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Circadian Calling Behavior of the Adult Female Brown-Banded Cockroach, *Supella longipalpa* (F.) (Dictyoptera: Blattellidae)

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The diel pattern of pheromone-releasing behavior (calling) of the adult female brown-banded cockroach, Supella longipalpa (F.), *was examined. Calling occurs discontinuously throughout most of the scotophase in a 12L:12D photoperiodic regime. Females exhibited a free-running calling rhythm after transfer to continuous light or dark conditions. Shifts in the temporal pattern of calling following changes in the timing of the photoperiodic cues indicated that "lights-off" is the Zeitgeber. Studies of insects under long- and short-day conditions suggest that, although insects within a population may call synchronously or asynchronously, respectively, the duration of an individual's calling bout is innately limited.*

KEY WORDS: circadian rhythm; cockroach; *Supella longipalpa*; calling; pheromone.

INTRODUCTION

The activities of insects, like those of other organisms, are often temporally limited to a portion of the diel cycle. These activities may include diverse aspects of reproduction such as sexual receptivity, mating behavior, pheromone synthesis and release, stridulation, copulation, sperm movement, spermatophore formation, and vitellogenesis (Saunders, 1982).

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Rhythms of pheromone synthesis and release have been amply studied, and in the Lepidoptera they are controlled by a combination of endogenous and exogenous factors (see Baker and Cardé, 1979; Delisle and McNeil, 1986; Schal and Cardé, 1986). In cockroaches, calling, a behavior presumably associated with pheromone release, has been reported for several species (Schal and Bell, 1985; Schal and Smith, 1990). However, the interactions of exogenous photoperiodic cues and the endogenous circadian system of calling have not been studied for any cockroach species.

Calling in the female brown-banded cockroach, *Supella longipalpa*, is characterized by elevated wings, a strongly recurved abdomen, and extended metathoracic legs (Hales and Breed, 1983). Recently, we demonstrated that it is associated with pheromone release (Smith and Schal, 1990). Calling occurs discontinuously in a diel pattern mainly during the scotophase, and although originally characterized as circadian (Hales and Breed, 1983), persistence of the rhythm in constant illumination or constant darkness was not demonstrated. We report that calling in *S. longipalpa* is under endogenous control (i.e., circadian), with the light-to-dark transition serving as the environmental cue by which the activity is kept in phase with the photoperiodic regime.

MATERIALS AND METHODS

Late-instar nymphs were collected from a colony and maintained at 27 ± 1°C under a 12L:12D photoperiodic regime. Adults were collected within 24 h after the imaginal molt and placed individually in vertically mounted petri dishes (15 × 100 mm) with pelleted Purina dog chow and water provided ad libitum. A wire mesh (1 × 3 cm) was embedded in the lid of each petri dish to provide a surface upon which the female could perch. Fluorescent lighting provided photophase illumination at 48 lux. Fluorescent lights, jacketed by photographic darkroom filters, were on constantly and permitted observation during the scotophase.

The insects were observed for calling for 20 min at the beginning of each hour. Specific manipulations of the photoperiod are described in the appropriate section under Results. Since data were collected from individual females, mean calling parameters (begin, midpoint, end, and duration) could be calculated for each cycle of calling. Duration, the length of time an individual spent calling on a given day, was defined as the difference (in hours) between begin and end times of calling for that day. Midpoint, for an individual insect, was defined as the median time of calling. Period is defined as the difference between the midpoints of calling on successive days.

RESULTS

Calling Activity in 12L:12D

Virgin females were observed from an adult age of 0 days (imaginal molt) through 10 days, under a 12L: 12D photoperiodic regime. The entrained rhythm of the population was monophasic (Fig. 1), with a difference of 23.9 ± 0.12 h (SE; $N = 70$; range, 20–27 h) between the midpoints of calling on successive days (Fig. 2). The mean age at which calling began was 6.15 ± 0.20 days ($N = 20$). Generally, peak calling occurred between 5 and 10 h after lights-off. There were no significant differences among the mean calling parameters (i.e., begin, midpoint, end, and duration) from day 6 through day 10 [(Table I; $P > 0.05$, Duncan's new multiple range test (NMRT)], thus permitting the association of subsequent changes in the parameters with specific manipulations in the photoperiod.

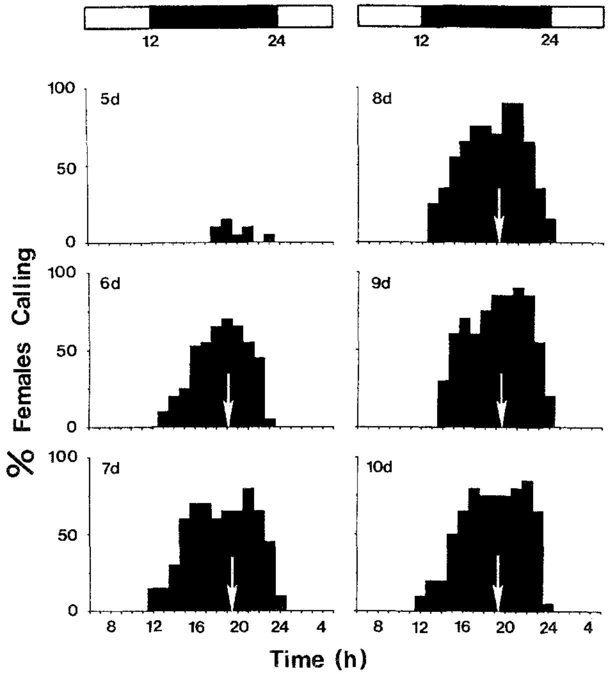

Fig. 1. Calling activity of adult female *S. longipalpa* under a 12L: 12D photoperiodic regime (top bar) on days 5–10 (*N* as in Table I). Arrows indicate the midpoint of calling.

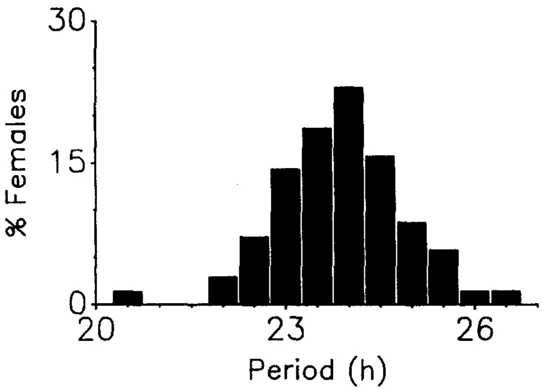

Fig. 2. Distribution of period lengths exhibited by adult female *S. longipalpa* under a 12L:12D h photoperiodic regime from day 6 to day 10 ($N = 70$). Period is defined as the difference between the midpoints of calling on successive days.

Calling Activity in LL and DD

Females were maintained under a 12L:12D photoperiodic regime for 8 days, then transferred to conditions of either continuous illumination (LL) or continuous darkness (DD) for 48 h to test the hypothesis that calling is under endogenous control. Under both sets of conditions, the behavior persisted and a free-running rhythm was apparent (Fig. 3, Tables II and III).

When transferred to LL, the free-running period (interval between midpoints of calling on successive days) increased, decreased, or remained the same

Table I. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L:12D (Lights-On at 12h) as a Function of Age[a]

Age	N	Begin	Midpoint	End	Duration
6	15	15.8 ± 0.33^a	19.1 ± 0.25^a	21.5 ± 0.24^a	6.7 ± 0.53^a
7	19	15.7 ± 0.66^a	19.4 ± 0.31^a	22.2 ± 0.27^a	7.5 ± 0.80^a
8	19	15.2 ± 0.49^a	19.2 ± 0.27^a	22.2 ± 0.25^a	8.0 ± 0.56^a
9	19	15.5 ± 0.35^a	19.6 ± 0.24^a	22.7 ± 0.20^a	8.3 ± 0.32^a
10	19	14.9 ± 0.35^a	19.3 ± 0.24^a	22.8 ± 0.25^a	8.9 ± 0.25^a

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's new multiple range test).

in 80, 17, and 3% of the insects, respectively (Fig. 4A), such that calling occurred later (Fig. 4B). The mean length of the free-running period increased significantly, from 24.0 ± 2.0 to 26.2 ± 1.4 h ($P < 0.05$, Student's *t* test). The duration of calling increased transiently on the first day in LL (day 9) but returned to normal on the following day (Table II).

Transfer to DD was more effective in maintaining the LD calling pattern: the period lengthened, shortened, or remained unchanged in 33, 54, and 13% of the insects, respectively (Fig. 5A). The mean lengths of the periods were not significantly different (23.6 ± 1.4 and 24.0 ± 1.3 h; $P > 0.05$, Student's *t* test). Thus, no phase shift in the calling pattern was observed (Fig. 5B). However, the duration of calling was significantly shortened in DD (Table III).

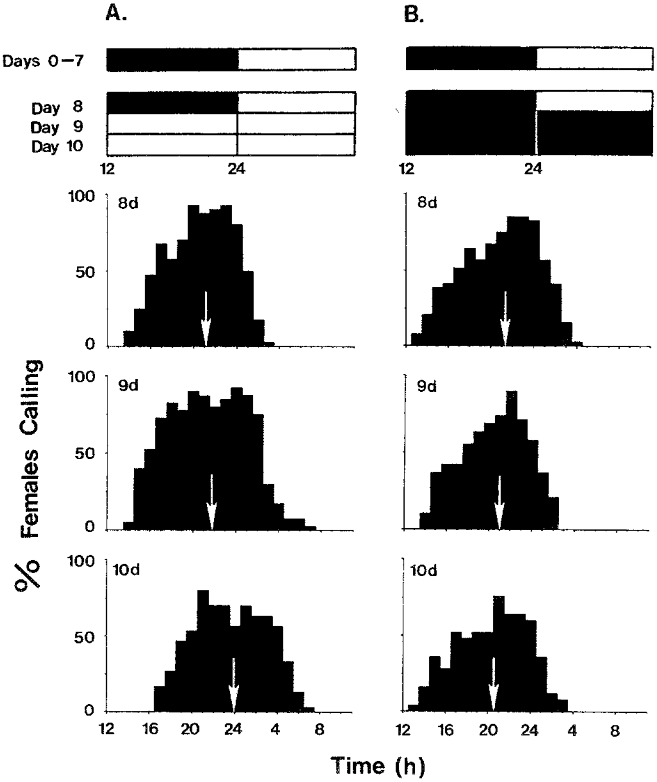

Fig. 3. Calling activity of adult female *S. longipalpa* in (A) LL ($N = 40$ females) and (B) DD ($N = 40$ females). Top bars indicate the photoperiod regime and arrows indicate the midpoint of calling.

Table II. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L : 12D on Day 8 and in LL on Days 9 and 10[a]

Day	N	Begin	Midpoint	End	Duration
8	40	16.7 ± 0.28^{a}	21.1 ± 0.18^{a}	24.5 ± 0.18^{a}	8.9 ± 0.31^{a}
9	40	16.6 ± 0.28^{a}	21.8 ± 0.24^{b}	26.2 ± 0.29^{b}	10.8 ± 0.29^{b}
10	30	19.7 ± 0.37^{b}	23.9 ± 0.37^{c}	27.0 ± 0.57^{b}	8.4 ± 0.59^{a}

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's new multiple range test).

Table III. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L : 12D on Day 8 and DD on Days 9 and 10[a]

Day	N	Begin	Midpoint	End	Duration
8	39	16.7 ± 0.44^{a}	21.3 ± 0.30^{a}	24.9 ± 0.26^{a}	9.2 ± 0.40^{a}
9	38	17.1 ± 0.43^{a}	21.0 ± 0.28^{a}	23.8 ± 0.27^{b}	7.7 ± 0.44^{b}
10	25	16.9 ± 0.56^{a}	20.6 ± 0.50^{a}	23.2 ± 0.61^{b}	7.3 ± 0.60^{b}

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's new multiple range test).

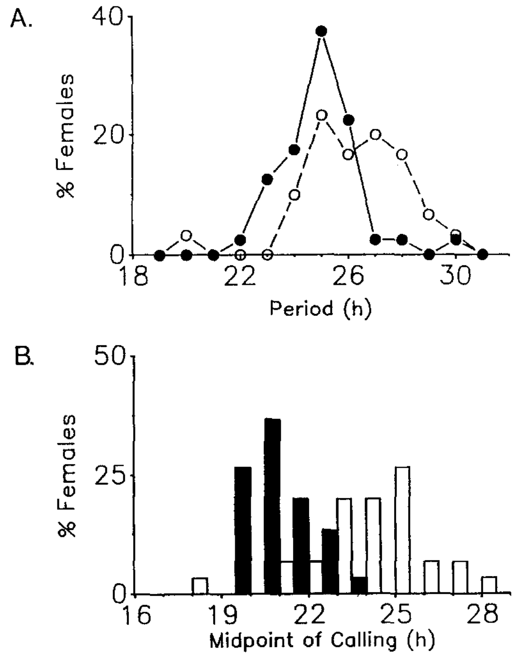

Fig. 4. (A) Distribution of period lengths after transfer to LL (filled circles, first period; open circles = second period). Period is defined as the difference between the midpoints of calling on successive days. (B) Distribution of midpoints of calling after transfer to LL ($N = 30$). See Fig. 3A for photoperiodic regime.

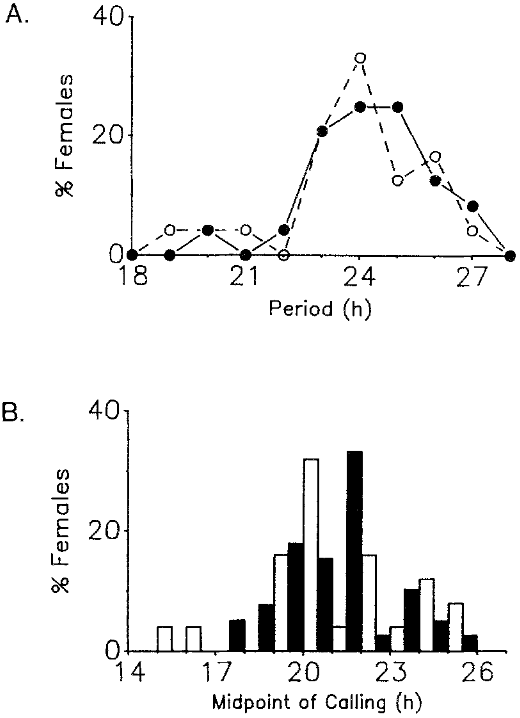

Fig. 5. (A) Distribution of period lengths after transfer to DD (filled circles, first period; open circles = second period). Period is defined as the difference between the midpoints of calling on successive days. (B) Distribution of midpoints of calling after transfer to DD ($N = 24$). See Fig. 3B for photoperiodic regime.

Calling Activity Following Shifts of the Photoperiodic Cues

Adult females were maintained under the 12L : 12D photoperiodic regime for 7 days, after which one of the photoperiodic cues (i.e., lights-off or lights-on) was shifted. When lights-on was advanced by 3 h on days 8 and 9, the only significant effect was that calling ended earlier (Fig. 6A, Table IV). Since there was no change in the mean beginning time of calling, the midpoint of calling advanced and the duration of calling shortened significantly.

However, a delay in lights-off was followed by a significant delay in the calling parameters (Fig. 6B, Table V). The midpoint of calling occurred later in 79% of the insects, compared with 13% exhibiting no change and 8% calling earlier. An advance in lights-off resulted in a moderate forward shift in the calling parameters (Fig. 6C, Table VI), but the differences were not statistically significant.

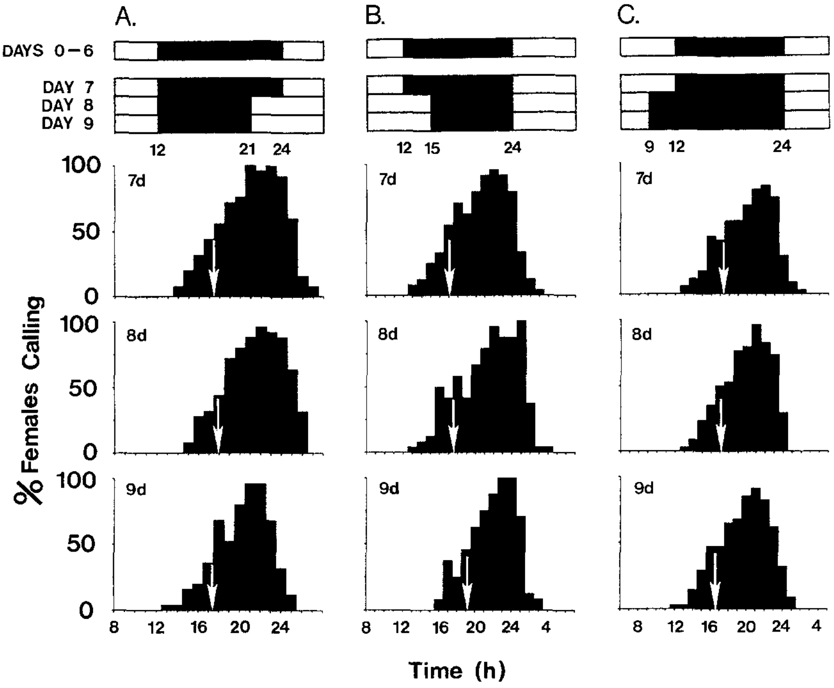

Fig. 6. (A) Calling activity of adult female *S. longipalpa* after a 3-h advance in lights-on (*N* = 25), (B) after a 3-h delay in lights-off (*N* = 24), and (C) after a 3-h advance in lights-off (*N* = 34). Top bars indicate the photoperiodic regime and arrows indicate the mean beginning time of calling.

Calling Activity in 20L:4D and 4L:20D

Two sets of cockroaches were reared from the oothecae under an abbreviated photo- or scotophase (4L:20D or 20L:4D, respectively). The imaginal females were collected during the photophase and observed under their respective photoperiod regimes on day 8. In 20L:4D, females began calling at a mean 3.6 h after lights-off compared to 3.2 h in 12L:12D (Table I), while in 4L:20D

Table IV. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L:12D on Day 7 and in 15L:9D on Days 8 and 9 Resulting from a 3-h Advance in ''Lights-On''[a]

Day	*N*	Begin	Midpoint	End	Duration
7	25	17.5 ± 0.40[a]	21.6 ± 0.25[a]	24.7 ± 0.18[a]	8.2 ± 0.38[a]
8	24	17.9 ± 0.37[a]	21.9 ± 0.24[a]	24.9 ± 0.23[a]	8.0 ± 0.39[a]
9	24	17.4 ± 0.40[a]	20.8 ± 0.27[b]	23.2 ± 0.20[b]	6.8 ± 0.34[b]

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's multiple range test).

Table V. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L : 12D on Day 7 and in 15L : 9D on Days 8 and 9 Resulting from a 3-h Delay in "Lights-Off"[a]

Day	*N*	Begin	Midpoint	End	Duration
7	24	17.1 ± 0.52^{a}	21.2 ± 0.32^{a}	24.3 ± 0.24^{a}	8.1 ± 0.50^{a}
8	24	17.5 ± 0.56^{a}	21.9 ± 0.33^{ab}	25.3 ± 0.24^{b}	8.8 ± 0.55^{a}
9	24	19.1 ± 0.45^{b}	22.5 ± 0.27^{b}	25.0 ± 0.18^{b}	6.9 ± 0.41^{b}

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's new multiple range test).

Table VI. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* in 12L : 12D on Day 7 and in 9L : 15D on Days 8 and 9 Resulting from a 3-h Advance in "Lights-Off"[a]

Day	*N*	Begin	Midpoint	End	Duration
7	34	17.3 ± 0.45^{a}	20.6 ± 0.26^{a}	23.0 ± 0.21^{a}	6.7 ± 0.48^{a}
8	34	17.1 ± 0.35^{a}	20.5 ± 0.23^{a}	22.9 ± 0.18^{a}	6.8 ± 0.30^{a}
9	34	16.7 ± 0.39^{a}	20.3 ± 0.28^{a}	22.8 ± 0.23^{a}	7.1 ± 0.32^{a}

[a] Means in columns followed by the same superscript are not significantly different ($P > 0.05$, Duncan's new multiple range test).

females began calling at a mean 10.2 h after lights-off (Fig. 7, Table VII). The long-day population restricted calling to a 10-h interval that extended 7 h into the photophase (Fig. 7A). The 4-h scotophase essentially served to synchronize the females such that they generally began and ended calling within a narrow range of time. Calling in short-day females was less synchronous and it occurred over an 18-h interval entirely within the scotophase (Fig. 7b). However, a significant correlation ($r^2 = 0.58$) between the beginning and the end of calling was observed: those females that called early ended early, and those females that called later ended later. Although the length of time the two populations spent calling differed by 8 h, the mean duration of calling for individual females was not significantly different between the two groups. Long-night females spent 7.0 ± 0.3 h calling, whereas short-night females spent 6.1 ± 0.3 h calling (Table VII). Females reared under 12L : 12D called for an average of 8.2 h (Table I).

DISCUSSION

Calling Activity in 12L : 12D. Supella longipalpa females, like other cockroaches, show distinct behavioral and physiological rhythms in locomotor activity, oviposition, mating, and adult ecdysis (Smith and Schal, unpublished). At 27 ± 1°C, the mean onset age of calling was 6.15 ± 0.91 days, compared

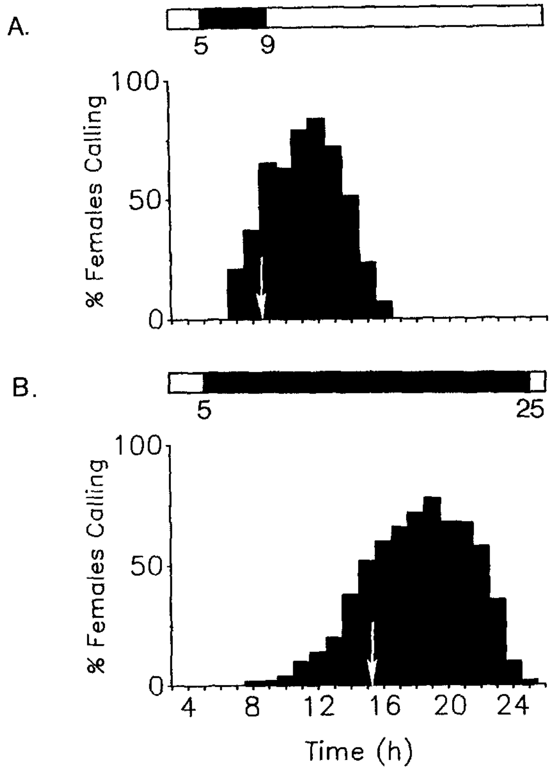

Fig. 7. Calling activity of 8-day adult female *S. longipalpa* reared under (A) a 20L:4D photoperiodic regime (N = 39) and (B) a 4L:20D photoperiodic regime (N = 50). Photoperiodic regimes indicated by top bars and the mean beginning time of calling indicated by arrows.

with 11 ± 4.3 at 25°C reported by Hales and Breed (1983). The difference is at least partly explained by the 2°C difference in temperature, since development is temperature sensitive (Adiyodi and Adiyodi, 1974). Under 12L:12D, the entrained rhythm was monophasic, with an interval (period) of 23.9 ± 1.0

Table VII. Mean (h ± SE) Calling Parameters of Adult Female *S. longipalpa* Reared from the Oothecae Under 20L:4D or 4L:20D[a]

Photoperiod	N	Begin	Midpoint	End	Duration
20L:4D	39	8.6 ± 0.21	11.6 ± 0.17	13.7 ± 0.22	6.1 ± 0.27
4L:20D	50	15.2 ± 0.39	18.7 ± 0.34	21.2 ± 0.33	7.0 ± 0.25

[a] Females were observed at an adult age of 8 days under their respective photoperiodic regimes.

h between midpoints of calling on successive days (Figs. 1 and 2), suggesting that calling could be coupled to a circadian system. As in *S. longipalpa*, the diel calling rhythm in a population of *Periplaneta americana* was monophasic (Seelinger, 1984). However, unlike *S. longipalpa*, calling in *P. americana* was not restricted to the scotophase, but rather it initiated near the end of the photophase and ceased several h before the end of the scotophase. Calling in anticipation of the scotophase was rarely seen in *S. longipalpa*, even under a short-night regime (Fig. 7A). Rather, *S. longipalpa* females continue to call into the photophase under such conditions. The maximum calling frequency (number of females per h) in *S. longipalpa* was 90% (Fig. 1), compared to 30% in *P. americana* (Seelinger, 1984). We attribute the difference in calling frequencies to the difference in the frequencies at which observations were made (20 and 1 min/h, respectively). *S. longipalpa* females do not call continuously but, rather, often cease for minutes at a time before resuming calling (Smith and Schal, unpublished). Had we made brief observations (i.e., 1 min/h), it is likely that lower calling frequencies would have been recorded. Turgeon and McNeil (1982) found that the frequency at which observations were made significantly influenced the calling parameters (e.g., number of calling bouts per day and duration of calling) in the armyworm, *Pseudaletia unipuncta*.

Calling Activity in LL and DD. A diel activity rhythm must satisfy two criteria to warrant designation as circadian: (1) the rhythm must persist in the absence of environmental cues, and (2) the free-running period must be nearly, but not consistently, equal to 24 h (i.e., the solar day) (Brady, 1974). Previous observations of *S. longipalpa* females (Hales and Breed, 1983) therefore described a diel, rather than a circadian calling pattern.

We observed free-running calling rhythms after transfer of females from LD to LL or DD (Fig. 3): 100 or 80% of the insects, respectively, had periods approximating, but unequal to 24 h. Hence, LL and DD do not suppress calling in *S. longipalpa*, and calling can conclusively be described as circadian. The behavior followed Aschoff's rule for arthropods (Aschoff, 1979): the free-running period lengthened within 48 h after transfer to LL in 80% of the insects (range, 25–29 h; Fig. 4A), such that a significant phase shift to later calling was observed (Fig. 4B, Table II).

Calling Activity Following Shifts of the Photoperiodic Cues. In order to test the influence of shifts in the photoperiodic cues (i.e., lights-on and lights-off), it was important to demonstrate that calling was not inhibited by LL (Fig. 3A) as has often been reported for cockroach locomotor rhythms (Lohmann, 1967; Dreisig and Nielsen, 1971; Dreisig, 1976; Leppla *et al.*, 1989). Consequently, changes in the calling pattern of *S. longipalpa* following shifts in the photoperiod could be attributed to the lights-on or lights-off cue, rather than to inhibition by light.

Under the 12L:12D photoperiodic regime, a small percentage of females began calling 1 h before lights-off (Fig. 1), suggesting that the timing of the activity phase was set by the previous lights-off. Confirmation that the light-to-dark transition served as the environmental cue (Zeitgeber) by which the endogenous rhythm is kept in phase with the photoperiodic regime was conclusively demonstrated by the similar directional shift in phases following a shift in lights-off (Figs. 6B, C).

In *S. longipalpa*, reentrainment of the calling rhythm following shifts in the light-to-dark transition was neither immediate nor complete over the 48-h observation period (Figs. 6B and C). We expect that after several additional days under the new LD conditions, resynchronization would have been realized, although oothecal production would have temporarily interrupted the calling pattern (Smith and Schal, 1990). A lag between the phase shift of the LD regime and reentrainment has been observed in other insects (review by Saunders, 1982). The appearance of transient cycles following phase shifts in the LD photocycle is a characteristic of circadian rhythms (Pittendrigh, 1965), providing further evidence that calling in *S. longipalpa* contains an endogenous component.

Calling Activity in 20L:4D and 4L:20D. Little information has been reported on the effect of the length of the scotophase on individual calling parameters of insects. Despite the 16-h difference in the lengths of the scotophases in the two photoperiodic regimes, the difference in the average duration of calling by individual *S. longipalpa* differed by only 0.9 h (Table VII), suggesting an inherent limitation to the time allocated to calling. It is interesting to note that when lights-off was advanced by 3 h, resulting in a longer scotophase, there was also no apparent increase in calling durations (Fig. 6C). As in *S. longipalpa*, the mean time spent calling by the female armyworm *P. unipuncta* remained relatively constant under scotophases ranging from 6 to 14 h (Delisle and McNeil, 1986). Moreover, like *S. longipalpa*, long scotophases served to lenghthen the time *P. unipuncta* populations spent calling (Delisle and McNeil, 1986), so that some females began and ended calling earlier, while others did so later. In both species, this suggests that, with long scotophases, the calling oscillators of individual females were out of phase with each other, resulting in a temporally dispersed population pattern. Conversely, with short scotophases, oscillators of individual females were in phase with each other relative to the Zeitgeber, resulting in a synchronously calling population.

Under 12L: 12D, males exhibit a diel response to extracts of virgin female *S. longipalpa*, with maximum response occurring during the interval corresponding to peak calling (Liang and Schal, 1990a,b). Consequently, we hypothesize, as have others for other insect species, that endogenous regulation of calling serves to synchronize mating activity. However, the ecological significance of the effect of the length of the scotophase on the onset of calling in female *S. longipalpa* is perplexing and difficult to explain for a species of tropical origin that would not normally experience extremes in the photoperiod. Although the amount of time that an individual female spends calling may be innately limited, the population responded to longer nights by calling later over a longer interval (Fig. 7B, Table VII). Possibly, under a prolonged scotophase, the ''necessity'' to mate becomes less critical so that other activities (e.g., feeding and foraging) take precedence in some individuals. Alternatively, the durations of other activities may be more plastic than the duration of calling behavior. Thus, as the scotophase lengthens, so do the durations of preceding activities, delaying calling relative to lights-off.

The data presented here may be extrapolated to suggest that other behavioral and physiological events associated with pheromone synthesis and release in *S. longipalpa* may be modulated by environmental (photoperiodic) factors. This study, then, underscores the importance of understanding the interaction of endogenous and exogenous cues in the timing of such events. It provides a foundation on which endocrine studies of this insect may be based, using physiologically and behaviorally synchronized insects.

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