NOTES ON THE LIFE HISTORY AND MATING BEHAVIOR OF *ELLYCHNIA CORRUSCA* (COLOEPTERA: LAMPYRIDAE)

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ABSTRACT

Population dynamics and reproductive activity were examined in a Massachusetts population of the common diurnal firefly, *Ellychnia corrusca*. Although closely related to nocturnal beetles in the genus *Photinus*, *Ellychnia* lack adult light organs. A mark-recapture study of overwintering adults demonstrated low winter mortality and supported the hypothesis that adults overwinter for a single year. By dissecting males and females sampled throughout late winter and spring, it was found that adults become reproductively active in early March, when male seminal vesicles first contained sperm and female ovaries first contained mature oocytes. Both sexes mated multiply during the approximately six-week mating season (early April through mid-May), and copulations lasted up to 28 h. Adults collected in fall had higher abdominal fat body volumes than those collected in spring, and females contained more fat body than

males. The life history and mating behavior of *E. corrusca* are discussed in comparison to *Photinus* fireflies.

Key Words: diapause, firefly, *Photinus*, population dynamics

RESUMEN

Dinámicas de población y actividad reproductiva fueron examinadas en una población de Massachussets de la luciérnaga común diurna, *Ellychnia corrusca*. Aunque están cercanamente relacionados a escarabajos en el genero nocturno *Photinus*, adultos de *Ellychnia* carecen órganos de luz. Un estudio de marca-recaptura de adultos que sobre-inviernan demostró mortalidad baja en invierno y apoyo la hipótesis que adultos sobre-inviernan por solo un año. Al disecar machos y hembras muestreados durante un periodo tarde en el invierno y primavera, se encontró que adultos se convierten activos reproductivamente temprano en Marzo, cuando las vesículas seminales contienen esperma por primera vez y los ovarios de las hembras contienen oocitos maduros por primera vez. Ambos sexos aparearon múltiples veces durante la temporada de apareamiento de aproximadamente seis semanas (temprano en Abril hasta mitad de Mayo), y copulaciones duraron hasta 28 h. Adultos colectados en otoño tuvieron volumen de grasa de cuerpo abdominal mas altos que esos colectados en primavera, y las hembras contuvieron mas grasa de cuerpo que los machos. La historia de vida y comportamiento de apareamiento de *E. corrusca* es discutido en comparación a luciérnagas de *Photinus*.

The *Ellychnia corrusca* L. species complex enjoys a wide geographical distribution across the eastern United States (Fender 1970). These beetles are conspicuous early spring inhabitants of forest habitats, yet little has been published on their life history or mating behavior. Williams (1917) reported that captive *E. corrusca* adults overwintered and mated in early spring. Adults have been described feeding on maple sap in spring, and on aster and goldenrod flowers in fall (Dillon & Dillon 1972).

In contrast to most other lampyrids, adult *Ellychnia* are diurnally active and are not luminescent, although light organs are present in larvae (Williams 1917). Based on external morphology, the genus *Ellychnia* has been placed in the same subtribe (Photinina) as the nocturnal firefly genus *Photinus* (LeConte 1881, McDermott 1964). A recent phylogeny based on mitochondrial cytochrome oxidase II sequence confirms a close association between *Ellychnia* and *Photinus*, and suggests quite recent divergence of these two genera (van der Reijden 1996).

E. corrusca also shows internal reproductive anatomy similar to that described for several *Photinus* species (van der Reijden et al. 1997, Rooney & Lewis 1999). During copulation, males transfer a complex, proteinaceous spermatophore to females. The male spermatophore is internally digested over the next several days within the female reproductive tract. Allocation of spermatophore-derived protein differs markedly between *E. corrusca* and *Photinus ignitus* (Rooney & Lewis 1999): *E. corrusca* females allocate male-derived protein primarily to somatic tissue (particularly fat body), while *P. ignitus* females allocate such nutrients mainly to maturing oocytes.

This study was conducted to elucidate additional aspects of *E. corrusca* life history and mating behavior. Overwintering survival was studied using mark-recapture methods, and reproductive status was monitored by dissecting males and females sampled at intervals throughout the winter and spring. Additional observations of feeding and mating behavior were made both in the field and laboratory.

Materials and Methods

Study Populations

The main study population occurred in a mixed pine and deciduous forest at the Habitat Sanctuary of the Massachusetts Audubon Society, located in Belmont, MA. Additional feeding observations were conducted on field populations at Wellesley College, Wellesley, MA, and additional observations of mating behavior were conducted in Lincoln, MA. The taxonomy of *Ellychnia* species has been difficult to resolve, especially within three complexes in the eastern United States (Fender 1970). Following Fender (1970), we refer to these large-bodied *Ellychnia* as *E. corrusca*, and individuals in this population ranged from 6 to 13 mm elytral length (Fig. 1).

Mark-recapture Study

The Belmont site was chosen for mark-recapture because the *E. corrusca* population is largely confined to a discrete area, occupying grooves in the bark of three Eastern black oaks (*Quercus velutina*): on adjacent trees there were few or no beetles. To estimate monthly survival of overwintering adults, *E. corrusca* were marked and resampled approximately every month from their fall appearance (October 1997) to spring dispersal (April 1998). Beetles were given date-specific marks on their left or

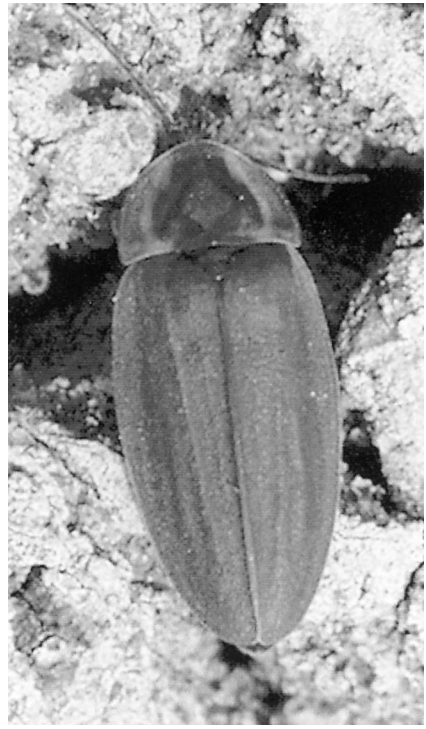

Fig. 1. Adult *E. corrusca* in overwintering position on bark of *Quercus velutina* (beetle length 1.3 cm).

right elytron using different colors of Mitsubishi UniPaint Fine Line PX-21 markers. At each census, the three *Q. velutina* trees were carefully searched from the ground up to 2 m height, and all observed *E. corrusca* adults were marked. Existing marks were recorded and used to determine for each beetle when it had most recently been caught. A total of 825 individuals were marked. Survival was estimated using Jolly-Seber methods designed for open populations (Greenwood 1996). Emigration out of the marked population during winter months was probably negligible since no *E. corrusca* adults were observed flying between late September and mid-March. Beetles did show limited walking movement along the bark surface during this time, but were never observed moving between trees. Thorough search of tree surfaces at each census and low overall mortality/emigration helped ensure that the Jolly-Seber assumptions of equal catchability of marked and unmarked beetles and no effect of marking on mortality or emigration were both met.

The proportion of the population surviving (and remaining in the study area) from the i^{th} to the $(i + 1)^{th}$ census, Φ_i, was calculated as:

$$\Phi_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}$$

where $\hat{M}$ is the number of known previously-marked individuals present, m_i is the number of previously-marked individuals sampled at the i^{th} census, and R_i is the number of individuals released after the i^{th} census (Greenwood 1996).

Timing of Reproductive Activity

To determine when *E. corrusca* adults become sexually mature, 10 males and 10 females were collected biweekly from 26 Feb to 19 April 1998, and monthly from August 1998 to November 1999. Individuals were frozen and later dissected to determine their reproductive status. Van der Reijden et al. (1997) provide details of male and female reproductive anatomy for *Photinus ignitus,* which closely resembles that of *E. corrusca* (Rooney and Lewis 1999). In males presence/absence of sperm bundles within the seminal vesicles and presence/absence of a pre-spermatophore within the spiral accessory glands were recorded. In females the number of mature oocytes (distinguished by diameter ≥600 μm) and presence/absence of developing follicles within the ovarioles were recorded. In addition, presence/absence of sperm in the female's spermatheca (sperm storage organ) was assessed by examining spermathecal contents at 400X.

To examine seasonal changes in stored resources for overwintering *E. corrusca* adults, the volume of abdominal fat body was estimated using the same beetles collected above. For each beetle, fat body nodules were carefully dissected out and placed in a graduated 1.5 ml microcentrifuge tube; samples were spun 30 s at 1000 rpm (Eppendorf microcentrifuge model 5415C), after which total fat body volume (in μl) was measured to the nearest 10 μl. Fat body differences between fall (August through November) and spring (late February through May), as well as sex differences, were examined using a fixed effects two-way ANOVA.

Mating and Feeding Behaviors

Feeding observations on *E. corrusca* adults were made in May 1997 and April-June 1998 at the Wellesley and Belmont sites. General behavioral observations were made throughout winter 1998-99 at the Belmont site. Mating behavior was observed at

times ranging from 0500 to 2100 hours during spring 1998 at Lincoln and Belmont sites. During April and May 1998, copulation durations and frequency of remating were determined from beetles kept in the laboratory in population cages and in pairs under natural photoperiod at room temperature (18-24°C).

RESULTS

Overwintering Mortality and Population Dynamics

Survival of overwintering *E. corrusca* adults estimated by mark-recapture at the Belmont site was high, with monthly survival ranging from 88% to 99% (Fig. 2). In spite of this high overall survival, additional observations suggest freezing and predation may be potential sources of mortality. During periods of below-freezing temperatures, several immobile, intact, adults were found on their backs in snow; some revived when warmed but one individual was dead. In addition, detached *E. corrusca* wing covers (some with V-shaped notches) were found at the base of overwintering trees in January and again in mid-April. In neither case was there any apparent mortality bias for marked vs. unmarked beetles.

While the *E. corrusca* population remained fairly constant through the winter (November through March), number of adults on trees declined dramatically beginning in April and continuing through May (Fig. 3). During late fall and winter (from 28 September to 7 March) adults were never observed to fly and could not be induced to do so, but by 18 March beetles flew back to the tree when held a short distance away and released. Starting in early March, adults also showed increased movement along the bark surface. Mating pairs were observed on trees from early April to mid-May.

From June through July 1998, no *E. corrusca* adults were found on trees at the Belmont study site, but adults began to congregate on the same three *Q. velutina* trees the following August (Fig. 3). Although a total of 825 *E. corrusca* adults had been marked the previous winter and spring, there were no marked beetles among these fall adults.

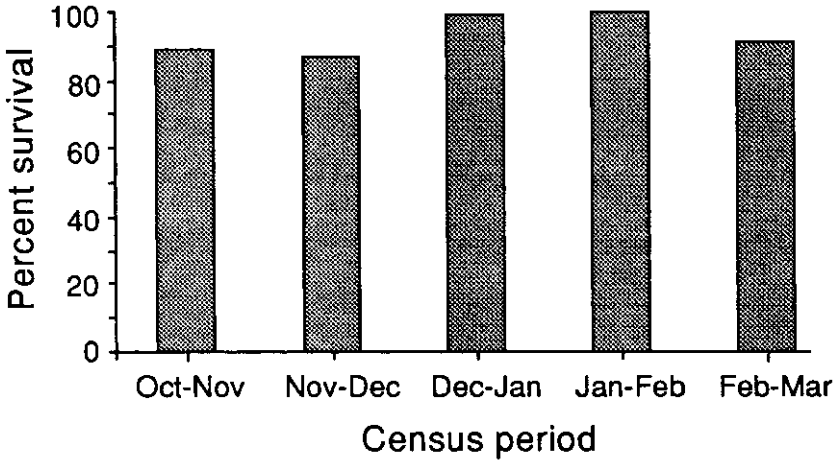

Fig. 2. Monthly survival determined by mark-recapture in a population of *E. corrusca* adults in Belmont, Massachusetts during 1997-98.

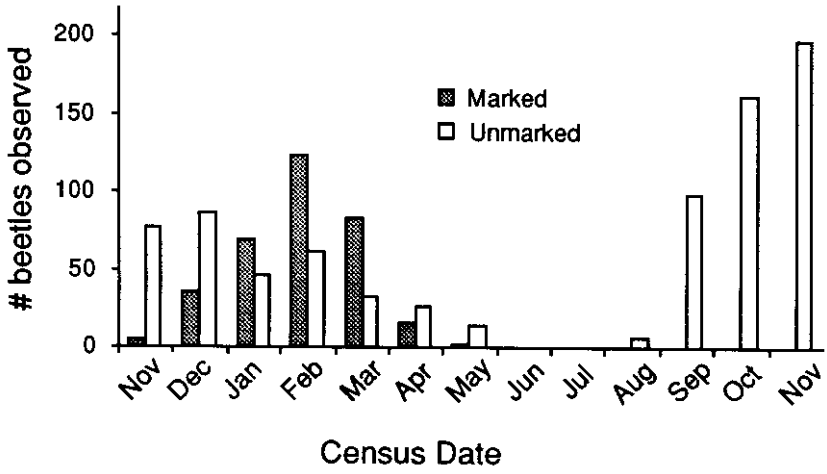

Fig. 3. Number of marked and unmarked *E. corrusca* adults during monthly censuses in Belmont, Massachusetts population during 1997-98.

Timing of Reproductive Activity

Although no mating pairs were observed until early April, there was a steady increase in reproductive readiness exhibited by both sexes beginning in mid-March. In females, this was marked by increasing numbers of mature oocytes present in female reproductive tracts (Fig. 4A) as well as by an increase in the percentage of females that contained sperm in their spermatheca (Fig. 4B). In contrast, females collected in fall and late winter were reproductively inactive, lacking both mature oocytes and any developing follicles. Fall-collected females also lacked sperm in their spermathecae.

A similarly-timed increase in reproductive readiness was observed for males, measured by the presence or absence of sperm in the seminal vesicles (Fig. 5). Males collected in fall and late winter lacked sperm in their seminal vesicles, while beginning in early March an increasing percentage of males contained sperm. Similarly, all spring-collected males contained pre-spermatophores in their spiral accessory glands, while pre-spermatophores were absent from all males collected during late winter or fall.

Fall-collected beetles (August through November) had higher mean volume of abdominal fat body compared to individuals collected in spring (February through May) (Fig. 6; fall vs. spring 2-way ANOVA $F_{(1,186)} = 179.9$, $p < 0.0001$). Fat body volume was higher for females across sampling dates (male vs. female, $F_{(1,186)} = 5.03$, $p = 0.026$; no significant interaction, $F_{(1,186)} = 0.2$, $p = 0.684$). Both sexes retained nearly 50% of maximum fat body volume when the mating season ended in May.

Feeding Behavior

Adult *E. corrusca* at the Wellesley site fed actively in early May on floral nectaries of *Acer platanoides L.* (Norway maple). At the Belmont site, adults were found in early April near sap flows on *Acer saccharum* (sugar maple) trees that had not been used for overwintering sites, and *E. corrusca* are commonly found drowned in sap-collecting buckets (Wihbey 1999). Throughout spring mating season, both males and females

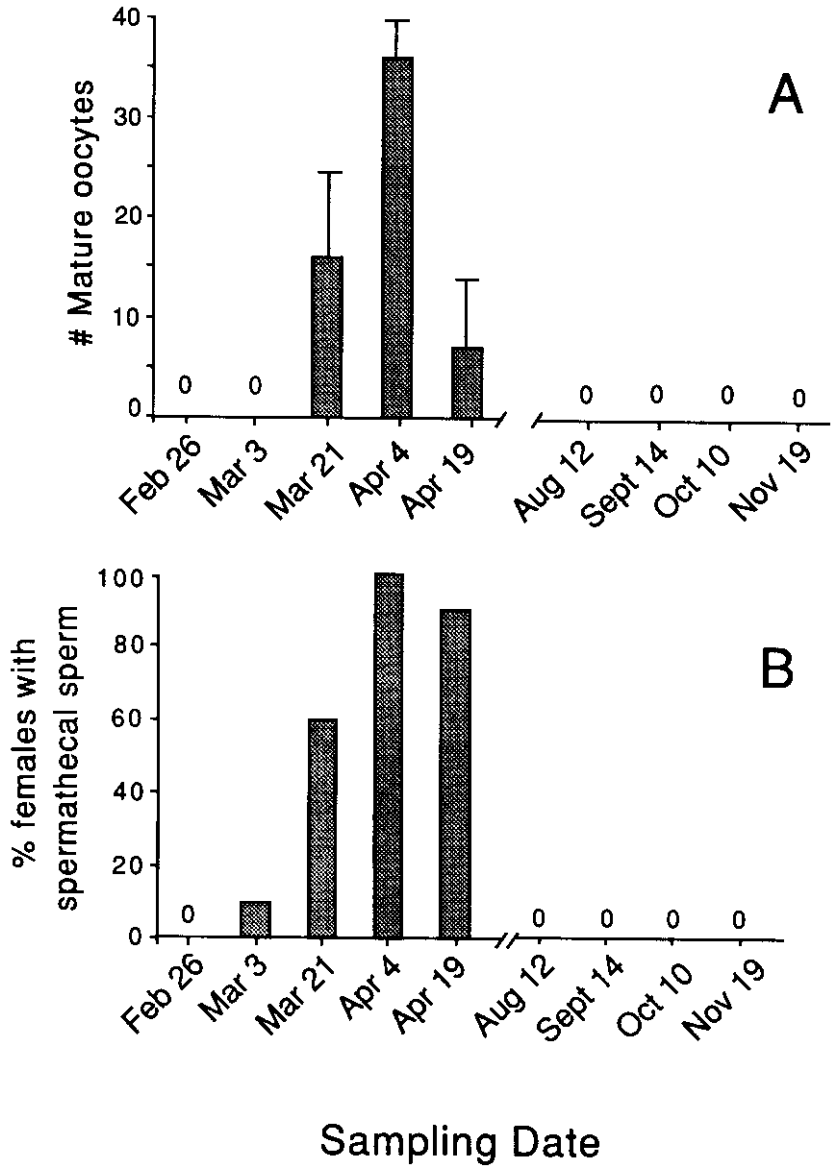

Fig. 4. Reproductive activity of *E. corrusca* females collected from Belmont, Massachusetts in 1998 (n = 10 females per sampling date). A) Mean (+1 SEM) number of mature oocytes (diameter ≥600 μm). B) Percent of females with sperm present in spermatheca (sperm storage organ).

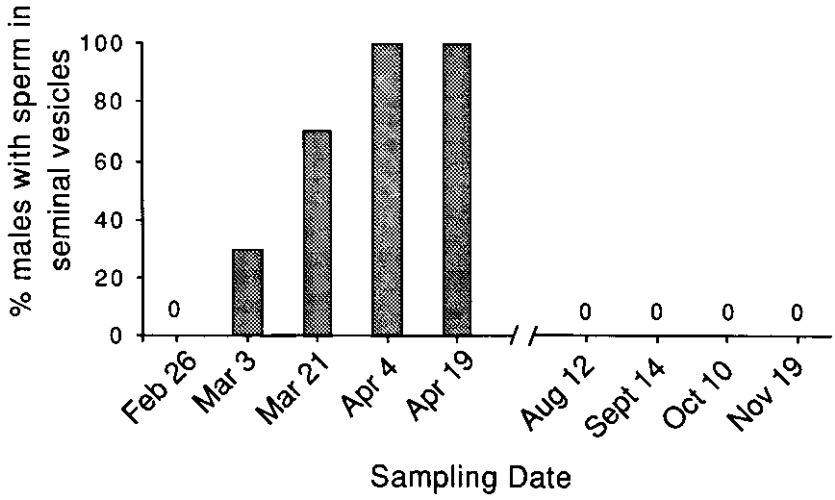

Fig. 5. Reproductive activity of *E. corrusca* males collected from Belmont, Massachusetts as percentage of males with sperm present in seminal vesicles (n = 10 males for each sampling date).

were occasionally found on soil at the base of trees, apparently drinking interstitial fluid. Although previous work has reported that *E. corrusca* adults appear on goldenrod and aster flowers in fall (Dillon & Dillon 1972), no beetles were observed on these flowers in late summer or fall, although these plants were abundant near known overwintering trees.

Mating Behavior

Copulating pairs were first found in the field on 7 April, although pairs mated in the lab as early as 17 March. The mating season lasted approximately six weeks, with the latest observed field copulation occurring on 21 May. *E. corrusca* mating took place primarily on tree trunks, but pairs were occasionally found at tree bases. Observations revealed two distinct stages of copulation, similar to those described for *Photinus* fireflies (Lewis & Wang 1991). During stage I, which lasted from 2 to 30 min, the male mounted the female dorsally, actively wiping his antennae across the female pronotum while contacting the junction between the female's pronotum and elytra with his maxillary palps. Stage II began when the male swiveled around to face in the opposite direction, and lasted for several hours. During stage II pairs often moved considerable distances. Because of their mobility it was difficult to measure field copulation durations; two monitored field copulations lasted 23.5 h and more than 15.5 h.

Copulation initiation was not limited to any specific time of day, as pairs were observed beginning stage I from 0730 h to 1800 h. Both males and females walked actively along the tree surface, and often contacted many beetles of the opposite sex before males initiated stage I by dorsally mounting a female. During stage II copulating pairs frequently contacted other adults, but no apparent interactions were observed.

In the lab males and females mated repeatedly, and field-collected adults lived up to 21 days. Individual males in either population cages or pairs observed in the lab

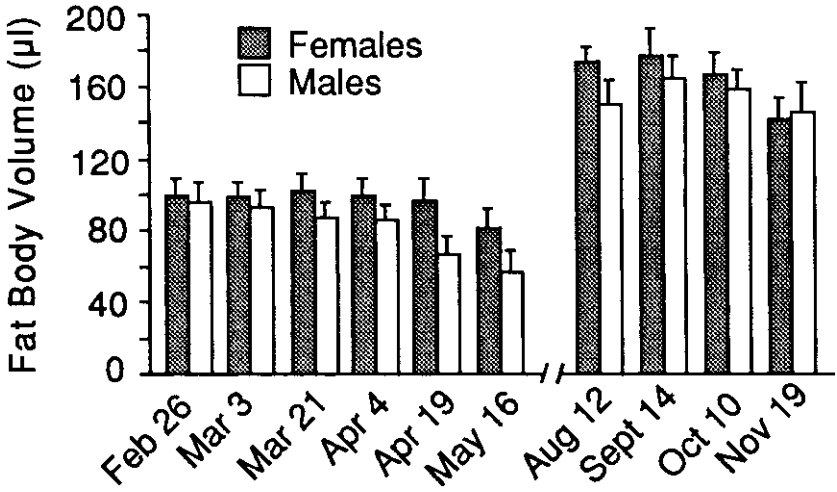

Fig. 6. Mean (+1 SEM) volume of fat body in male and female *E. corrusca* collected from Belmont, Massachusetts in 1998-1999 (n = 10 of each sex for each sampling date, except n = 5 of each sex for 16 May).

mated between 0 and 11 times, with a median of 3 lab matings per male (n = 9 males). Males that mated more than once often mated on consecutive days, with a median 2 d interval between matings (based on 32 matings for 7 males that mated more than once). Females mated between 1 and 11 times, with a median of 4 matings per female (n = 7 females), and a median inter-mating interval of 1.5 d (based on 32 matings for 5 females that mated more than once). In population cages or pairs, copulation durations ranged from 1.7 h to 28 h, with a median of 12.5 h (n = 34 copulations). Females oviposited in moss and on moist filter paper, and greater than 90% of eggs kept at 28°C and 70%RH hatched in 16 (±2) d.

Discussion

This mark-recapture study revealed high overwintering survival of *E. corrusca* adults, confirming Williams' (1917) limited observations based on 18 adults confined in a windowbox. Our field observations also indicate that some overwintering mortality may be caused by freezing and predation (possibly by birds or small mammals). However, predation on *E. corrusca* adults may be minimized by chemical deterrents. When disturbed, *E. corrusca* adults exhibit reflex bleeding similar to that described for other lampyrids (Blum & Sannasi 1974), and their extremely bitter taste (personal observation) suggests the presence of lucibufagins (Eisner et al. 1978) or related compounds.

This study suggests that in New England *E. corrusca* spends approximately 10 months as adults (August through May), overwintering a single year. *E. corrusca* collected in fall exhibit extensive fat body reserves typical of pre-diapausing adults (Leather *et al.* 1993), and reduced fat body in spring-collected adults suggest a portion of stored reserves are used for metabolic maintenance during overwintering. *E. corrusca* mate in early spring on their overwintering trees, with onset of reproductive activity perhaps triggered by temperature or daylength cues (Leather *et al.* 1993). Adults die in late spring or early summer, and *E. corrusca* adults that appear on trees

the following fall probably represent newly emerging individuals from eggs laid in spring. Several lines of evidence support this interpretation of *E. corrusca* life history. While 825 overwintering adults were marked in fall and winter 1997-98, no marked individuals were found among hundreds of adults observed on the same trees between August 1998 and June 1999. Additional evidence suggesting that fall- collected *E. corrusca* adults have recently emerged is that these females appear to have not yet mated, based on their inactive ovaries and absence of sperm in their spermathecae.

Several aspects of *E. corrusca* life history, including their diurnal activity, adult feeding and overwintering, and early spring mating period distinguish them from most other lampyrids (Lloyd 1997). However, in reproductive anatomy and occurrence of male spermatophores *E. corrusca* closely resembles *Photinus* fireflies (Lewis & Wang 1991, van der Reijden *et al*. 1997, Rooney & Lewis 1999). This study demonstrates further similarities in copulatory behavior, with *E. corrusca* exhibiting two copulatory stages described for *Photinus* (Lewis & Wang 1991), and spermatophore transfer occuring approximately 1 h after stage II begins (J. A. R., unpublished data). Copulation durations lasting up to 24 h beyond the time required for spermatophore transfer may function as copulatory mate guarding (Alcock 1994) in *E. corrusca*.

The life-history differences described in this study may explain some differences in female allocation of spermatophore-derived protein between *P. ignitus* and *E. corrusca*. *P. ignitus* females allocate 62% of male-derived protein to their developing oocytes, with 27% allocated to female somatic tissue (Rooney & Lewis 1999). In contrast, *E. corrusca* females allocate male-derived protein primarily to somatic tissue (64%), particularly fat body, with lower allocation to oocytes (21%). Thus, *E. corrusca* females may rely on both male-donated nutrients and adult feeding to support egg production over the course of their mating season.

E. corrusca is unusual among lampyrid beetles in its diurnal activity period and lack of bioluminescent courtship signals (Lloyd 1997). This shift in activity period may be associated with low nightly temperatures during the early spring mating season, which may preclude nocturnal flight and bioluminescent courtship display. Future studies on lampyrid phylogeny will help shed light on the evolution of life histories and mating behavior within this family.

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