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Author: Faust, Lynn Frierson

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NATURAL HISTORY AND FLASH REPERTOIRE OF THE SYNCHRONOUS FIREFLY *PHOTINUS CAROLINUS* (COLEOPTERA: LAMPYRIDAE) IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

LYNN FRIERSON FAUST
11828 Couch Mill Rd., Knoxville, TN 37932
E-mail: TNLFAUST@Gmail.com

ABSTRACT

The synchronous firefly *Photinus carolinus* (Green) of the moist cove hardwood forests of the Great Smoky Mountains National Park attracts much public attention during its spectacular month-long mating display known as The Light Show. In previous studies flash synchrony among *P. carolinus* males has been investigated, but little is known about its natural history and mating behavior. This study provides additional information on the habits, flash signal variation, mating strategies, predation and historical records of *P. carolinus*. The polyandrous females remate throughout their approximately 3-week adult lifespan, laying successive clutches of eggs. While stationary females generally respond to male courtship signals with a *receptive* doublet flash signal, they also produce a rhythmic flash while walking, and can revert back to the receptive state. In this protandrous species, the average number of flashes per flash train in male courtship signals increases after females have emerged. I describe *pseudo-female* male flashes and group *chaos* flashing associated with mating clusters as well as conditions causing *distress* flashing in both sexes. With a backdrop of changing habitat and increasing human pressure, observations taken from the past 18 years and over 1000 h spent in the field additionally describe male guarding of a female pupa, mate guarding via prolonged copulation, common predator and phorid infestation challenges for this firefly.

Key Words: synchronous flash behavior, polyandry, protandry, lightning bug, phorid

RESUMEN

La luciérnaga sincronizada, *Photinus carolinus* (Green), de los bosques de madera noble en áreas húmedas del Parque Nacional de las Montañas "Great Smoky" atrae mucha atención pública durante su exposición espectacular de apareamiento que dura un mes conocido como "El Espectáculo de Luz". En estudios anteriores, la sincronización de los destellos entre los machos de *P. carolinus* ha sido investigada, pero poco es conocido sobre su historia natural y su comportamiento de apareamiento. Este estudio provee información adicional sobre los hábitos, variación en las señales de destellos, estrategias de apareamiento, depredación y registros históricos de *P. carolinus*. Las hembras poliandrosas aparearon de nuevo durante la duración de su vida de aproximadamente 3 semanas, poniendo masas de huevos sucesivos. Mientras que hembras estacionarias generalmente responden a las señales de cortejo sexual de los machos con una señal *receptiva* de un destello doble, ellas también producen un destello rítmico cuando están caminando, y pueden revertir de nuevo al estado receptivo. En esta especie protandrosa, el número promedio de los destellos por los machos en el tren de señales del cortejo sexual aumentan después de que las hembras emergen. Se describen los destellos de tipo *pseudo-hembra* de los machos y el destello de caos del grupo asociados con grupos de apareamiento además de condiciones que causan el destello por *angustia* en ambos sexos. Con el acumulo de cambios en el hábitat y la presión humana creciente, observaciones hechas en los últimos 18 años y en más de 1000 horas en el campo, adicionalmente se describen el comportamiento guarda (protección) de la pupa de la hembra por el macho, y la guardia de su pareja por medio de la copulación prolongada, los desafíos de depredadores e infestaciones comunes de moscas foridas para esta luciérnaga.

Fireflies are unique; they are one of the few insects readily recognized and even admired by many people. Among the most spectacular firefly displays is "The Light Show" (Emily Faust pers.com. 1968; Landry 1994; Faust et al. 1998; Strogatz 2003) produced on Jun nights by synchronizing *P. carolinus* males in the former logging town of Elkmont, TN (Weals 1991) within the Great Smoky Mountains National Park (GSMNP). This display consists of

thousands of flying males which flash in discontinuous synchrony (Copeland & Moiseff 1995) with each male producing flash trains containing 4-8 flashes given at 0.5 second intervals followed by 6-9 seconds of dark, both time intervals being temperature dependent. Beginning 37-43 min after sunset (Lloyd 1966), on peak nights (Faust & Weston 2009) thousands of males flash in unison and then go dark in unison, signaling together for up to 3 h.

Lloyd (1966) further detailed its range and habitat by mapping the locations of small, scattered populations stretching from the north Georgia Appalachians to western Pennsylvania. Faust & Weston (2009) added that this species is found in lower elevations as it moves higher in latitude and appears earlier in the season the further south it is found. Green (1956), when first describing the morphology and range of *P. carolinus*, considered this “an Appalachian offshoot of the more northern *P. ardens* Leconte”. Bole (2001) offered additional contemporary evidence linking *P. carolinus* closely to *P. consimilis* Green and *P. ardens*.

Lloyd (1966), Copeland & Moiseff (1995), and Bole (2001) provided excellent studies on the details of *P. carolinus* flash signals under natural and controlled settings. While males signal in flight, females remain stationary and well-hidden in the leaf litter or low ground cover. Females respond to male advertisements by emitting a *receptive* doublet flash given midway through the 6 s dark phase, averaging 3 s after the final flash of the male flash train (Bole 2001; Moiseff et al. 2001). Copeland et al. (2008) described male landing distance to the signaling females and Moiseff et al. (2001) the formation of competitive male mating clusters around the receptive female, involving both satellite and nuclear males.

Marshad et al. (2008) designed a bioengineering model for analyzing the visual performance of the sexually dimorphic eyes of *P. carolinus*. Faust & Weston (2009) presented a degree-day prediction model and described the phenology of *P. carolinus* and 13 additional East Tennessee lampyrids. *Photinus carolinus* is protandrous, with the first males appearing on May 24 on average, approximately half-peak male abundances reached by Jun 5, first females by Jun 9, with the final night of peak male activity being Jun 11 (Faust & Weston, 2009).

This paper seeks to elucidate aspects of the natural history of the southern Appalachian populations of *P. carolinus*, occurring primarily in the GSMNP or private lands bordering the Park. Emphasis is on descriptions of male and female mating, non-courtship flash variations and comparisons of the 2 different female flash behaviors as related to mating receptivity, polyandry, remating, ovipositing and phorids. Historical records of the presence of this species through the past 60 years in the GSMNP is provided as is a brief discussion of the changing impact of man and the habitat on this species.

MATERIALS AND METHODS

Study Sites

In the GSMNP, *P. carolinus* is found in the highest densities at 732m (2400'), though isolated

individuals have been found as low as 488m (1600') and as high as 1524 m (5000').

Photinus carolinus is found in the maturing second growth cove hardwood forests in mountain river valleys throughout the National Park. Tulip poplar (*Liriodendron tulipifera* L.) is the primary tree with oak (*Quercus alba* L. and *Q. rubra* L.), maple (*Acer saccharum* L.), yellow buckeye (*Aesculus octandra* Marsh), hemlock (*Tsuga canadensis* L.) and *Rhododendron maximum* L. with doghobble (*Leucothoe fontanesiana* Steudal) also common. The prime display areas are open woodlands bordering former or current open areas and abandoned railroad grades and trails, often near or on a steep hillside and within a 100 m of a stream or river. The rainfall averages 168 cm/yr (66") (NADP 2007) in these temperate near-rain forest mountain valleys. Night temperatures during the mating season typically range from 15-21°C (59-70°F).

Every summer since 1992, the author has traveled to Elkmont, TN in Sevier Co. (35°39'13"N, 83°34'50"W) in the GSMNP to observe *P. carolinus* from the nights of first male emergence in late May, through the peak display season in mid Jun, until the final nights of the last remaining *P. carolinus* of the season in early Jul. Additional sites within and just outside of the Park have been utilized for observations and collections.

Field Observations

Nightly field notes, data charts and observations regarding all aspects of the *P. carolinus* life history were recorded from over 1000 h spent in the field in the past 18 years. Additionally, for the past 5 years, a Kodak Z740 Easyshare, an Olympus SW720, a Sony super-nightshot Handycam DCR-HC48, and a Bushnell Nightwatch 26-0224 night vision scope have been used to visually record thousands of observations. An Olympus VN2000 pocket voice recorder, a Digiwalker SW651 stopwatch, a Mannix HDT303K digital thermometer, and a Petzl TacTikka XP LED Headlamp with blue filters were used for data collection and observation. An Omano 7.5x-35x Stereo Trinocular Microscope was used for details, egg, phorid and external parasite counts.

Study Organism

Field marks for correctly identifying *P. carolinus* in its native setting were determined as there are at least 13 Lampyridae species commonly found in Elkmont during the *P. carolinus* season including *Photinus pyralis* L., *P. macdermotti* Lloyd, *P. marginellus* Leconte, *P. carolinus*, *Photinus versicolor* complex Fab. and *P. lucicrescens* complex Barber, *Pyraetomena borealis* Randall and *P. angulata* Say, *Phausis reticulata* (early and late varieties) Say, *Ellychnia corrusca* L., *Lucidota atra* and *Pyropyga minuta* Leconte. Additionally, since *P. carolinus* are

difficult to find except during mating flight times, concentrated effort was made in 2007, 2008, and 2009 to determine the after-display and daytime location of *P. carolinus* and where captured adults go upon release. NPS permit (Faust #GRSM-2009-SCI-0026) guidelines stress sample numbers must be kept as low as possible to protect this resource in the National Park.

Male and Female Flash Repertoires

Photinus carolinus frequently exhibit different types of flash behavior in addition to the species-specific courtship flashes. Behavior was recorded with data sheets, voice recorders, video cameras, and a stopwatch to more accurately describe the appearance and context for 5 additional flash behaviors: walking/flashing female, pseudo-female male flash, male/female dialogue single flashing, group chaos flashing, and distress flashes.

Variation in Male Flash Signals

In May through Jul 2007 and 2008, I examined whether male flash signals changed after females had emerged. Over 4500 individual flashes (617 flash trains) of *P. carolinus* were counted by 3 observers using data sheets and voice recorders beginning on the earliest nights of first male emergence, and continuing until the final nights of the mating season 6 weeks later. Times, weather, moon phase, and temperatures during flash train counts were recorded. No display occurred below 10°C. We only recorded trains produced by flying males in which the first flash in the train was seen. Because of their predictable rhythm and flight path, individuals could be followed for an entire flash train. Any counts that could have included more than 1 male were discarded. Students *t*-test compared male flashes within each flash train before females emerged (early season) to flash numbers per flash train after females were present (later season).

Female Flash Behavior, Mating/Remating, and Oviposition

From Jun 12-24, 2009, 20 *P. carolinus* females were captured and labeled as displaying either the typical *receptive* female flash or the more rhythmic *walking/flashing* flash to determine if flash behavior indicated future mating, remating and oviposition outcomes. Females were kept separately in 4-oz containers with dampened filter paper and a small amount of moss and soil from their collection site, at natural temperatures, humidity and photoperiod. Field-captured males were placed into females' containers at dusk each night, and pairs were observed with blue light every 15 min for mating activity. A couple was counted as mated if stage 2 copulation, in which

spermatophore transfer occurs (Lewis & Wang 1991; Demary & Lewis 2007), was achieved for at least 1 h. Each morning males were removed and all eggs were counted and set aside for release. To compare mating outcomes for females exhibiting *walking-flashing* vs. *receptive* flash behavior, the percentage of females that mated at least once was compared between groups by Fisher's Exact test on a 2 × 2 table. This test also was used to compare percentage of females that remated between these 2 groups. For all captive males and females, the presence and number of mites and parasitic phorid larvae (Brown 1994; Lewis & Monchamp 1994) on or emerging from each host was noted. The percentage of females parasitized by phorid flies was compared between 2 separate *P. carolinus* populations by Fisher's Exact Test.

Photinus carolinus and Man

Interviews were conducted with former residents of Elkmont, fishermen, campers, Eastern Band of the Cherokee Nation tribal elders, and manuscripts for records of when this synchronous species was first noticed in the Elkmont area and the Cherokee lands of *Shaconage*, now known as GSMNP. Additional information was gathered on the presence of and changing perceived densities of this species in specific locales around Elkmont through the past 50 years and the impact of man on the habitat of this species in these same years.

RESULTS

Field Marks for Identifying *P. carolinus*

Averaging a live total body length of 12.5 mm, *P. carolinus* falls midway in size between the larger *P. pyralis* and the smaller *P. macdermotti* and *P. marginellus*, all of which can be found flashing in Elkmont during the *P. carolinus* season in similar habitats (Fig. 1). Both sexes often have a noticeable black margin on the anterior lateral aspects of the black, pink and opaque pronotum. Though alate (winged), the female, who is often slightly wider than the male, is rarely seen flying. Females have 1 dimpled half moon shaped lantern in the center of abdominal sternite 6; males have 2 lanterns on sternites 6 and 7 (Fig. 2a, b, c). As opposed to the other very morphologically similar local *Photinus* species, which sometimes have light abdominal markings near the lanterns on the ventral surface, both male and female *P. carolinus* are usually dark ventrally except for the lanterns. I have noted that it is often easier to distinguish similar firefly species in the field by comparing female (if available) lantern shape and structure vs. male comparisons. Adults occasionally have retained vestigial larval lanterns. Males fly flashing their synchronous display in roughly horizontal flight

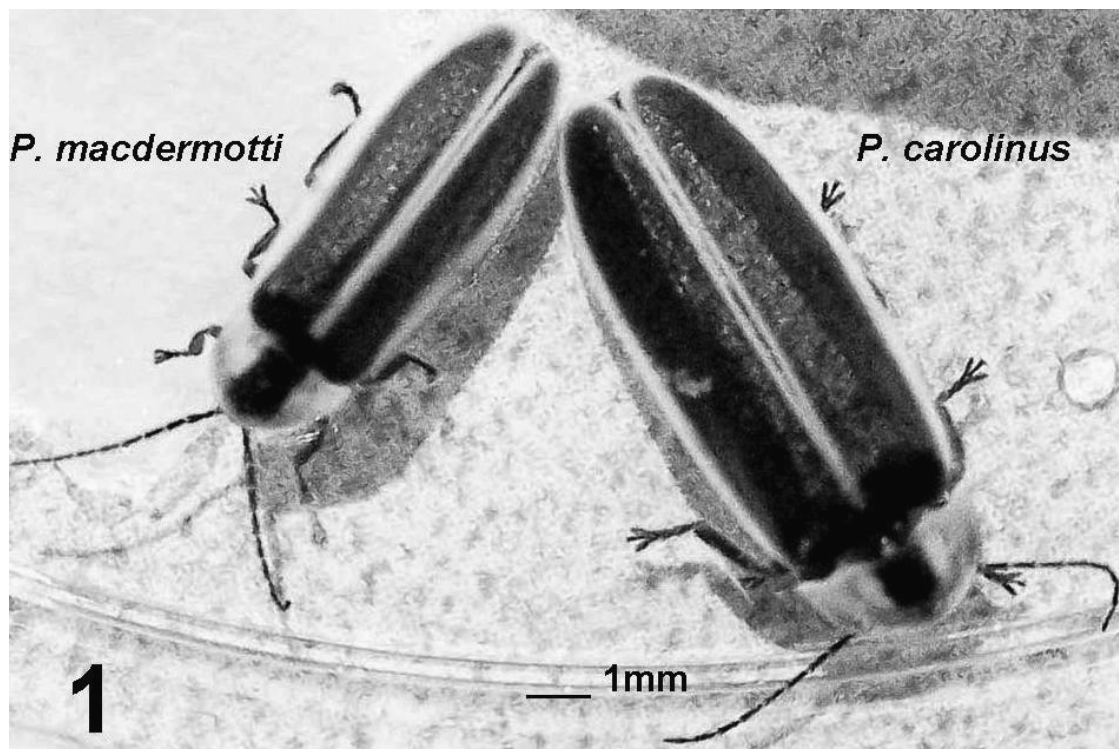


Fig. 1. Size comparison of *Photinus macdermotti* (L) and *Photinus carolinus* (R). Because 13 sympatric Lampyrid species occur in Elkmont in Jun, proper field identification is critical.

paths 1-3 m off the ground covering up to 5 m per flash train. These field marks, combined with the distinctive male flash train pattern, the female doublet and response delay, the specific habitat, seasonality, and elevation parameters make field identification relatively reliable in the GSMNP.

At the end of the evening's mating flight, the majority of the *P. carolinus* males appeared to flash their final train as they rose high into the treetops. In 2009, captive males ($n = 20$), released at their original collection site during the day, flew up into the trees instead of seeking shelter in the dense, lower ground vegetation. By season's end many of the males were perched instead of flying as they flash during their nightly display time.

Life Cycle Observations

Eggs. Egg counts from 1993-2005 showed that captive *P. carolinus* females ($n = 21$) laid an average of 24 (range 1-83) off-white, 0.75-1.0 mm eggs in up to 4 successive clutches over a period of 1-13 d. If provided with a sprig of moss or native soil, the captive female individually placed each egg; otherwise, egg retention was common with all the eggs being expelled in a mass just prior to death.

Larvae. *Photinus carolinus* larvae, because of their subterranean habit, were seldom seen in the wild. In Jul 1993, I hatched 44 *P. carolinus* larvae from 47 eggs laid 18 d earlier. Laterally pink, these tan-brown-gray smooth, narrow-bodied 2-3-mm larvae were fed tiny earthworms. The 25-d-old larvae died in their second instar when their container was accidentally destroyed. Typical of other *Photinus* larvae, the larvae had active multifingered pygopodia (caudal tail organ) and 3 longitudinal pale dorsal lines. It is unknown whether *P. carolinus* larvae become dormant in the cold winter months or simply dig deeper into the soil. As the time for pupation nears in May, the occasional final instar ($n = 3$) appeared under the leaf litter, often near damp rotting logs or moss, where, glowing, they soon pupated.

Pupae. In Jun 2006, an adult male *P. carolinus* was observed clasping the body of a glowing pink pupa which eclosed into an adult female 6 d later. Two other *P. carolinus* males with antennae actively moving, and 1 pair in copula were found on top of the moss <5 cm above where the female pupa and the adult male lay buried. Because I removed only the female to gain a positive sexual identification upon eclosion, the male was prevented from further guarding the pupa.

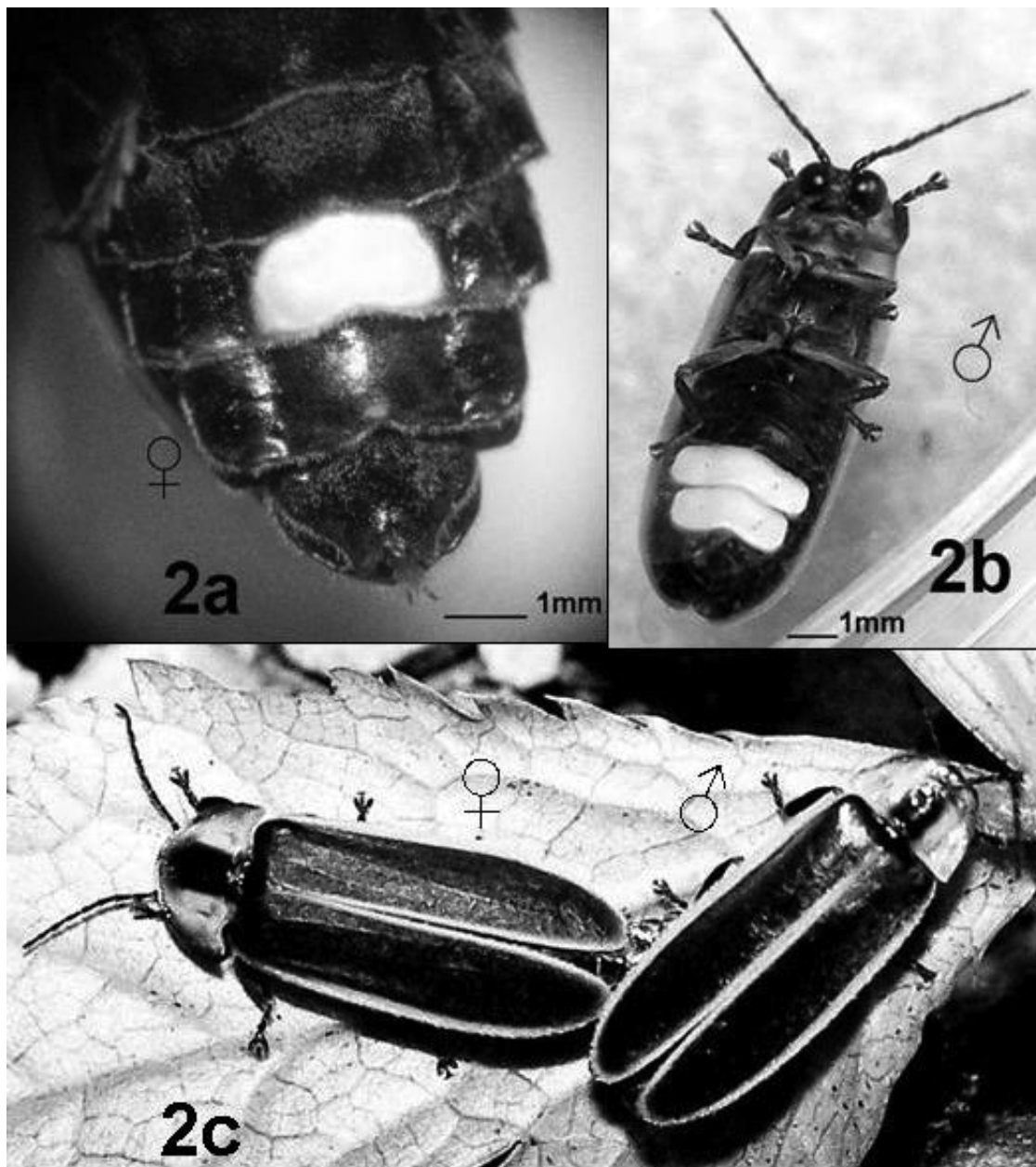


Fig. 2. 2a, Comparison of female (L) and 2b, male lanterns (R). In the field, the female lanterns of the sympatric species are often more distinct than the male lanterns. 2c, Stage 2 copulation. The female (L) is often slightly wider posteriorly than the male (R).

Male and Female Flash Repertoire

Female walking/flushing behavior. In addition to the typical doublet response flash given by receptive females, *P. carolinus* also displayed *walking/flushing* behavior. This very rhythmic flash was most often seen on or after peak nights, usu-

ally more than an hour after sunset. Females produced these rhythmic doublet flashes every 1.2-2.5 s while walking out in the open. *Walking/flushing* females were highly visible and active, with antennae moving rapidly, and often hopped and flew <15 cm, then continued walking rapidly. This very conspicuous flash did not appear to at-

tract males. On cool evenings (below 15°C) the *walking/flashing* females often approached humans crouched on the ground and care needed to be taken not to crush them. Females also sought out the softer margin of the raised gravel (former) railroad bed, which measured as much as 1°C warmer than the road-bed. *Walking/flashing* females appeared particularly vulnerable to the large crowds coming to see The Light Show, as they were the most exposed to trampling, as well as easiest to see and to capture.

Male and female single flashing courtship dialogue. When a male and female *P. carolinus* began their close range mating dialogue, the male switched from his multi-flash courtship signal to give single flashes as he began to circle the female. At this point, the female also often switched to give single flashes, although occasionally she continued her doublet flash. During this dialog of alternating, aimed flashes the male continued to approach the female, first flying, then walking. In the absence of competing males, these pairs usually achieved Stage 2 copulation within minutes (Fig. 2c). Once coupled, females occasionally continued to sporadically emit single flashes or doublets, and males sometimes gave slower than normal flash trains, but generally the couple ceased flashing and moved to a sheltered location (undersides of leaves or beneath leaf litter). If uncovered, the female often attempted to crawl back under cover, pulling the male backwards behind her. Copulations often lasted until dawn with mean duration of 11.4 ± 1.0 h ($n = 5$).

Chaos flashing behavior. *Chaos* describes the sudden appearance of rapidly alternating, single flashes emitted by multiple males gathered <20 cm around a single responding female. Looking like a miniature laser show, chaos lasted less than 10 s before ending abruptly. When examined (with a night vision scope or infrared camera) within minutes after *chaos* flashing stopped, many males were found in a tight cluster around the female, often completely obscuring her from view; sometimes these males formed stacks of up to 6 males on the female. These clustered males grappled with one another by shoving, pushing, and dislodging their competitors from the back of the female. Eventually, 1 male succeeded in achieving Stage 1 mating with the female. However, females were often observed rejecting these apparently successful males after a few minutes in Stage 1 by dislodging, twisting, or walking away from the suitor who initially attempted to remount the female. When rejection did occur, scramble competition (Demary et al. 2006) described by (Copeland et al. 2008) as frenzy resumed among the nuclear males that remained, and a new cluster quickly reformed around the female. *Chaos* flashing did not normally recur this second time.

From years of field observations and video footage review it appeared that both large and

small males were successful in securing Stage 2 copulations with females, although body size could not be measured without disturbing the clusters. Larger males appeared to have the advantage when shoving their way in to reach the female, but the smaller males appeared more agile, and could slip into the cluster more easily. Flashing does not appear important at this stage of courtship.

Male pseudo-female flash behavior. Courtship clusters of up to 30 males competing for 1 receptive female have been described by Moiseff et al. (2001) and Copeland et al. (2008). It was not uncommon in the mating clusters for the female to reject a male after a few minutes of Stage 1 copulation. When this occurred, the rejected male often gave female-like rhythmic doublet flashes repeated every 1.5-2.5 s while crawling away from the cluster and female. Other males were often attracted to this *pseudo-female* flashing and dropped from the air or abandoned the female they were courting to briefly follow this doublet-flashing male. After crawling some distance from the cluster, rejected males were observed resuming their typical courtship flash pattern.

Distress flashing. *Photinus carolinus* adults caught in spider webs or by harvestmen (Phalangidae) emitted rhythmic flashes repeated every 1.5-3 s. These *distress* flashes were sometimes simple single flashes, while at other times they appeared bimodal (as in female response doublets). Distress flashes were produced by both sexes, and also occurred when adults had fallen into water, got caught in rhododendron sap or become injured. *Distress* flashing often attracted other males that subsequently became caught. When males giving *distress* flashes were removed from the water or spider webs, they often resumed their normal courtship flash trains after a short recovery.

Variation in Male Flash Signals

Flash trains given by *P. carolinus* males had significantly more flashes/pulses later in the season after females had emerged compared to flash trains before female emergence (Fig. 3; Student's $t = 9.93$, $df = 615$, $P < 0.0001$). Across both years, the overall average was 6.77 flashes per male flash train ($n = 617$ flash trains or > 4500 pulses), although on peak nights male flash trains included as many as 9-11 flashes, compared to the earliest nights where many 4 pulse flash trains were seen. On the nights included in this study, early season temperatures averaged 22.4°C; late season averaged 20.6°C.

Female Flash Behavior and Mating/Remating

During 2009, females that were collected giving either the normal courtship *receptive* ($n = 6$)

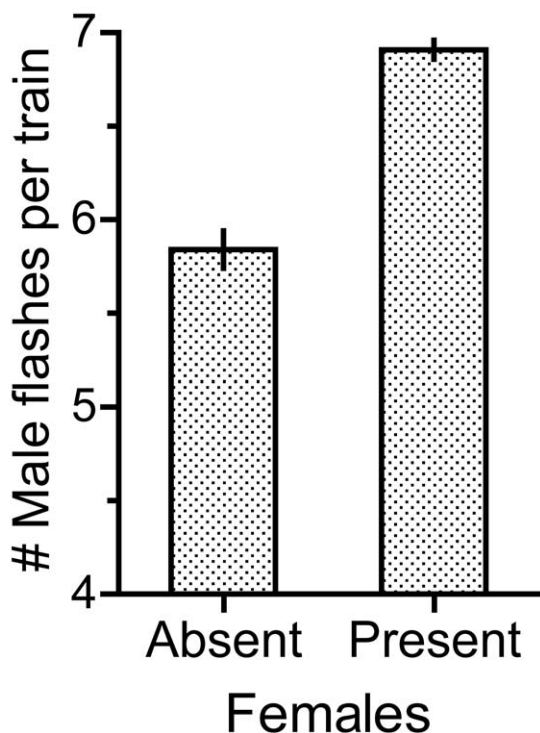


Fig. 3. Number of flashes per flash train given by *P. carolinus* males early season, before females have emerged (5.84, $n = 102$ flash trains) vs. late season when females are present (6.91, $n = 515$ flash trains); means \pm SE shown.

doublet response or *walking/flashing* ($n = 9$) behavior were tested for receptivity to mating, remating, and subsequent egg laying. When *P. carolinus* females in captivity were given access to males, there was no significant difference in the proportion that mated between walking-flashing vs. receptive females (Fisher's Exact test, $P = 0.329$). Similarly, there was no significant difference in the proportion of females that remated between these 2 groups (Fisher's Exact test, $P = 0.200$).

In 2-13 d of captivity, 10 *P. carolinus* females with both flash behaviors mated 23 times (range 1-5). Although prior mating and ovipositing history was unknown before capture, both types of females laid eggs, with clutch sizes ranging from 1-44 eggs in up to 4 separate clutches. Walking-flashing females averaged 3.4 d ($n = 5$) until first ovipositing and receptive flash females averaged 3.5 d ($n = 6$). Parasitic phorids were found in females showing both flash behaviors (Table 1).

Natural Enemies

Orb-weaving spiders (Araneidae) prey on *P. carolinus*. Late at night, after all courtship flash-

ing had ceased, often the only lights visible were the rhythmic distress flashes or the steady glow of fireflies caught in webs. In addition, harvestmen (Phalangidae) often were seen carrying glowing pupae, adult fireflies, or only the still glowing firefly lantern, perhaps scavenged from another predator. Incidence of mites on *P. carolinus* is low.

Though local *Photuris* fireflies readily eat captive *P. carolinus* and regularly fly and signal within the dense display areas of male *P. carolinus*, predation by *Photuris* sp. of *P. carolinus* in the wild has not yet been observed.

Phorid flies (*Apocephalus antennatus* Malloch) parasitize *Photinus* fireflies by ovipositing eggs within the firefly's body (Brown 1994; Lewis & Monchamp 1994), and these parasitoid larvae were found emerging from *P. carolinus* males and females. In 2009, a significant difference (Fisher's Exact test, $P = 0.0048$) in degree of phorid infestation was noted between captive populations of *P. carolinus* females from 2 different watersheds within the GSMNP with 62.5% ($n = 8$) parasitized at one site; none ($n = 11$) were parasitized at the other site (Table 1).

Local Ethnology of *Photinus carolinus* and Man

From interviews conducted in 2005 and 2008, native American Cherokee Nation tribal elders Jerry Wolf of Cherokee, NC, Alfred Wolf of the Snowbird Blue Clan, and Dr. Michael Abram, folklorist of the Cherokee Tribal Museum, agree that, although named *atsisdadagesgoya*, meaning "bug that makes a spark", there is no mention of fireflies in their tribal history and mythology. This is consistent with previous descriptions of pre-1900 Cherokee culture, which also noted lack of any mention of fireflies (Moody 1912). This omission is curious, as much of the traditional tribal lands in and surrounding the GSMNP are prime *P. carolinus* habitat, in addition to sheltering at least 20 additional local firefly species (Mayor 2006).

Former residents of Elkmont first remember seeing The Light Show in the early 1960s when the display occurred over 2 kilometers upstream of the Elkmont community in more mature forest. By the 1970s, the Light Show had spread down river and was visible in the open mown lawns and surrounding forest of the Little River portion of Elkmont, but not on the upper Jakes Creek Rd of Elkmont a kilometer away. After the removal of the Elkmont street lights in 1995, there appeared to be an explosion of *P. carolinus* throughout the entire community. This expansion could additionally be related to the growing openness of the maturing forest, which was approaching 75 years or more in most areas of the Park. In 2009, *Photinus carolinus* continued to be abundant throughout the open forest surrounding the community, but *P. carolinus* had disappeared from the previously

TABLE 1. INCIDENCE OF PHORID PARASITOIDS *APOCEPHALUS ANTENNATUS* AND OVERALL FECUNDITY IN *P. CAROLINUS* FEMALES COLLECTED JUN 2009 FROM 2 LOCATIONS IN THE GSMNP.

Location in GSMNP	Total # females	% parasitized	Ave # phorid larvae per infected female	% firefly ovipositing	Ave # of eggs per ovipositing female
Little River watershed	8	62.5	5.8	50	5.2 ± 4.4
West Prong Watershed	11	0	0	78	13.3 ± 12.8

mown lawn areas, which had become tangled thickets since the NPS vacated the residents and their lawn mowers from Elkmont in 1992.

Prior to 1992, Elkmont was a quiet summer retreat where residents, before going to bed, observed The Light Show from their porches. Since 2000, each year as many as 26,000 visitors come to see The Light Show during its 10-d peak season, with the accompanying trampling of the ground and vegetation. Flickering flashlights, the now mandatory NPS visitor “firefly-shuttle” buses, human noise, bug spray, and general disturbance that up to 2000 people a night cause to a normally quiet, dark area, all create potential impacts to this population. Despite the crowds, however, the Light Show remains breathtakingly spectacular on peak nights (NPS 2009).

DISCUSSION

This study provides new descriptions of variation in the flash behavior of male and female *P. carolinus* observed in the field, and also provides new information on their mating system. This study documents a major change in male flash behavior, with males producing more flashes per flash train once females have emerged; on peak nights, male flash trains can contain up to 11 flashes. This finding agrees with Carlson & Copeland’s (1985) discussion of how male firefly flashes are dependent on state of arousal; and also agrees with Bole (2001), who found that female *P. carolinus* are more likely to respond to male flash trains containing more than the average of 6-7 flashes. In other *Photinus* species, such selection pressure from females preferring more conspicuous male flashes is balanced by increased predation costs for these flashier males (Demary & Lewis 2006; Woods et al. 2007).

Several male flash behaviors are described here for *P. carolinus* for the first time. *Photinus carolinus* males that have been rejected after contacting a female sometimes produce doublet flashes resembling those of females. Papi (1969), Lloyd (1979), and Cicero (1983) described pseudo-female flashes given by males under similar circumstances of intense male-male competition in several other firefly species. The group flash interaction that takes place during *chaos* flashing in *P. carolinus* has not yet been described in other synchronic or *Photinus* species. Further studies

will be needed to determine whether this *chaos* display signifies male to male competition, aggression, communication of intent, species identification, male and/or female choice, or is simply the accumulated visual spectacle created when many courting males engaged in flash dialogues with 1 female in a small area. Though witnessed infrequently, *chaos* display is used by researchers to find the cryptic females and evolving clusters. The *P. carolinus* *distress* flash described here could be considered similar to the non-courtship or agitated flashes that have been discussed by Lloyd (1984), Carlson & Copeland (1985) and Buck (1990) in other species. Because they are quite common, the function of these other flash behaviors calls for further investigation.

This study also provides new information about different female flash behaviors and *P. carolinus* mating systems. Females displaying both the *receptive* doublet response flash and *walking/ flashing* behavior were observed to mate, to oviposit, and often to remate on succeeding nights. The high percentage of female remating clearly demonstrates that *P. carolinus* females are polyandrous like many, but not all, other *Photinus* species (Wing 1984, 1985; Lewis & Wang 1991; Lewis & Cratsley 2008). The unexpected finding of large differences in phorid infestation between separate populations needs to be explored further. The function of the *walking/ flashing* female behavior remains unknown, although the fact that this behavior is exhibited by females crossing open areas is consistent with its being used as an aposematic warning signal. This flash behavior is unlikely to signal oviposition readiness, as no difference in egg-laying behavior was observed between the *receptive* flashing females and the *walking—flashing* females.

In many *Photinus* species, males transfer spermatophores to females (Lewis et al. 2004), and comparisons of male reproductive structures suggests that this also occurs in *P. carolinus* (Demary & Lewis 2007). Spermatophore-producing *Photinus* species have longer copulation durations (Wing 1985; Lewis & Cratsley 2008), which is consistent with the prolonged copulations seen here in *P. carolinus*. Such prolonged copulations may serve as copulatory mate-guarding, as they exceed the time required for spermatophore transfer (Lewis & Wang 1991; van der Reijden et al. 1996).

Several previous studies have described courtship interactions in other *Photinus* species. As in other *Photinus* species (Cicero 1983; VencI & Carlson 1998), *P. carolinus* females often continue responding to other males' signals after establishing a flash dialog with 1 male; this augments male competition and potentially increases female mate choice. As in other species, males are also attracted to male-female dialogs and aggregations of males. Direct interference competition among males appears intense in *P. carolinus*, and the mating clusters described here are similar to Maurer's (1968) "love knots" described in *P. pyralis*. Scramble competition among males, found in many species (Lloyd 1979; VencI & Carlson 1998; Demary et al. 2006) appears common. *Photinus carolinus* females appear to exert mate choice even in these clusters, as often females were seen to reject males during the first, dorsal-mounting stage of copulation by twisting or tucking the abdomen or walking away from the rejected male and then proceed to copulate with a different male. Much more work is needed to further understand the evolutionary dynamics of these large mating clusters and the roles of male and female choice.

Finally, the observation of an adult male *P. carolinus* guarding a female pupa suggests the possibility that some matings may occur without any flash interaction. *Pyractomena borealis* males often locate and guard both female larvae (unpublished data) and pupae (Lloyd 1997) for several weeks until female eclosion; males then couple with the newly emerged female adults, often while the teneral female is still in the white, untanned cuticle stage (unpublished data). Buck (1938), Lloyd (1979), Lewis & Wang (1991), and Copeland et al. (2008), noted the high male/female ratio for various firefly species including *P. carolinus*. If future studies show male guarding of female pupae or adults to be a common behavior, then it could be possible that human observers simply never see some of the females who could be mated as soon as they eclose, thus slightly skewing the perceived operational sex ratio of these polyandrous females.

CONCLUSIONS

Unlike so many other firefly sites in the USA and the world, the GSMNP fireflies are relatively unaffected by light pollution and habitat destruction, although human presence is certainly increasing (GSMNP 2009). I hope that these observations on flash behavior, mating systems, natural history, and parasitoid challenges will help in the management, conservation, field identification, and understanding of *Photinus carolinus* and ultimately other Lampyridae. No species can be properly conserved until it can be easily identified and its life history is known. After 18 years

of studying *Photinus carolinus* and a lifetime of appreciating their display as a thing of magic and beauty, I am constantly humbled by how much remains to be learned about this tiny bright creature.

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