

THIEVES IN THE NIGHT: KLEPTOPARASITISM BY FIREFLIES IN THE GENUS *PHOTURIS* DEJEAN (COLEOPTERA: LAMPYRIDAE)

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ABSTRACT

Food theft is a common foraging strategy in birds, and many arthropods steal prey trapped by orb-weaving spiders. Some fireflies (Coleoptera: Lampyridae) within the North American genus *Photuris* Dejean (Coleoptera: Lampyridae) are specialist predators which actively hunt for and sequester chemical defenses (lucibufagins) from other fireflies. Here we present the first description of kleptoparasitic behavior by female *Photuris* fireflies, which we have observed stealing wrapped fireflies of the genus *Photinus* Laporte from spider webs. *Photuris* females thus appear capable of three distinct foraging strategies: hawking, aggressive flash mimicry, and kleptoparasitism. We discuss some factors that might have favored the evolution of kleptoparasitism by this specialist predator.

Key Words: foraging behavior, food theft, spiders, lucibufagins, *Photinus*

Kleptoparasitism is a form of interference competition in which one animal steals resources, usually food, from a conspecific or heterospecific individual. The term was first introduced by Rothschild and Clay (1952) to describe the behavior of arctic skuas (*Stercorarius parasiticus* [L.]) stealing food from gulls (Laridae). Kleptoparasitism as a foraging strategy is widespread among birds (reviewed by Brockmann and Barnard 1979; e.g. Radford *et al.* 2010).

Orb-weaving spiders attract numerous kleptoparasites, perhaps due to the spiders' lengthy handling times for prey, as well as to the webs facilitating the capture and storage of multiple prey items (Sivinski and Stowe 1980; Iyengar 2008). The most common thieves associated with orb-weavers are other spiders (Whitehouse 1986; Rypstra 1981; Vollrath 1984), but kleptoparasitic behavior has also been described in such insects as wasps (Jeanne 1972), ants (Leborgne *et al.* 2011), flies (Eisner *et al.* 1991), and scorpionflies (Thornhill 1975).

Here we describe for the first time the occurrence of kleptoparasitic behavior by predatory fireflies in the genus *Photuris* Dejean (Coleoptera:

Lampyridae), which actively seek, grapple for, and pirate certain prey trapped by orb-weaving spiders. We also discuss factors that might favor the evolution of kleptoparasitism in *Photuris*, as this is an unusual foraging strategy for a specialist predator.

Most fireflies do not feed after they become adults (Williams 1917), but certain species within the genus *Photuris* are specialist predators of other lampyrids (Lloyd 1965, 1984, 1997). *Femme fatale Photuris* actively hunt for fireflies in the genus *Photinus* Laporte, from which they sequester defensive compounds known as lucibufagins (Eisner *et al.* 1978, 1997). Previous work has described two foraging strategies used by predatory *Photuris* females: aggressive mimicry of prey courtship signals by these *Photuris femmes fatales* (Lloyd 1965) and aerial hawking (Lloyd and Wing 1983).

MATERIAL AND METHODS

Observations of kleptoparasitism by *Photuris* were made in Hardin Valley along a two-km trail near Beaver Creek in Knox County, Tennessee, USA (35°56'44.02" N, 84°12'24.54" W, elevation

274 m) from mid-June through July, covering the peak of *Photinus* mating seasons from 2006–2011. Habitat consisted of Appalachian oak-hickory forest and margins along open fields. Surveys were conducted by looking for bioluminescent flashes emitted by perched *Photuris*, as well as for the distress flashes that are frequently emitted by fireflies trapped in spider webs (Buschman 1972; Lloyd 1973; Faust 2010; Lewis *et al.* 2012). When a *Photuris* was seen approaching a web, behavioral observations were made using a voice recorder and final outcomes noted and photographed when possible. Sexual identification of kleptoparasitic *Photuris* in the field was not always possible without disturbing these behavior interactions, but when sex could be confirmed, it was noted.

Photuris is a taxonomically difficult group in need of revision, and although the predatory fireflies observed here have been tentatively identified as belonging to the *Photuris lucicrescens* Barber complex (J. E. Lloyd, personal communication), we refer to them here simply as *Photuris*.

RESULTS

Female *Photuris* were often seen flying or perched near or in webs constructed by spiders in the family Araneidae. On nine nights, 12 explicit events and many more incidentally noted episodes of kleptoparasitism were observed from late June until late July over five years. In each case, a female *Photuris* was seen feeding on a silk-wrapped *Photinus* firefly (rarely a *Photuris*) that was hanging in a spider's web. However, the outcomes of these incidents varied. Sometimes these large and active female *Photuris* were able to keep the spider at bay and retain hold of the silk-wrapped *Photinus* firefly (Fig. 1). Sometimes the spider thwarted the theft by: a) aggressively approaching and driving off the female *Photuris*; b) cutting strands to release the female *Photuris* from the web; or c) subduing the female *Photuris* and wrapping her in silk, either alone or with her prey (Fig. 2a). Even when female *Photuris* were wrapped in silk, they occasionally managed to

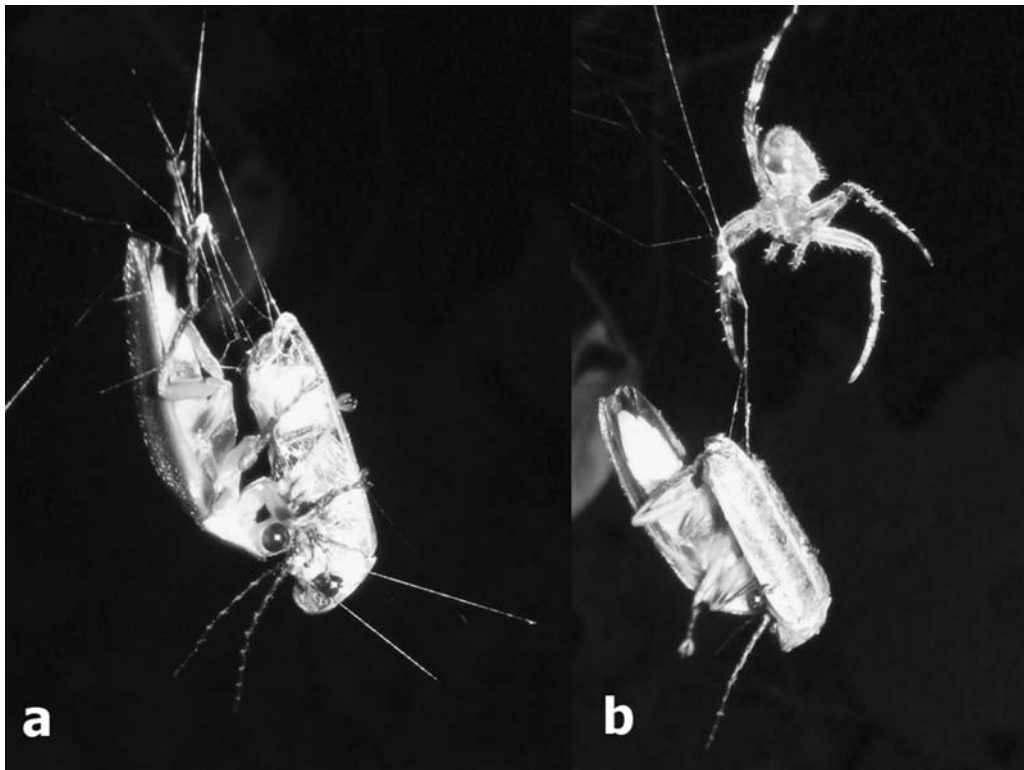


Fig. 1. a) Kleptoparasitism by female *Photuris* sp. on *Photinus pyralis* as prey, b) After a failed attempt to chase away the kleptoparasitic *Photuris*, the spider cut both the kleptoparasitic firefly and the wrapped *Photinus* from the web and commenced web repair while the *Photuris* continued to feed on the wrapped *Photinus* firefly from the ground. (Photos by L. Faust).

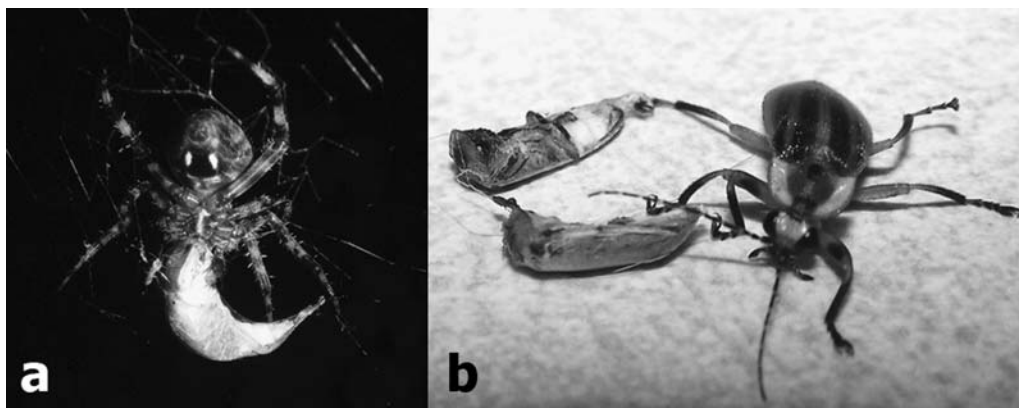


Fig. 2. a) Failed attempt at kleptoparasitism by a female *Photuris* that flew into the web of a large *Araneus* spider which had snared a male *Photinus brimleyi*, but the *Photuris* was quickly subdued and wrapped by the web owner, b) Kleptoparasitic female *Photuris*, which had been wrapped together with its intended prey, has removed most of its silken wrapping but remains tethered to two wrapped male *Photinus* fireflies. (Photos by L. Faust).

escape, though the majority, once wrapped, were eaten by the spiders. In some cases, the spider cut both the female *Photuris* female and its previously wrapped prey out of its web (Fig. 2b). Additional predatory *Photuris* were often seen perched near these spider webs, perhaps waiting to scavenge scraps or to attempt stealing prey again. Similar to the findings of Cangiolosi (1991) with kleptoparasitic spiders, it was noted that when *Photuris* fireflies were captured in webs of relatively smaller spiders, they were not often wrapped but usually cut out. Larger spiders, more similar in size, were more apt to attempt to attack or wrap the *Photuris* firefly.

Such kleptoparasitism by *Photuris*, although not previously reported, appears to be a common phenomenon. The first author initially observed ten incidences of apparent kleptoparasitism by female *Photuris* in July 2006. Table 1 summarizes outcomes witnessed from *Photuris*-spider-prey incidents observed from 2006 to 2011. Note that in this study all observed actively hunting kleptoparasitic *Photuris* were females, but the already captured and silk-wrapped *Photuris* were both male and female.

DISCUSSION

Our observations reveal an entirely new foraging strategy used by female *Photuris* to obtain prey — kleptoparasitism from spider webs. Notes by 20th century *Photuris* expert Herbert Barber (Barber 1951) mention female *Photuris* “quietly feeding” on silk-wrapped *Photinus* males “in an orb web from which the spider had departed.” Our studies reveal that the kleptoparasitic *Photuris* not only scavenge but actively hunt the spiders’ prey by stationing themselves near occupied webs,

“divebombing” into the webs, seizing and feasting on the silk-wrapped prey, often grappling with the spider for the prize, sometimes winning, sometimes losing. The genus *Photuris* includes highly specialized predators that attack mainly fireflies in the genus *Photinus* (Lloyd 1997). Unable to manufacture their own lucibufagins, *Photuris* must obtain these defensive compounds from their prey (Eisner *et al.* 1997). By consuming *Photinus* fireflies, female *Photuris* gain protection for themselves as well as for their eggs (González *et al.* 1999). Studies of these predatory fireflies have previously described two types of foraging behavior: aerial hawking, in which female *Photuris* use bioluminescent signals to find and attack flying prey (Lloyd and Wing 1983); and aggressive mimicry, in which female *Photuris* attract male *Photinus* by mimicking the response given by prey females (Lloyd 1965, 1984).

Because previously described instances of kleptoparasitism involve opportunistic feeders (Iyengar 2008), the occurrence of kleptoparasitic behavior in specialist predatory *Photuris* is quite unusual. However, this interaction does appear to fulfill several of the ecological criteria suggested to facilitate evolution of kleptoparasitic behaviors (Brockmann and Barnard 1979; Iyengar 2008). For *Photuris*, kleptoparasitism of spider webs appears to provide a predictable source of high quality, lucibufagin-containing prey (Eisner *et al.* 1997), as many different *Photinus* fireflies are trapped in spider webs (Lloyd 1973; Day 2011). Furthermore, during peak mating season, multiple *Photinus* are frequently found within a single web (Lewis *et al.* 2012). This kleptoparasitic web-feeding behavior might serve an additional function by aiding the *Photuris* in obtaining the

Table 1. Incidents of attempted or successful kleptoparasitism by female *Photuris* fireflies.

OBS	DATE	TIME	INCIDENT (sex noted when known)	OUTCOME
1	10 July 2006	10:30	<i>Photuris</i> ♀ flew into web, eating silk-wrapped <i>Photinus brimleyi</i> Green ♂. Three <i>Photuris</i> (sex unknown) stationed beside web.	Spider cut both from the web. <i>Photuris</i> ate 20 minutes before being cut out of web along with its prey.
2	10 July 2006	10:45	<i>Photuris</i> ♀ flew into a web to prey on another wrapped <i>Photuris</i> sp. ♂.	Spider cut out both.
3	11 July 2006	10:04	<i>Photuris</i> ♀ in web eating <i>Photinus</i> sp. ♂.	Spider cuts most strands and retreats.
4	12 July 2006	9:57	Silk package contained two <i>Photinus</i> ♂ and one <i>Photuris</i> ♀ which had been attracted to steal.	<i>Photuris</i> was more loosely wrapped on top of the tightly wrapped <i>Photinus</i> and struggled free within the hour. Spider avoids silk bundle.
5	16 July 2006	9:30–11	Survey of 6 incidents of <i>Photuris</i> hunting in webs observed on 2-km trail in one evening, sex not recorded.	Reality of phenomenon now confirmed. Year 2006 of extremely high <i>Photuris</i> density.
6	July 2007	9:45–11:30	General observations-many <i>Photuris</i> ♀ hunting in and near webs this month.	<i>Femme fatale Photuris</i> usually escape the silk. <i>Photuris frontalis</i> LeConte (congener complex) ♂ are usually eaten when caught. <i>Photinus</i> , <i>Photuris</i> , <i>Phausis</i> Say, <i>Pyraclomena</i> LeConte prey usually eaten but occasionally cut out of webs with/without <i>Photuris</i> predator present.
7	8 July 2008	10:15	<i>Photuris</i> ♂ and <i>Photinus</i> ♂ in three webs	All wrapped in silk. None escaping.
8	22 July 2008	10:05	<i>Photinus pyralis</i> L. ♂ wrapped in web along with two other singly wrapped fireflies - <i>Photinus</i> ♂ and <i>Photuris</i> sex unknown	One <i>Photinus</i> and one <i>Photuris</i> eaten. One <i>Photinus</i> escapes and removes silk by next morning. *only observed incidence of wrapped <i>Photinus</i> escaping web and clearing silk from body.
9	27 July 2009	9:41	<i>Photuris</i> ♀ and <i>Photinus</i> ♂ wrapped next to one another in web	Spider feeds on both prey.
10	19 June 2011	9:15	Spider wrapped a <i>P. pyralis</i> ♂. A <i>Photuris</i> ♀ was observed flying and landing on a leaf next to the web and subsequently flew in and commenced eating the silk-wrapped prey.	By 10 pm, the spider had returned to the firefly prey remains and a <i>Photuris</i> , we assume it was the same individual, was observed perched on a leaf next to the web.
11	30 June 2011	10:00	<i>Photuris</i> ♀ landing and feeding on silk-wrapped <i>P. pyralis</i> ♂ prey in web.	After 5 minutes, the <i>Araneus</i> spider tries and fails to chase the <i>Photuris</i> away. The spider then cut the web, causing both prey and kleptoparasitic <i>Photuris</i> to fall, while the spider began repairing its web. <i>Photuris</i> continued to eat the <i>Photinus</i> from the ground.
12	30 June 2011	10:30	<i>Photinus brimleyi</i> ♂ caught in a spider web; <i>Photuris</i> ♀ flew into the web, attempting to steal the prey.	The larger spider quickly wrapped the <i>Photuris</i> tightly in silk, ensnaring both original prey and kleptoparasite into one flashing package. Both became spider's prey.

needed lucibufagins, while avoiding a mouthful of white, sticky reflex bleeding (Blum and Sanasi 1974) emitted by many *Photinus* during attack. *Photinus* can often escape while the *Photuris femme fatale* struggles to clear its glued mouthparts (Lewis

et al. 2012); yet these immobilized *Photinus*, often covered in dried, white hemolymph under the silk wrapping, have already emitted their defensive bleeding (Bateman and Fleming 2009) when the spider first attacked.

Another novel approach to obtain lucibufagins by *Photuris femina fatales* occurred in four episodes in late June and mid-July 2011 when four newly captured *Photuris* were observed by the first author to scavenge dead (recent to 24+ hours old) *Photinus*. This corpse-eating behavior could possibly help explain why local *Photuris* become more abundant toward the end, instead of before the peak, of the main *Photinus* firefly season.

Male fireflies, both *Photinus* and rarely *Photuris*, are more frequently captured in webs (Lewis *et al.* 2012), presumably because more males are flying and searching for mates. On 14 June 2007, the first author observed a female *Photuris* capture a male *Photinus* while perched 1 m aboveground on vegetation. Within minutes, a male *Photuris* landed and began copulation while the female continued to feed, a behavior also reported by Day (2011). Further studies are needed to determine if male *Photuris* might also station themselves near webs to locate potential female mates who are available, yet occupied while feeding, thus ensuring a “safer” copulation by minimizing the courting male’s risk of becoming a meal for the *femina fatale Photuris*.

It seems likely that predatory *Photuris* can facultatively switch among these foraging strategies as conditions change. When orb-weaver density and web capture rates of *Photinus* are high, it may become more efficient for female *Photuris* to resort to thievery.

This alternative foraging strategy is not without risk, however, as host spiders were sometimes able to subdue, wrap, and later eat *Photuris* interlopers. Another insect kleptoparasite of orb-weavers, scorpionflies in the genus *Panorpa* L., can escape from webs by regurgitating a brown fluid that deters spiders and dissolves the silk strands (Thornhill 1975). For *Photuris* fireflies, the success of this feeding strategy seems to depend on the relative size of the kleptoparasite and the spider. *Photuris* fireflies are relatively large, agile, and long-legged, which may give them a size advantage in direct contests with spiders over prey ownership. This may also enhance their ability to escape from webs, even when they are partially wrapped in silk.

Spider hosts are negatively affected by this interaction in two ways. When successful, kleptoparasitism by *Photuris* directly reduces the number of prey available to the host spider. Even when *Photuris* are not successful in stealing prey, their struggles often damage the web; spiders appeared to avoid this by cutting *Photuris* out of their webs.

Finally, it is worth considering what mechanisms kleptoparasitic *Photuris* might use to locate *Photinus* fireflies that are trapped in spider webs. When fireflies become trapped in spider webs, they often emit rhythmic flashes of light or continuous glows (Faust 2010; Lewis *et al.* 2012). Such visual signals seem

most likely to attract *Photuris*, as these predators rely on flash cues to locate prey when they are hunting on the wing (Lloyd and Wing 1983; Woods *et al.* 2007) or they use aggressive mimicry (Lloyd 1965). Yet, chemical attraction of kleptoparasites is also possible. When certain stink bugs (Heteroptera: Pentatomidae) and squash bugs (Heteroptera: Coreidae) are caught in spider webs, they release a defensive spray containing *trans*-2-hexenal and hexanal, which attracts kleptoparasitic milichiid flies (Eisner *et al.* 1991). When *Photinus* fireflies are disturbed, they release lucibufagins through reflex bleeding (Blum and Sanasi 1974; Eisner *et al.* 1978), and it is possible that these chemicals might be detected by kleptoparasitic *Photuris*.

There are many fascinating questions about this novel firefly foraging behavior that remain unanswered. What specific factors trigger a shift by female *Photuris* from predatory to kleptoparasitic foraging? Are male *Photuris* ever kleptoparasitic? Do male *Photuris* perch and search near webs to find mates? Are *Photuris* only attracted by the visual cues from flashing or glowing prey, or do they wait by empty webs until appropriate prey is caught? Is there intra-specific kleptoparasitism *i.e.*, do female *Photuris* steal prey from one another? Could scavenging dead and dying fireflies, using neither flash cues nor movement in detection of prey, be an additional strategy used by these predatory *Photuris*? Further study is needed to explore these questions.

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