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.ON SEXUAL SELECTION IN FLORIDA'S *PYRACTOMENA BOREALIS* (COLEOPTERA: LAMPYRIDAE)

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ABSTRACT

To what extent can a small animal with limited mobility use behavior to take advantage of its environment and how might this influence the population as a whole? This was examined in a firefly species *Pyractomena borealis* (Randall), by looking at the features of the microhabitat where larvae pupate, how developmental rates are influenced by extrinsic factors, and how the population's spatial distribution differed according to sex. In two populations of *P. borealis* in Gainesville Florida, larvae pupated at the warmest locations on trees, potentially causing a faster development rate than individuals in cooler areas. In these populations males pupated sooner and in warmer areas than females, suggesting males chose their pupation locations in order to have a shorter development period and an earlier emergence date than females. This is the first evidence of protandry being experimentally linked with behavioral usage of habitat.

Key words: protandry, Microhabitat, Microclimate, Pupation Duration, Ectotherm, Behavior

RESUMEN

Hasta que punto puede un animal pequeño con mobilidad limitada usar el comportamiento para aprovecharse de su ambiente y como esto puede influenciar la población completa? Esto fué investigado en una especie de luciérnaga *Pyractomena borealis* (Randall), al observar las características del microhabitat donde se empupan las larvas, como las tasas de desarrollo son influenciadas por factores extrínsicos, y como la distribución espacial de la población varia de acuerdo al sexo. En dos poblaciones de *P. borealis* en Gainesville Florida, las larvas se empuparon en las localidad más cálidas de los arboles, potencialmente causando una tasa de desarrollo más rápido que en los individuos en áreas más heladas. En estas poblaciones los machos empuparon más pronto en las áreas más calidas que las hembras, sugeriendo que los machos escogen las localidades donde van a empupar para tener un periodo de desarrollo más corto y una fecha de emergéncia de las hembras más temprana. Esta es la primera evidencia de protandria que experimentalmente conecta el comportamiento del uso del habitat.

Virtually all aspects of the life history of an ectotherm (physiology, development, activity levels, reproduction, etc.) are strongly influenced by ambient temperature (Fagerstrom & Wiklund 1982; Branson 1986; Zonneveld & Metz 1991; Wiklund et al. 1996; Olsson et al. 1999; Hemptinne et al. 2001). Behavioral responses to the limitations of being an ectotherm may be an important factor in the evolution of a species. There is no clearer example of this than the behavior that is involved in pupation.

Arboreal Pupation

Unlike most lampyrids, which pupate underground, members of the genus *Pyractomena* (and perhaps all of the fireflies in the tribe Cratomorphini) pupate above ground, mostly on vegetation (Lloyd 1997). *Pyractomena borealis* (Randall) larvae climb up tree trunks and glue the holdfast organ (at the tip of their abdomens) to the tree trunk (Lloyd 1997; Archangelsky & Branham 1998). Pupae hang upside down, generally with their ventral surface against the tree, the same position they use during ecdysis between larval instars (Archangelsky & Branham 1998).

There are many potential costs associated with arboreal pupation that are not as extreme for species that pupate underground. An underground burrow buffers environmental temperature fluctuation while arboreal pupation provides little shelter from such extremes. Similarly, burrows are moist environments, whereas arboreal pupation presents a greater risk of desiccation. Finally, underground pupae are less exposed to predation and parasitism compared to the often highly visible *P. borealis* pupae. Given these additional costs of arboreal pupation, why should this unusual mode of pupation exist at all?

Lloyd (1997) suggested that *Pyractomena* evolved aerial pupation as a way to avoid floodwaters, since the habitats they are found in are prone to flooding. While arboreal pupation may also expose the firefly to extremes of temperature, they may be exposed to much warmer average temperatures than species that pupate in the ground; thus, there is a potential for more rapid development and earlier eclosion (Regniere et al.

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1981; Fagerstrom & Wiklund 1982; Branson 1986; Wagner et al. 1987; Leather 1990; Wiklund et al. 1996; Hemptinne et al. 2001). *P. borealis* is unique in Florida because adults can emerge as early as mid-February.

Protandry

Protandry (males maturing to a reproductive stage earlier than females) occurs commonly in ectotherms and has been found in many insect species (Wiklund & Fagerstrom 1977; Wiklund & Solbreck 1982; Regniere et al. 1981; Fagerstrom and Wiklund 1982; Bulmer 1983a, b; Parker & Courtney 1983; Branson 1986; Zonneveld & Metz 1991; Wedell 1992; Wiklund et al. 1992; Nylin et al. 1993; Wiklund et al. 1996; Zonneveld 1996; Bradshaw et al. 1997; Carvalho et al. 1998; Harari et al. 2000). Protandrous systems have been shown to have sexual advantages for males (Fagerstrom & Wiklund 1982; Zonneveld & Metz 1991; Wedell 1992; Nylin et al. 1993; Harari et al. 2000). Emerging early gives males the advantage of having virgin females to mate with, increased time to produce sperm, and assurance that they will not emerge after the female population begins to decline resulting in either no or low quality females remaining (Wiklund & Fagerstrom 1977; Wiklund & Solbreck 1982; Fagerstrom & Wiklund 1982; Wiklund et al. 1992; Wiklund et al. 1996; Zonneveld 1996b; Carvalho et al. 1998; Olsson et al. 1999). It has also been suggested that females may not merely be passive participants in protandry, but may actually benefit from emerging after males and therefore be selected to do so (Wiklund & Solbreck 1982; Zonneveld & Metz 1991; Wedell 1992; Wiklund et al. 1996). Protandry could reduce the chances of pre-reproductive mortality in females (Wiklund & Solbreck 1982; Zonneveld & Metz 1991; Wedell 1992; Wiklund et al. 1996; Harari et al. 2000) and also act as a mechanism for passive female choice by assuring that females mate with old and therefore, by way of longevity, the fittest males (Wedell 1992).

Protandry has not been reported in any *Pyractomena* species (Buschman 1977), though this may be because it has not been specifically looked for. However it has been suggested that protandry may occur in the firefly *Photinus knulli* (Cicero 1983) and in other *Photinus* species (Lewis & Wang 1991).

P. borealis is vulnerable to extreme temperature variation during pupation. Therefore it is possible that the microhabitat of a pupation site influences the developmental rate of individuals, and if there is a sex difference in microhabitat usage, it is possible this may influence the dynamics of protandry across a population (Regniere et al. 1981; Bulmer 1983a; Fagerstrom & Wiklund 1982; Parker & Courtney 1983; Branson 1986; Leather 1990; Zonneveld & Metz 1991; Wiklund et al. 1992; Nylin et al. 1993; Wiklund et al. 1996; Harari et al. 2000; Hemptinne et al. 2001).

Behavioral manipulation of emergence timing has been suggested by Regniere et al. (1981) for the Japanese beetle (Scarabaeidae: *Popillia japonica*). Since the duration of pupation is dictated by temperature, males might pupate at different soil depths according to surface temperature to decrease pupation duration and to emerge before females. Similarly, there is high variation in the arboreal microhabitats of *P. borealis* and thereby the potential to exploit certain microhabitats. This study looks at how behavioral manipulation of emergence timing by individuals could potentially impact the population dynamics through protandry.

Materials and Methods

The Study Areas

This study was performed in mid-January, 2001 at two locations in Gainesville, Alachua County Florida (Latitude = 29°41'N, Longitude = 82°16'W). Study area A was a flood plain forest located in a residential area between Blues Creek and Devil's Millhopper Geological Site. Study area B was located in Possum Creek, also a flood plain forest. Deciduous trees dominated both habitats. The specific plots were 30.5 m by 30.5 m areas with high concentrations of *P. borealis* larvae. All of the trees in these plots were numbered and categorized according to bark roughness on a scale of 1-5 (1 = the smoothest, 5 = the roughest). Similarly, tree calipers were used to measure all the tree's width (east to west axis) and depth (north to south axis) at 1.22 m from the ground.

Collection Techniques and Measurements

Between 18th of January 2001 (day-of-year 18) and 18th of February 2001 (day-of-year 49) all trees at both plots were scanned daily for attached *P. borealis* larvae, pupae, and adults. Larval collection date was also their attachment date because of the daily scans. Trees were scanned between ground level and up to nine meters. Once an individual was located, I assigned a number to it and recorded the stage (larvae or pupae), tree number it was found on, height above ground, and the aspect of the individual using a Suunto® compass. For this study, aspect is considered the compass direction the individual was facing (i.e. the face of the tree it was on). These data were used to describe the microhabitat, that is, the apparent key features of the specific location at the point of attachment described at the scale that is relevant to that individual. If the individual was within reach, I collected the firefly by scoring the bark approximately 2.5 cm around the individual with a contractor grade Stanley utility blade; the

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section of bark was then pried from the tree with a wood-carving chisel. The specimen was placed in a semi-opaque plastic film canister covered with netting secured with a rubber band.

Rearing Temperatures

The specimens were immediately taken back to the laboratory and randomly and evenly distributed amongst three rearing chambers. Two of the chambers were Florida Reach-in Chambers® set at a constant temperature of 13 and 24°C respectively. The other chamber was an Environator® set at a constant temperature of 18°C. All three chambers maintained a constant humidity of 70% and nine hours of light (8 am-5 pm) simulating the natural hours of daylight at the start of the field season. I monitored the fireflies every day and recorded their date of pupation and eclosion, sex, and adult weight.

Field Temperature Monitoring

At study area A the ambient temperature was monitored on eleven trees randomly selected within the marked plot. I refer to these data as the microclimate measurements, not to be confused with the microhabitat data collected for individual pupation locations. Microhabitat is defined by the features of a specific location (tree size, aspect, height, bark roughness); microclimate in this study is considered the temperature regime for a specific point on a tree.

I used four Optic StowAway® Temp loggers (Onset Computer Corporations, Bourne, MA) on each tree to measure microclimate. The loggers were placed at 0°N and 0.61 m above ground, 0°N and 2.44 m above ground, 180°S and 0.61 m above ground, and 180°S and 2.44 m above ground. The loggers recorded the temperature every 30 seconds for 66 hours.

I used two approaches to analyze the temperature data. The first was to find the mean hourly temperature and standard deviation (as a measure of temperature variability within hours) for each location. As successive temperature readings are not truly independent, for the second method of analysis, I randomly selected five percent of the total recorded data. The random selection increased the independence of the individual temperature readings. This process was repeated ten times to ensure accurate representation of the data by the random selection. In this case, there was no measurement of standard deviation.

Statistics

I conducted the statistical analyses using SPSS version 9.0® (SPSS Inc., Chicago, Illinois). All data sets were examined for normality using a Kolmogorov-Smirnov test. When data were normally distributed, or could be transformed to be normally distributed, I utilized parametric tests for subsequent analyses. I analyzed non-normal data using appropriate non-parametric tests. The specific tests used are detailed in the results section.

Results

The Habitat Data

To ensure equality of tree distribution between the two sites, I first had to compare the size of the trees. Tree width and depth were not normally distributed at either study area. There was no difference in tree width between study area A and B (Mann-Whitney U = 6099, Z = -1.191, p = 0.234) and no difference in depth (Mann-Whitney U = 6148.5, Z = -0.998, p = 0.318).

In order to find physical characteristics of a microhabitat that would influence the microclimate, I analyzed the mean and the standard deviation of the hourly temperature for each microhabitat. The mean and standard deviation of the hourly temperature were not normally distributed. I developed a stepwise linear regression model using the mean hourly temperature as the independent variable to examine the potential causes of temperature variation. The putative explanatory variables entered were the vertical height up the tree, the side on the tree (North = 0°, South = 180°), the tree width (representing the tree's girth), the bark roughness, the day of the year, how many hours from noon it was, and whether it was AM or PM. I split these data into the two latter variables for analysis to reduce the circular nature of time.

All significant variables had positive correlations with the mean hourly temperature. Beginning with the most significant, these variables were: The time of day according to the number of hours from noon (Adjusted R^2 = 0.285, Pearson Correlation = 0.533, F Change = <0.001), the day of the year (Adjusted R^2 = 0.184, Pearson Correlation = 0.434, F Change = <0.001), if the sample was taken in the AM or the PM (Adjusted R^2 = 0.101, Pearson Correlation = 0.357, F Change = <0.001. A positive correlation means that it was warmer in the PM), the size of the tree (Adjusted R^2 = 0.061, Pearson Correlation = 0.138, F Change = <0.001), or if the microhabitat was facing north or facing south (Adjusted R^2= 0.003, Pearson Correlation = 0.053, F Change = <0.001. The positive correlation meaning that the south was warmer than the north). These variables explained a total of 63.2% of the variation in the mean hourly temperature.

I repeated the same regression model, but used data from 5% randomly selected temperatures as the dependent variable for all ten replicates. The mean adjusted R^2 value for these ten trials was 0.622, and the standard deviation

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0.003. In all ten cases the same variables occurred in the same order as the hourly mean values. However, in four out of ten trials the height up the tree was included as the last variable in addition to the other five variables. The mean adjusted R^2 change when adding the height variable was less than 0.001.

To examine the potential causes of the variation in the fluctuation of temperature, I conducted a stepwise linear regression using the square root of the standard deviation of the mean hourly temperature. The square root of the standard deviation was used as the dependent variable to make the data more normally distributed. The independent variables included for analysis were the same as the stepwise linear regression of the mean temperatures.

In order of significance, the variables with a positive correlation to the variance of the hourly mean temperature were: The time of day according to the number of hours from noon (Adjusted R^2 = 0.353, Pearson Correlation = 0.594, F Change = <0.001), if the microhabitat was facing north or facing south (Adjusted R^2 = 0.017, Pearson Correlation = 0.135, F Change = <0.001. The positive correlation means the south was more fluctuating than the north), if the sample was taken in the AM or the PM (Adjusted R^2 = 0.016, Pearson Correlation = 0.195, F Change = <0.001) A positive correlation means that it was more fluctuating in the PM), the day of the year (Adjusted R^2 = 0.004, Pearson Correlation = 0.061, F Change = <0.001), and the bark roughness (Adjusted R^2 = 0.003, Pearson Correlation = 0.024, F Change = <0.001). The size of the tree was negatively correlated with the variance of the mean hourly temperature (Adjusted R^2 = 0.013, Pearson Correlation = -0.041, F Change = <0.001). These variables explained a total of 40.4% of the variation in the variance of the mean hourly temperature.

Distribution of Fireflies at Study Areas A and B

I compared the physical characteristics of those trees with and without fireflies to determine any differences between the trees fireflies "chose" to pupate on and those they did not. Trees with fireflies were larger than trees without fireflies (Width: Mann-Whitney U = 2777.5, Z = -7.224, p < 0.001; Depth: Mann-Whitney U = 2814.5, Z = -7.101, p < 0.001). Trees with fireflies were also rougher than trees without fireflies (Chi square = 12.7, p < 0.01, df = 3).

To examine differences between the distribution of males and females, I analyzed height, girth, and aspect of pupation locations with respect to sex. Males were found higher up the trees than females (Mann-Whitney U = 2230, Z = -2.148, p = 0.032). Males were also found on larger trees than females (Width: Mann-Whitney U = 2301, Z = -1.993, p = 0.046; Depth: Mann-Whitney U = 2287.5, Z = -2.044, p = 0.041). Females deviated more from 180° than males did, i.e. males were more clustered on the south side of the trees than females (Mann-Whitney U = 2250.500, Z = -2.071, p = 0.038) (see Fig. 1 for females, and Fig. 2 for males). The descriptive statistics for the distribution of female and male *P. borealis* can be found in Tables 1 and 2, respectively.

Attachment Timing

I looked at the population wide pattern of development in order to begin examining protandry in *P. borealis*. The collection dates of the larvae (i.e. attachment dates, expressed as Day-of-Year or DY. January 1st is 1 DY, February 1st is 32 DY) were not normally distributed. Overall, females were collected and therefore had attached later than males (Females: N = 70, Mean = 28.21 DY, Median = 27 DY, SD = 7.13; Males: N = 81, Mean = 23.84 DY; Median = 22 DY, SD = 5.36; Mann-Whitney U = 1464, Z = -3.915, p < 0.001).

Developmental Timing According to Ambient Temperature

I compared the development rates for individuals reared under the three different temperature regimes to determine temperature effect on pupation. None of the developmental parameters that were measured were normally distributed. The duration of the attached larval stage, pupation, and emergence all decreased with increasing temperature (see Tables 3 and 4). The general descriptive statistics for all variables at 13°C, 18°C, and 24°C can be found in table 4.

In all three temperature regimes females pupated and also emerged as adults on later dates

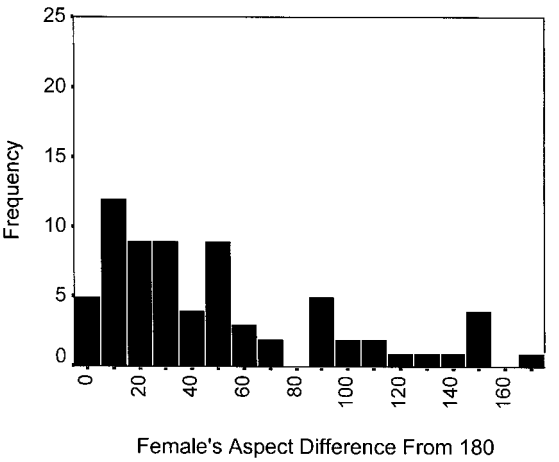


Fig. 1. The Female's Aspect Deviation from 180°. On the X axis 0 represents south, because it is the difference from 180.

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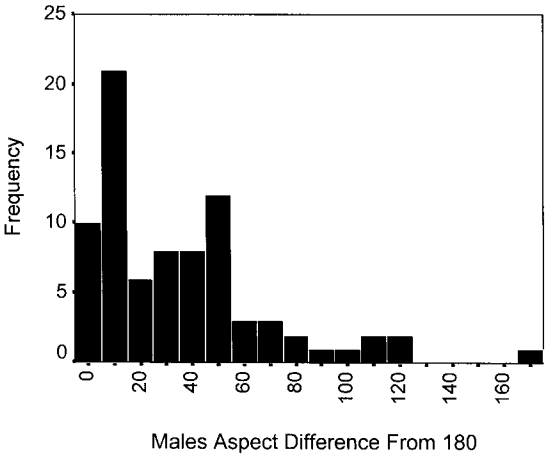


Fig. 2. The Male's Aspect Deviation from 180°. On the X axis 0° represents south, because it is the difference from 180°.

than males (see Tables 5, 6, and 7). At 13°C and 24°C the length of time it took from attachment to pupation was longer in females (see Tables 5 and 7). However, at 18°C and 24°C the length of pupation was longer for males than for females (see Tables 6 and 7). At 13° the total length of time from collection to emergence was significantly longer in females (see Table 5). The descriptive statistics for all of the significant results are found in Table 8.

To examine the potential causes of variation in the total duration of development, from attached larvae to eclosion, I developed a stepwise linear regression model using the total number of days from collection to emergence as the independent variable. Date of collection, rearing temperature, sex, and adult weight were entered as the possible explanatory variables. The temperature the individual was reared at was negatively correlated with the duration of development (Adjusted $R^2 = 0.748$, Pearson Correlation = -0.865, F Change = <0.001). The sex of the individual was positively correlated with the duration of the development; meaning that individuals with longer development times tended to be female (Adjusted $R^2 = 0.016$, Pearson Correlation = 0.287, F Change = 0.003). These two variables explained 76.0% of the total variation of development times.

Discussion

In this study I have shown that *P. borealis* tends to pupate in the warmest microhabitats and that warmer temperature leads to faster pupation rates. In addition there were temporal and spatial differences between males and females. Males not only attach earlier than females, but they also pupate in warmer areas than females. These two behaviors would lead to males emerging earlier than females; this suggests that protandry is found in *P. borealis* and the degree of protandry in a population may be influenced by the behavior of individuals.

Microhabitat Features

The largest features in the variation of temperature were not surprisingly associated with time. The first three features were related to the time of day and the day of the year. However, tree size and the aspect of attachment were also significantly important contributors to the variation of mean hourly temperature. Larger trees were warmer than smaller trees; large trees retain absorbed heat from the sun more than smaller trees. This was also shown by Lloyd (1997) through his physical model experiment that simulated different microhabitats that *P. borealis* might encounter. In addition, the south side of the tree was warmer than the north side. This result is also expected because the south side of the tree receives direct sunlight (and therefore solar radiation) where the north side does not. This also corresponds with the results of Lloyd's physical models (1997).

Interestingly, height was not a feature that influenced the variation of mean hourly temperature between microhabitats. This seemingly contradicts the results of Lloyd's (1997) model trees that found height to be positively correlated with temperature. This result may also be due to half of the data coming from the north side, therefore the data with significant differences in height from the south side would had less of an influence on the data set as a whole. However, upon closer examination,

Table 1. Descriptive statistics of female distribution.

	N	Mean	Std. deviation	Percentiles		
				25th	50th (median)	75th
Deviation from 180° aspect	70	49.971	44.559	14.50	37.00	74.50
Height up tree (m)	70	1.625	0.574	1.120	1.646	2.073
Tree width (m)	70	0.203	0.137	0.086	0.180	0.318
Tree depth (m)	70	0.200	0.133	0.086	0.180	0.326

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TABLE 2. DESCRIPTIVE STATISTICS OF MALE DISTRIBUTION.

	N	Mean	Std. deviation	Percentiles		
				25th	50th (median)	75th
Deviation from 180° aspect	80	34.738	34.060	5.250	26.500	52.250
Height up tree (m)	80	1.818	0.592	1.379	1.905	2.240
Tree width (m)	81	0.245	0.139	0.131	0.216	0.318
Tree depth (m)	81	0.244	0.137	0.127	0.218	0.326

when viewed at a tree-by-tree basis, Lloyd's findings are in fact corroborated by this study. Height was important in four out of the ten trials examining 5% of the randomly selected data. This may reflect the inconsistent nature of solar exposure to trees in the same forest. Not all trees are in areas of uniform solar exposure; therefore on some trees height is an important feature for maximizing heat. The randomly selected data would not contain an equal representation of all trees, so those trees in areas of patchy sunlight where height was important may have had a larger representation in the four trials where height was important.

Time of day also plays a key role in the fluctuation of temperature, but the second most important feature is the aspect. Areas on the south side of the tree fluctuate much more than areas on the north side; the north side continuously being in shadow, and the south side receiving more or less solar radiation depending on cloud cover, shadows, etc. . . . Finally, tree size is negatively correlated with temperature fluctuation; larger trees have more stable microclimates than smaller trees. This is corroborated by Lloyd's study of model trees (1997). This is probably for similar reasons as to why large trees are warmer, because large trees have a smaller surface to volume ratio, they can maintain absorbed heat longer than small trees, therefore making them more stable.

The contribution of microhabitat features on the microclimate may appear to be minor, but it is important nonetheless (Ohsaki 1986). All fireflies are exposed to the same daily and seasonal effects of temperature, but aspect, tree size, and height are all features that individuals can control through behavioral decisions. An individual that has selected to pupate on the south side of a large tree will, over the course of several days, have the advantage because of the cumulative effect of the warmer temperature throughout development. If this behavior were genetically based, it would be a source of selectable variation among individuals.

Pupation Site Selection Behavior Based on Microhabitat

It is important to note that there was no significant difference of tree characteristics between the two sites, therefore we may assume the microclimate data collected for study area A can also be applied to study area B. The overall distribution of *P. borealis* suggests that the fireflies are taking advantage of the best microhabitats to maximize the temperature of their microclimate. Trees with fireflies were larger and had rougher bark than trees without fireflies. This study also confirms Lloyd's findings in 1997 that *P. borealis* prefer the south side of the tree, but does not support his findings that individuals preferred smoother trees; this difference may be due to differences in habitats and the availability of bark types. Height also seemed to be an influencing factor; as suggested by Lloyd (1997), *P. borealis* pupate higher than is necessary to avoid floodwaters. On some trees this may take advantage of areas with more direct sunlight. The features that determined the distribution of *P. borealis* were also the same features that maximized the mean temperature.

The distribution of *P. borealis* stands in stark contrast to that of *P. limbicollis*. *P. limbicollis* pupate low to the ground on the northeastern side of small trees; they also emerge several weeks after *P. borealis* (Lloyd 1997). The distribution of *P. limbicollis* suggests that these fireflies are in fact taking advantage of the cooler more stable envi-

TABLE 3. COMPARISONS OF DEVELOPMENT AMONG INDIVIDUALS REARED AT 13, 18, AND 24°C. IN ALL CASES, THE VALUES FOR 13°C ARE LARGER THAN 18°C, WHICH IS LARGER THAN 24°C.

	Kruskal-Wallis	df	p
Pupation date	31.081	2	<0.001
Emergence date	94.496	2	<0.001
Attached larvae duration	67.659	2	<0.001
Pupa duration	105.868	2	<0.001
Attached larvae to emergence duration	110.300	2	<0.001

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TABLE 4. DESCRIPTIVE STATISTICS OF DEVELOPMENT AT THREE DIFFERENT TEMPERATURES. THE PUPATION AND EMERGENCE DATES ARE IN UNITS OF THE DAY-OF-YEAR (DY). THE ATTACHED LARVAE DURATION, PUPA DURATION, AND LARVAE TO PUPA DURATION ARE IN UNITS OF NUMBER OF DAYS (D).

	Temperature	N	Mean	Std. deviation	Percentiles		
					25th	50th (median)	75th
Pupation date (DY)	13°C	40	42.38	11.60	32.00	45.00	51.00
	18°C	45	34.44	8.22	26.50	36.00	42.00
	24°C	54	29.67	6.97	24.00	28.50	33.25
Emergence date (DY)	13°C	37	76.57	15.60	67.00	78.00	88.00
	18°C	49	48.57	7.62	42.00	49.00	55.50
	24°C	56	36.68	6.90	31.00	35.00	41.00
Attached larvae	13°C	40	16.93	7.24	10.25	17.50	24.00
Duration (D)	18°C	45	8.07	4.45	5.00	8.00	11.00
	24°C	54	4.33	2.07	3.00	4.00	6.00
Pupa duration (D)	13°C	35	35.83	6.23	35.00	36.00	37.00
	18°C	44	15.93	7.06	13.00	14.00	16.00
	24°C	53	7.36	0.56	7.00	7.00	8.00
Larvae to emergence	13°C	37	51.22	11.60	45.00	54.00	60.00
Duration (D)	18°C	49	21.41	5.42	17.50	22.00	25.00
	24°C	56	11.38	2.40	10.00	12.00	13.00

ronments (the lower stability of small trees is probably counterbalanced by the preference for the north side). In this case, they would also not need to pupate high up the trees to maximize light, but merely high enough to avoid flood waters (Lloyd 1997). *P. limbicollis* is considerably smaller than *P. borealis*, so it may be that *P. limbicollis* is too small to overcome the potentially desiccating effects of direct sunlight.

Developmental Timing According to Ambient Temperatures

All insects have a temperature threshold above which they can develop, and warmer temperatures cause faster development rates in insects (Regniere et al. 1981; Branson 1986; Wagner et al. 1987; Leather 1990; Miller 1992; Wiklund et al. 1996; Hemptinne et al. 2001); *P. borealis* is no exception. In this study, pupal development was shown to be shorter at warmer temperatures, and temperature was the largest influence on development time. This suggests that the selective behavior of *P. borealis* to pupate in microhabitats with the warmer microclimates will result in reduced developmental durations. The laboratory conditions *P. borealis* were reared in were conservative compared to the actual field sites. This suggests there may be more highly variable development rates based on microclimate in the field than were seen in the laboratory.

Protandry

Protandry is evident in *P. borealis*. In the field males attach before females. In the laboratory males pupate and emerge earlier than females. However, there are differences at each of the three temperatures, suggesting that the patterns of development of the sexes are not consistent throughout a wide range of temperatures. At 13°C females have a longer development time, but at 18 and 24°C there is no difference in the total development time between the sexes at $p < 0.05$. However, sex was a determinant of developmental duration in the linear regression; meaning an individual with a long developmental time would most likely be a female.

TABLE 5. COMPARISONS OF THE DEVELOPMENTAL STAGES BETWEEN MALES AND FEMALES REARED AT 13°C.

	Mann-Whitney U	Z	p	Value higher for (see real numbers in Table 8)
Pupation date	54.50	-3.44	0.001	Female
Emergence date	57.50	-3.34	0.001	Female
Attached larvae duration	54.00	-3.46	0.001	Female
Pupation duration	94.00	-1.72	0.086	Not significant
Larvae to emergence duration	62.00	-3.19	0.001	Female

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TABLE 6. COMPARISONS OF THE DEVELOPMENTAL STAGES BETWEEN MALES AND FEMALES REARED AT 18°C.

	Mann-Whitney U	Z	p	Value higher for (see real numbers in Table 8)
Pupation date	74.5	-2.67	0.008	Female
Emergence date	113.0	-2.70	0.007	Female
Attached larvae duration	109.5	-1.55	0.121	Not significant
Pupa duration	70.0	-3.07	0.002	Male
Larvae to emergence duration	176.0	-1.11	0.266	Not significant

This latter result is consistent with studies of *P. lucifera* in which females have a longer duration of the larval stage and therefore males pupate sooner than females (Buschman 1977). Interestingly, in both of these systems, the actual duration of the pupal stage is longer for males than for females (Buschman 1977). The explanation for this extended pupation duration is unknown. However, regardless of the developmental differences there has been no suggestion of protandry in *P. lucifera* (Buschman 1977). Protandry may be limited in this system because the male's slow pupation duration negates any time advantage they gained by attaching early.

Microhabitat Influences on Protandry

When looking at all the individuals collected, there is a significant difference between the pupation locations of males and females. Overall, males were found on larger trees and were located on the south side more often and were higher up the trees. From what we know about microhabitat, the males appear to be maximizing developmental rates through microclimate more than the females.

It is unclear whether the females are "intentionally" choosing smaller trees, lower down and deviating from the south more than males in order to slow their development or are simply choosing a "large enough" tree without using up time looking for the largest tree to pupate on. It may also take more effort to find the southern most part of a tree, and so females may not be that specific in their site selection to save time and energy. Similarly, it was shown on some trees that height positively influences microclimate and so it is also unclear if females are specifically selecting low pupation sites on the trees or if they are pupating just high enough for successful development. In contrast, the behavior of males seems to have an obvious result. By pupating on large trees on the southern-most part and pupating significantly higher than females males can take advantage of microhabitat to decrease their development time.

In *P. borealis* there is an obvious benefit to males that emerge early, it gives them more time to search for adult females and more time to "tend" pupae and mate with eclosing females (Lloyd 1997). The benefits for females are not as evident. Many have suggested that females can benefit from protandry through reducing premating mortality (Wiklund & Solbreck 1982; Fagerstrom & Wiklund 1982; Zonneveld & Metz 1991; Wedell 1992; Wiklund et al. 1996; Harari et al. 2000). However, females seem more vulnerable as immobile pupa than as mobile adults and so it is unclear why they would want to prolong this stage. It has also been suggested that females benefit from protandry through passive female choice (Wedell 1992). However, because the pupal "tending" behavior by males is greatly enabled by protandry, the benefits of female passive choice must be considered in light of the costs associated with being "tended" as a pupa.

Previously published models that discuss protandry suggest that developmental timing is primarily under physiological control (Wiklund & Fagerstrom 1977; Wiklund & Solbreck 1982; Regniere et al. 1981; Parker & Courtney 1983; Branson 1986; Zonneveld & Metz 1991; Nylin et al. 1993; Bradshaw et al. 1997). In the case of *P. borealis*, developmental timing is influenced by behavior with regard to the choice of pupation site.

TABLE 7. COMPARISONS OF THE DEVELOPMENTAL STAGES BETWEEN MALES AND FEMALES REARED AT 24°C.

	Mann-Whitney U	Z	p	Value higher for (see real numbers in Table 8)
Pupation date	12.500	-2.617	0.009	Female
Emergence date	14.500	-2.599	0.009	Female
Attached larvae duration	17.500	-2.307	0.021	Female
Pupa duration	22.000	-2.288	0.022	Male
Larvae to emergence duration	26.500	-1.887	0.059	Not Significant

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TABLE 8. DESCRIPTIVE STATISTICS OF DEVELOPMENT AT THREE DIFFERENT TEMPERATURES BETWEEN MALES AND FEMALES. THE PUPATION AND EMERGENCE DATES ARE IN UNITS OF THE DAY-OF-YEAR (DY). THE ATTACHED LARVAE DURATION, PUPA DURATION, AND LARVAE TO PUPA DURATION ARE IN UNITS OF NUMBER OF DAYS (D).

	Temperature	Sex	N	Mean	Std. deviation	Percentiles		
						25th	50th (median)	75th
Pupation date (DY)	13°C	Female	9	40.00	9.54	32.50	36.00	51.00
		Male	12	32.92	8.35	26.25	31.00	39.00
	18°C	Female	21	38.10	7.74	32.50	38.00	44.00
		Male	15	30.87	7.04	25.00	30.00	37.00
	24°C	Female	21	33.10	7.06	27.00	33.00	37.50
		Male	33	27.49	6.063	23.00	25.00	29.50
Emergence date (DY)	13°C	Female	9	74.78	9.50	67.00	71.00	85.50
		Male	12	65.50	15.85	62.00	67.00	76.25
	18° C	Female	22	51.96	7.43	48.25	51.50	57.25
		Male	20	45.60	6.68	41.00	45.50	51.75
	24°C	Female	21	40.19	6.88	35.00	40.00	44.50
		Male	35	34.57	6.07	31.00	32.00	37.00
Attached larvae	13°C	Female	9	15.11	5.47	11.50	14.00	19.50
Duration (D)		Male	12	11.42	6.27	7.00	9.50	17.00
	18°C	Female	21	9.10	4.70	5.50	9.00	13.00
		Male	15	6.67	3.60	5.00	6.00	9.00
	24°C	Female	21	5.62	1.75	4.00	6.00	7.00
		Male	33	3.52	1.86	2.00	4.00	5.00
Pupa duration (D)	18°C	Female	21	13.62	1.36	13.00	13.00	14.00
		Male	16	19.69	10.76	14.00	16.00	16.75
	24°C	Female	21	7.10	0.44	7.00	7.00	7.00
		Male	32	7.53	0.57	7.00	7.50	8.00
Larvae to emergence	13°C	Female	9	49.89	5.30	46.00	49.00	54.50
Duration (D)		Male	12	44.25	14.25	42.25	45.50	53.75

It is clear that future models should also consider behavior as a mechanism for protandry.

This study is the first to experimentally link protandry with behavioral usage of the environment. The variation in microhabitat and its potential effects on individual success provide a basis upon which selection can occur (Regniere et al. 1981; Parker & Courtney 1983). This suggests that fine scale variations in the environment can influence the dynamics of protandry and sexual selection in the population as a whole.

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