods of rest (D. Orr, personal communication). Like *G. pennsylvanicum*, resting in these species also occurs in aggregations under laboratory conditions. These findings suggest that tucking and cyclical resting behavior may be common family attributes of the Scelionidae.

Tucking spans a large proportion of the 24-h cycle and is characterized by its diel periodicity and its persistence. Once initiated, this resting behavior lasts for several hours. Furthermore, unlike the resting behavior we categorized as "motionless" (in which slight agitation causes a wasp to become active), adults engaged in tucking are not easily disturbed.

In our laboratory colonies, both female and male *G. pennsylvanicum* undergo tucking in aggregations. Although aggregative resting has been found for other insects (Linsley 1962, Matthews & Matthews 1978, Motte & Burkhardt 1983), it has not been reported previously in the Parasitica.

During morning hours, *G. pennsylvanicum* adults cease tucking and undergo a rapid increase in activity. On the other hand, the return from activity to tucking in the afternoon and evening appears to involve a sequence of activities; i.e., a gradual progression from active behavior to motionless to tucking. No intervening behavior (i.e., motionlessness) was exhibited between tucking and morning activity.

The factors that stimulate posttucking activity are unknown. They may involve a delayed response to the onset of the photophase which, in the laboratory, occurred about an hour before active behavior resumed. A circadian rhythm may underlie this periodicity, for even after a temporary disturbance in tucking was observed when lights were switched on, parasitoids quickly resumed the tucking posture.

Our field data (Fig. 2) confirm that tucking in *G. pennsylvanicum* occurs under natural conditions and has a diel periodicity similar to that observed in the laboratory. It is less clear whether the aggregative behavior observed in the laboratory colonies at high wasp densities occurs in natural, or released, field populations of *G. pennsylvanicum*.

Diel behavior in parasitoids may provide important clues for elucidating the temporal occurrence of biological events such as oviposition in the field. For example, a recombination of our laboratory data shows that, with the exception of one interval (0415–0815 hours), probing by *G. pennsylvanicum* females on host egg masses was most frequent during periods when most eggs were laid (Fig. 5). In some egg parasitoids, probing is associated both with host feeding and oviposition (see Jervis & Kidd 1986 for review). However, detailed observations of *G. pennsylvanicum* in the laboratory indicate that this parasitoid does not host feed. Thus, probing is an unambiguous indicator of oviposition in this parasitoid.

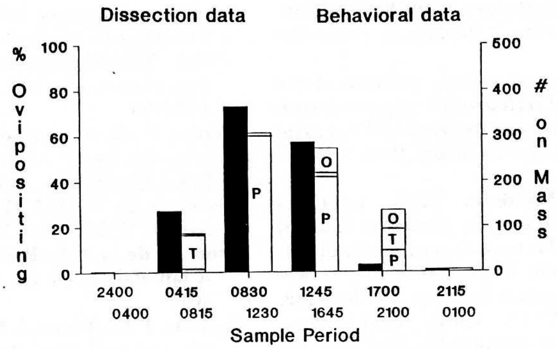

Fig. 5. Relationship between *G. pennsylvanicum* diel oviposition patterns and incidence of various adult female parasitoid behaviors on egg masses. The percentage of females ovipositing is shown on the left Y axis; the total frequency of females present on host egg masses is shown on the right Y axis. Female behavior on egg masses is partitioned as follows: Probing (P); tucking (T); other behavior (O). Bar graphs show categories O, T, and P from top to bottom, respectively. Behavioral data were not available for the 2400–0400-hour sample period. For the 0415–0815-hour period, P = 9 and O = 2; for 0830–1230 hours, T = 0 and O = 5; for 1245–1645 hours, T = 14; for 2115–0100 hours, the five wasps on the mass were all tucking. ■, % Ovipositing; □ no. on mass.

Gryon pennsylvanicum maintains a relatively fixed pattern of daily ovipositional activity in the laboratory (i.e., most oviposition occurs during morning hours). Although we do not know the diel oviposition pattern of this parasitoid in the field, our results agree with recent field studies that have shown an ovipositional periodicity in other insect species (e.g., Chadee & Corbet 1987; Chadee et al. 1987, 1989).

Little is known about the diel periodicity of oviposition, resting, and other behavior of parasitoids, and yet this kind of knowledge would have direct applications for biological control. For example, pesticide applications could be timed to avoid peak periods of searching and oviposition in *G. pennsylvanicum*, the times when these insects are probably most vulnerable to chemical sprays. Also, augmentative releases of *G. pennsylvanicum* might more effectively be made in the morning hours when wasps are active and more likely to encounter hosts. Finally, diurnal resting (tucking) in the field may enable *G. pennsylvanicum* to avoid, reduce direct exposure to, or tolerate, high daily temperature extremes. For example, the onset of tucking in the laboratory (1330 hours) coincides with peak daily field temperatures during the summer months. *G. pennsylvanicum* may move to cool microhabitats within the plant canopy or lower its metabolic rate during tucking (or both), thus conserving energy.

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Table 1. Total number of *G. pennsylvanicum* eggs laid, total number of females ovipositing, and number of eggs laid per female[a,b]

Sample period, hours	Total no. eggs laid	Total no. ♀♀ ovipositing	Eggs/♀, $\bar{x} \pm$ SD (range)
2400–0400	1	1	0.04 ± 0.18 (0–1)
0400–0800	17	8	0.57 ± 1.40 (0–7)
0800–1200	122	22	4.06 ± 2.50 (0–14)
1200–1600	62	17	2.07 ± 3.10 (0–11)
1600–2000	15	9	0.50 ± 0.94 (0–4)
2000–2400	4	3	0.13 ± 0.43 (0–2)

[a] Number of females = 30; experiment conducted in a 16:8 (L:D) photoperiod, 27°C, RH about 20%.
[b] $\chi^2 = 11.48$; $P \leq 0.05$.

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