

Landing distance in a synchronic North American firefly

JONATHAN COPELAND¹, ANDREW MOISEFF² and LYNN FAUST³

¹Department of Biology, Georgia Southern University, Statesboro, GA, U.S.A., ²Department of Physiology and Neurobiology, University of Connecticut, Storrs, CT, U.S.A. and ³11828 Couch Mill Road, Knoxville, TN, U.S.A.

Abstract. The flash communication system of *Photinus carolinus* in Great Smoky Mountain National Park (Tennessee) is characterized by male firefly synchrony. *Photinus carolinus* males signal a conspecific female with synchronic trains of flashes. A solitary responding female attracts several males, which is not common in North American rover fireflies. The female and the group of males that she attracts are called a cluster. It is hypothesized that the first male attracted to the female would land closer to the female than would additional males because there would be less tendency for visual confusion. This hypothesis is explored under controlled conditions by replacing the responsive female with an appropriately flashing light-emitting diode (LED) located in the center of a flat target area. When infra-red videography is used to measure the first male and the additional males' landing distances from the counterfeit female (LED), most fireflies land within 15 cm of the target LED, and the first male does not land closer than the additional males. It is suggested that cluster formation is a by-product of male synchrony and is facilitated by the tendency of males to land near, but not on, females.

Key words. Bioluminescence, fireflies, insects, landing, mating behavior, synchrony.

Introduction

Nocturnal flying animals have evolved sophisticated, sensitive and effective systems to detect, accurately locate, and obtain a mate or prey (Feng & Ratnam, 2000; Hoy, 1991; Miller & Surlykke, 2001; Robert & Goepfert, 2002; Konishi, 2003). Male fireflies are nocturnal insects that detect a receptive female at a distance, locate her in space, court and mate. They rely on their visual system to respond to photic signals (flashes) based on timing (Buck, 1937; Lloyd, 1966; Lloyd, 1971; Carlson & Copeland, 1985). The flash is a species specific Morse code-like signal system that is dependent on the timing (interval and delay) between a male's species specific flashes and the responding conspecific flash.

When only one male and one female are involved, the mating protocol in its simplest form consists of recognition, which leads to localization, courtship and mating in that sequence (Mast, 1912; Barber, 1951; Lloyd, 1966; Lewis &

Lloyd, 2003). However, when the number of males flying and flashing is more than one, they can simultaneously attempt to court the same female (Carlson *et al.*, 1975). This is called flash competition and the males are called rival males (Carlson *et al.*, 1983, 1988; Carlson & Copeland, 1985). Multiple males approach the female by air or ground and, eventually on the basis of certain flash parameters, size and agility (Vencl & Carlson, 1997), one male copulates with the female (Carlson *et al.*, 1975).

In other species, the ratio of male to female fireflies becomes large (Buck, 1938, 1988; Mauer, 1968; Otte & Smiley, 1977; Copeland & Moiseff, 1995). For example, in three species of North American rover firefly (*Photinus pyralis*, *Photinus consimilis* and *Photinus carolinus*), courtship normally involves many males and a single female. As is the case with all fireflies, the flying male must locate the female, land near her, find her and mate. However, with many males present, flashing and landing, the female signal can occur amidst much conflicting (male) signal noise (Mauer, 1968; Otte & Smiley, 1977; Buck, 1988; Copeland & Moiseff, 1995).

Flying male *P. carolinus* produce a species specific flash pattern that consists of a 2–3 s train of four to eight flashes

Correspondence: Jonathan Copeland, Department of Biology, Georgia Southern University, Statesboro, GA 30460-8042, U.S.A. Tel.: +1 912 0681 0529; fax: +1 912 0681 0845; E-mail: copeland@georgiasouthern.edu

repeated rhythmically every 6–12 s. When more than one male is present and flashing in an area, the males flash synchronously (Copeland & Moiseff, 1995). A female responds to the flying male's flash by producing one to four double-peaked flashes at a delay of approximately 3 s. The courtship flashing of *P. carolinus* males with a female is characterized by many males walking rapidly, often in circles, in the vicinity of a responding female (Moiseff *et al.*, 2001), and this group of several males and a single female is called a cluster.

Because mating group formation is rare in North American fireflies, and because landed congregations of males are only regularly found in synchronic fireflies in North America (*P. carolinus*, *P. pyralis*, *P. consimilis*, and *Photinus jamaicensis*) and synchronic fireflies in Southeast Asia (*Pteroptyx malaccaae*, *Pteroptyx tener*, *Pteroptyx valida* etc.), it is of interest to investigate how the cluster is formed, how the cluster influences mating, and what the contribution of synchrony might be to the development of a cluster.

Materials and methods

The landing distance, defined as the distance from the male's landing spot to the light-emitting diode (LED), was studied in *P. carolinus* in June 2003 and 2006 from 09.20 h to 23.30 h along hiking trails in Great Smoky Mountains National Park (Tennessee) (Permit #: GRSM-2006-SCI-0027).

A Sony camcorder (DCR-TRV120; Sony Corp., Tokyo, Japan) in Nightvision mode was used to record and later measure a male firefly's landing distance from the LED. To provide maximal control over the flash signal, a green LED was triggered manually to produce double-pulsed flashes that acted as counterfeit female flashes. The flashes were rectangular in shape (intensity vs. time) unlike the Gaussian shaped curve of the natural firefly flash. The intensity of the LED's flashes were adjusted to be less than that of *P. carolinus* to insure that the stimulus was not supernormal. The counterfeit female's response was delayed 1–3 s from the last male flash.

Because the substrate was uneven and because the work was undertaken in darkness, to determine the landing distance from the LED, a white poster board target (30 × 30 cm) was used with concentric circles drawn at 5-cm intervals. This target arena was placed along the surface of a hiking trail in an area containing *P. carolinus*. The camcorder was located 2.0 m above and behind the target's centre and the LED was placed in the centre of the target.

Each trial was 3–8 min in duration. The end of each trial was determined arbitrarily. A trial began when the first firefly landed on the target. The first firefly to land (and sometimes the only firefly to land, $n = 9$) was termed the 'solo' firefly. Because no other fireflies were present, it was assumed that 'solo' fireflies were responding to the LED alone (i.e. not to other landed fireflies). All subsequent fireflies were termed 'additional' (i.e. all non-solo landed males). Some of the fireflies were seen landing 30–50 cm from the

centre of the target or were already on the ground when the trial began. These were not counted because the landing distance could not be measured against the dark background dirt. After each trial, the target was moved 3–5 m along the hiking trail.

Caged or uncaged females were used to observe male and female behaviour. A single female was placed within a closed, clear Petri dish (9 cm in diameter) or in a clear-stoppered glass vial (2 oz, 5 cm in length). Flash behaviour and firefly movements were recorded by the tripod-mounted camcorder and by voice descriptions.

Results

Male landing behavior in the field

In a natural courtship, a *P. carolinus* female responded to the species-specific flash pattern of a flying *P. carolinus*. The female produced one to four flashes and each flash was double-peaked. The male, still flying, turned toward the responding female, sometimes hovered, and landed. After landing, the male walked towards the female, although some did not exhibit any clear orientation towards the female. The landed male flashed intermittently and, after the female's flashed response (to himself or to another male), proceeded to move in the female's direction. In the natural environment, the terrain over which the male walked or jumped contained vegetation that could act as obstacles to moving directly to the female. Courtships on the ground sometimes lasted for less than 1 min but were usually longer. We did not follow courtships in the field longer than 45 min due to time constraints. Successful courtships in the field ended with a female and male *in copulo* for as long as 7–8 h.

Target and LED

A target comprising an LED on a white posterboard background provided a landing area around the LED (i.e. counterfeit female) that was free of any obstacles between landed males and the LED. Once the target was deployed, one to three double-peaked counterfeit female flashes were presented 1–3 s after a train of male species-specific flashes. The counterfeit female flashes attracted flying male *P. carolinus*. The time to attract males to the target depended on the abundance of males flying in the area of the target and could be as rapid as few seconds after the counterfeit flashes were produced. Because the target was placed in the field among naturally flying males, factors such as the number of males in the vicinity, the male firefly's elevation about the ground, light intensity and flight path could not be controlled.

Male landings were usually preceded immediately by a hovering flight or an apparent dive. Landings started 0.01–1 m above the target. To determine the landing distance of a male from the LED, measurements were made (during videotape playback) of the landing distance of a 'solo' male and

all subsequent ('additional') fireflies to land. Landing occurred over the entire measurement range (1–30 cm), but occurred more often in the 1–15-cm class than in the 16–30-cm class (χ^2 , goodness of fit, $P < 0.05$; Fig. 1). There was no significant difference between the total 'solo' and total 'additional' landing distances (χ^2 , goodness of fit, $P > 0.05$; Fig. 1). When the landing distances of 'several' males were viewed in sequence, no pattern was seen. For example, one male might land near the LED (1–5 cm) and the next two far from the LED (26–30 cm) and the next one near the LED.

To determine the direction that a male firefly faced when he landed, landings were tallied as toward the LED or away from the LED (Table 1). The direction that the males walked immediately after landing was also tallied (Table 1).

Fewer 'solo' fireflies faced the LED when landing on the target than faced the LED when 'additional' fireflies were viewed (χ^2 , $P < 0.05$, goodness of fit; Table 1).

More males landed facing away from the LED (χ^2 , $P < 0.05$; Table 1), but there was no difference in the number that subsequently walked toward the LED (χ^2 , $P > 0.05$).

Cluster behaviour

Typically, a *P. carolinus* female on the ground or a shrub was surrounded by males (a cluster). (Single male–female pairs were occasionally found late in the night's flashing period, when most of the males were no longer flying).

There was a loose structure to the cluster. The males closest to the female (within 20 cm of the female) were called nuclear males. They were characterized by their fast walking, frequent turning, or loitering in the neighborhood of the female. Only occasional flashes were produced by nuclear males, and these flashes were single flashes or an occasional male species specific flash. Males also landed outside of this nucleus (> 20 cm from the female) and these individuals were referred to as peripheral males. By contrast to the

Table 1. The direction the firefly faces when landing and the direction the firefly walks in once landed.

	Land		Walk	
	To LED	Not to LED	To LED	Not to LED
First male to land	10	27	16	21
First male to land and all subsequent males	38	75	48	53
	χ^2 , $P < 0.05$		χ^2 , $P > 0.05$	

LED, Light-emitting diode.

nuclear males, peripheral males produced the species-specific flash regularly and synchronized their flashes with one another or with the flying flashing males in their vicinity. Clusters containing as many as 23 nuclear males were found, but the average cluster size was 6 ± 3.1 nuclear males ($n = 9$).

Flashing from nuclear males had an irregular interflash interval and occurred infrequently. Suddenly, a rapid flashing occurred from the nuclear males from different geometric positions around the female. This flashing looked like flash bulbs going off on different sides of the female. These flashes were not species specific flashes and showed no temporal relationship to the flashing of flying male fireflies. The rapid flashing occurred over a period of seconds, not minutes.

When close inspection of the cluster prior to mating was possible, it was observed that the nuclear males would vigorously mount each other or the courting female or both. Piles of grappling males formed and engaged in extensive grappling, walking, attempted coupling. The term frenzy refers to this highly energetic group behaviour.

After a variable interval, the courting males found the female. The female did not necessarily copulate with the first male to reach her. A female could walk away from a male(s), toss the male(s) off her dorsal surface, or allow stage I

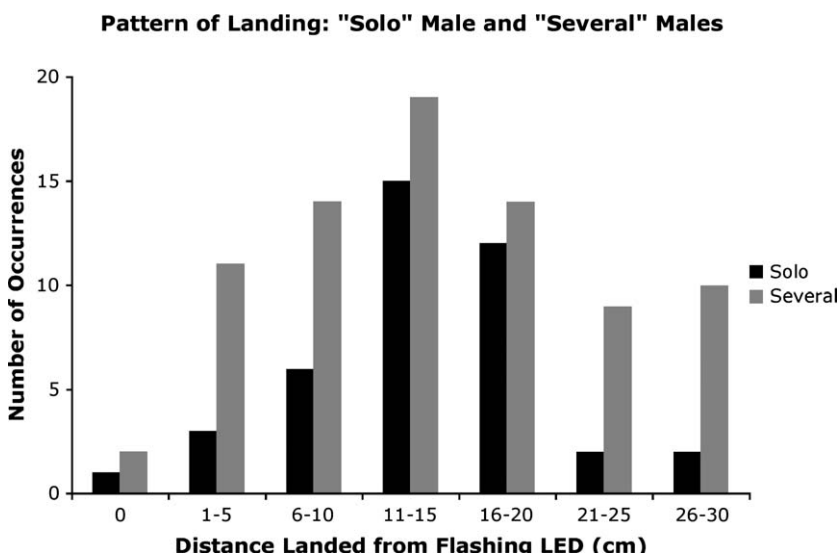


Fig. 1. Landing distance of individual fireflies and sequentially landing groups of fireflies. Individual fireflies are marked 'solo' and sequentially landing groups of fireflies are marked 'additional'. In both 'single' and 'additional' categories, there were more fireflies in the 1–15-cm category vs. the 16–30-cm category (χ^2).

mating to begin but not proceed (Fig. 2) (Cratsley & Lewis, 2005).

In stage I mating, the male and female stood dorsal side up, both facing the same direction with the male on top of the female (Fig. 2, top). A male in stage I might be displaced by another male or might not be accepted by the female. In stage II, male and female were posterior-to-posterior in a straight line (Fig. 2, bottom). At this point, the female sometimes began to walk, pulling the (smaller) male behind her into the leaf litter. A male could produce the species-specific flash when *in copulo*, but this was not a frequent occurrence. Similarly, the female *in copulo* was observed (although rarely) emitting her double-flash in response to flashing by other males. Throughout stage I, rival males tried to uncouple the mating pair mechanically.

Frenzy continued until a male–female pair had formed *in copulo*, and it stopped when the mating pair were in tail-to-tail, stage II mating (Fig. 2, bottom). At this time, almost all of the non-copulating males decamped quickly.

Discussion

Landing distance

It is hypothesized that a ‘solo’ male would not be confused by other males in the vicinity and would land closer to the counterfeit female than ‘additional’ males. On average, more *P. carolinus* males (‘solo’) land near a flashing LED (1–15 cm) and fewer land at a distance. The same is true of ‘additional’ males. This suggests that the males were not confused or distracted by extra males.

For ‘solo’ males, direct male–male competition cannot occur after landing because only one male firefly interacts with the female. Thus, the range of landing distances exhibited by ‘solo’ males suggests that the variability in distance is inherent in the male’s landing behavior and not due to competition among males. The source of this variability remains to be determined, but it could lie in the structures responsible

for detection and/or processing of visual information or, alternatively/additionally, in sensory–motor coordination. For ‘additional’ males, the possibility exists for male–male competition to occur prior to landing, but their landing distance is not significantly different from that of ‘solo’ males, suggesting that competition between males does not occur at this point in mating behaviour.

The assumption made in the present study is that the goal of the males is to locate, land and court the female represented by the counterfeit LED. If this is the case, males would be expected to land as close to the counterfeit female as possible, and the landing distance would represent the precision or accuracy of the targeting. However, in the present study, males have perfect accuracy (i.e. three males land on the LED) in only three trials. These results could be interpreted as indicating error in the ability of males to locate and/or land on the female but, if there is a selective advantage for landing near, but not on the female, the apparent error could represent the desired outcome.

Another possibility is that the landings could be an adaptation to avoid predation. Predation by harvestmen and web weaver spiders is possible (Lloyd, 1971). In the present study, harvestmen were observed carrying a glowing firefly lantern, suggesting that there could be harvestman predation on fireflies in the study site, but harvestmen were also observed walking by and not preying upon courting flashing fireflies. Thus, harvestman predation may occur, but this is probably not a strong selection pressure.

Predation by web building spiders is not uncommon. Repetitively flashing captured *Photinus* males are often found struggling in a web. The effect of one repetitively flashing captured male on the landing of another male has not yet been investigated. We also do not know the ultimate fate of a firefly that has been trapped in a spider’s web. Spiders are occasionally seen envenomating and wrapping fireflies but, in some cases, the captured firefly is cut free by the spider.

Predation by *Photuris* females is also possible. A few species of *Photuris* females are reported to prey on heterospecific males by employing a flash similar to the flash of a heterospecific female (Carlson & Copeland, 1985). This is termed aggressive mimicry (Lloyd, 1965, 1971; Nelson *et al.*, 1975; Venzl & Carlson, 1997). Landing at a distance from a potential predatory heterospecific female might allow a male additional time to assess the veracity of the female’s flash and potentially differentiate between con- and heterospecifics. Thus, a 15-cm landing distance might provide a safety margin for the male *P. carolinus* to avoid a predatory *Photuris* female.

Two different flash patterns are produced by flying flashing *Photuris* males in fields where *P. carolinus* is found. Flying flashing *Photuris* females producing a sequence of single flashes are also observed walking or stationary flashing females can produce single or doublet flashes on the ground. These *Photuris* species have not been identified, and it is not known whether these flashes are conspecific *Photuris* courtship flashes or predatory flashes. To be predatory flashes, the *Photuris* female flashes would have to be shown

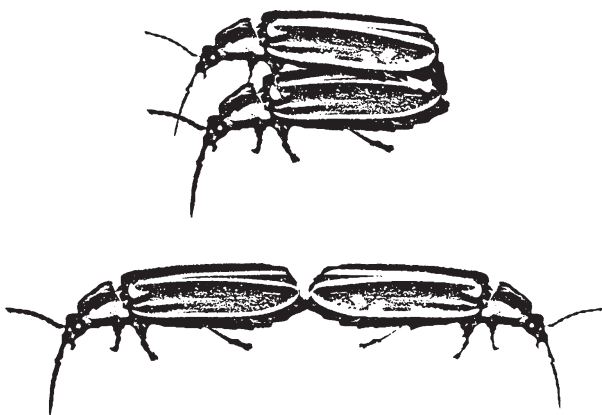


Fig. 2. Stage I (top) and stage II (bottom) mating. Drawings illustrate mating positions.

to attract *P. carolinus* males and that attraction would have to lead to capture and subsequent ingestion of the *P. carolinus* by the *Photuris* female.

Landing distance could be influenced by the optics of the firefly's compound eye. Many insects are near-sighted (Klowden, 2003) and a male *P. carolinus* could aim at the LED with each landing, but limitations in the insect's far-sighted vision might limit any spatial acuity. In terms of far-sighted vision, visual resolution is usually not acute in insects (Klowden, 2003). However, a male *P. carolinus* can hop or fly from perch to perch as he moves toward the female, and this probably requires good near-sighted resolution. Little is now known about the characteristics of near- and far-vision in fireflies.

Cluster formation

In fireflies, groups of males near a female are found in synchronous or semi-synchronous species (*P. pyralis*, 'love knot', Mauer, 1968; *P. consimilis*, Otte & Smiley, 1977; *Pt. tener*, Case, 1980); *Pt. malacciae*, Buck, 1988; *P. carolinus*, Copeland & Moiseff, 1995). This raises the possibility that clusters are an emergent consequence of synchrony.

To form a cluster, a responding *P. carolinus* female need only respond (i.e. flash appropriately) to the flashes of a single male. In doing so, she is flashing functionally at a group of several flying synchronizing *P. carolinus* males. In other words, the courtship dialog involves a single courting male directly and, indirectly, all the synchronizing males that can see her. If, after the next burst of male flashes, she now flashes at another male, possibly a new male, more *P. carolinus* fireflies will be attracted. These males will land on average 0–15 cm away from the female creating a cluster.

Thus, cluster formation may be the consequence of a male–female communication channel that is not one-to-one. It may also form by default if the male's target is the female but he is physiologically unable to reach his target exactly. Because there is so little species specific flashing by nuclear males, the cluster is probably not a lek, as proposed to be the case in *Pteroptyx* (Buck, 1988).

The trigger for frenzy is unknown. It could be include photic, chemical, tactile or other triggers. A period of rapid non-species specific flashing occurs and then frenzy is seen, so flashes of light may be involved. Because chemical cues are involved in mating behaviour in other genera, the possibility of their occurrence in the present study is raised (Shibue *et al.*, 2000, 2004; DeCock & Matthysen, 2005). Vencl & Carlson (1997) show that scramble competition occurs in *P. pyralis*, a firefly that forms 'love knots'. The authors suggest that male selection for locomotory skills may be occurring in this species. In *P. carolinus*, once the scramble for the female occurs in frenzy, no flashing occurs.

The triggers for stage I and stage II mating are also unknown. Without flashing, the male(s) finds the female. Because the female, often larger than the male, can throw off any number of males before moving to stage I mating with a

single male, it is likely that the final stage of courtship does not involve photic cues. The same is true for stage II mating.

Cluster formation influences the operational sex ratio (OSR), where OSR is defined as the ratio of the number of males courting a female to the number of females. It is difficult to obtain OSR data for fireflies using a methodology that employs objective measures that are observer-independent (Lewis *et al.*, 2004). Measurements of OSR that rely on competing (near to the female?) males and a female to calculate the OSR are misleading inasmuch as the female's range for distance vision is not known. Accurate measurements of OSR that rely on subjective field observations are difficult because of the inherent uncertainty in identifying individual flying males under conditions of no or low ambient illumination, as well as in determining distances to fireflies at night.

The *P. carolinus* clusters described in the present study represent an environment where multiple males engage in behaviour that culminates typically with one male successfully mounting a female. As such, this represents the OSR. The average cluster size in the present study is approximately 6 : 1 and the highest is 23 : 1 (as seen at the height of the mating season).

Synchrony brings males into proximity with a female and thus raises the population density of males locally. We propose that cluster formation may be the result of a flash communication system where the female's response attracts multiple, synchronously flashing males. However, how cluster formation affects male–male competition or female-choice remains unknown. The present data do not address this aspect of mating behaviour, nor do they differentiate whether the goal of the landing system is to have the male land at a distance to avoid possible predation or to land near or on the female.

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