

Reproductive Responses to Photoperiod by a South Florida Population of the Grasshopper *Romalea microptera* (Orthoptera: Romaleidae)

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ABSTRACT Reproductive tactics of some insects are affected by photoperiod because daylength is a reliable cue indicating seasonal change in environmental suitability. We tested the hypothesis that late-season (short-day) photoperiod affects the length of the oviposition cycle of the eastern lubber grasshopper, which is from a subtropical area with a winter dry season. We predicted that oviposition would occur sooner in short-day (11.5:12.5 [L:D] h) than in long-day (13.75:10.25 [L:D] h) individuals, and that costs associated with earlier oviposition would be expressed as smaller eggs or fewer eggs per female under the short-day photoperiod. Two diets (low and high food quantity) were tested at each photoperiod. Although MANOVA yielded no significant main effect of photoperiod on the timing of oviposition, number of eggs, and mean egg dry mass, there was a significant multivariate interaction between photoperiod and food for these variables. In the low food treatment, the short-day animals produced fewer, smaller eggs than did the long-day animals, but this multivariate difference between short-day and long-day animals was absent in the high-food treatment. Photoperiod and its interaction with food did not affect timing of oviposition in either multivariate or univariate analyses. The absence of the predicted change in timing of reproduction in an autumn photoperiod suggests that seasonal constraints on reproduction do not exert a strong influence on reproductive timing of this population. Our alternative hypothesis is that the combination of short days and low food availability serve as a cue to lubber grasshoppers of an oncoming dry season with potentially limiting food, and that they respond to this cue by reducing the mass of reproductive output but not by accelerating reproductive timing. Thus, we propose that these subtropical grasshoppers adjust reproductive investment in response to seasonal changes in resource availability.

KEY WORDS time constraints, season, oviposition, reproductive output, photoperiod, life history

SEASONAL CONSTRAINTS ON life histories of insects have received considerable theoretical and empirical study (e.g., Forrest 1987, Rowe and Ludwig 1991, Landa 1992, Tanaka et al. 1993, Abrams et al. 1996, Olvido and Mousseau 1998, Johansson and Rowe 1999). Timing of life history transitions such as metamorphosis, oviposition, and hatching can influence fitness whenever there are seasonal cycles of temperature, precipitation, or food availability (Rowe and Ludwig 1991). Insects may modify the time or body mass at which life history transitions occur based on season (e.g., Forrest 1987, Mousseau and Roff 1989, Landa 1992, Tanaka et al. 1993, Johansson and Rowe 1999), with transition typically occurring at an earlier age or at a lower body mass as unfavorable seasons approach (Forrest 1987, Rowe and Ludwig 1991). Such a change in life history can be advantageous whenever the unfavorable season leads to an increased probability of mortality and

therefore realized fitness, thus favoring accelerated development (Tanaka et al. 1993, Johansson and Rowe 1999). For a univoltine insect having obligate winter egg diapause (as described by Johansson and Rowe 1999) adults that fail to lay eggs before the onset of the unfavorable season pay a high fitness price. Thus, we would expect reproductive development to be accelerated by late-season conditions, even at the cost of reduced reproductive investment (number or size of eggs). Given the central role of seasonally-related mortality, it is not surprising that most tests of time constraints on life history have been conducted on insects from environments with an unfavorable cold season (i.e., a freezing winter—e.g., Forrest 1987, Tanaka et al. 1993, Leimar 1996, Johansson and Rowe 1996). As a result, we know relatively little about the life history responses of insects from environments in which the unfavorable period is a dry season, with little risk of freezing (e.g., Mediterranean or subtropical climates). In such environments the increase in mortality due to the unfavorable season is potentially lower.

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For many insects, photoperiod is the principal cue to season (Tauber et al. 1986), and timing of life history events often changes in response to photoperiod (e.g., Verdier 1976, Hewitt 1985, Tanaka et al. 1993, Miles et al. 1998, Nakao 1998, Ishihara 2000, Zhou 2001). Photoperiod is an ideal seasonal cue as it changes in a predictable pattern throughout the year. When nymphs of *Lestes congener* Hagen are subjected to a photoperiod simulating late-season conditions, they undergo metamorphosis earlier, show greater molting rate, reduced size at maturity, and reduced growth rate (Johansson and Rowe 1999). The price these damselflies paid for accelerating development was an increased exposure to cannibalism and decreased size at maturity. Johansson and Rowe (1999) review other studies showing similar effects on metamorphosis. With regard to reproductive tactics, both *Megalurothrips sjostedti* (Trybom) and a northern population of *Locusta migratoria* L. have shorter pre-oviposition periods and reduced egg production when exposed to shorter photoperiods (Tanaka et al. 1993; Ekesi et al. 1999).

Adequate tests for life history responses to seasonal constraints must evaluate the effects of late-season photoperiod on reproductive tactics over a range of controlled feeding rates (Leimar 1996, Johansson and Rowe 1999). Well-fed animals typically exhibit rapid reproductive development (e.g., Moehrlin and Juliano 1998, Hatle et al. 2000), often regardless of photoperiod (e.g., Tanaka et al. 1993). Thus, if tests for effects of photoperiod on reproductive tactics are done only with well-fed animals, changes in reproductive timing and any associated costs of that change may be difficult to detect (Leimar 1996). Further, food availability or quality may also be a cue to season (Tauber et al. 1986), and thus may play a role in inducing life history responses to season.

The eastern lubber grasshopper, *Romalea microptera* Beavois (= *R. guttata* Houttuyn), is found in the southeastern United States. This species is univoltine, deposits multiple clutches per year (usually about three), and overwinters only as eggs (Stauffer et al. 1998). The timing of reproductive development and number of eggs per clutch is plastic in response to food availability (Moehrlin and Juliano 1998, Hatle et al. 2000) and temperature (A. Young and S.J., unpublished data). These large grasshoppers appear to acquire the resources for reproduction via adult feeding (as opposed to nymphal feeding) and they invest a very large amount of resources in reproduction (Stauffer and Whitman 1997, Moehrlin and Juliano 1998, Hatle et al. 2000).

Hypothesis and Predictions. We hypothesized that the winter dry season of south Florida imposes a seasonal constraint on reproduction of *R. microptera*, and that this species is adapted to that constraint via flexibility in reproductive tactics. We predicted that lubber grasshoppers will adjust timing of reproduction and reproductive investment in response to short photoperiods characteristic of the onset of the dry season. Specifically, we predicted that females exposed to short days will oviposit sooner, and pay a price of less

mass invested in egg clutches, than will females exposed to long days. Smaller clutches may contain either fewer or smaller eggs.

Materials and Methods

Experimental Animals. Grasshoppers used in this study were from a laboratory colony originating from Copeland, FL, USA. This site in southwest Florida is characterized by limited probability of freezing (Southeast Regional Climate Center 2001) and a pronounced seasonal cycle of precipitation. Rainfall averages >300 mm/month from June to September, and declines in October to a dry season average of <50 mm rainfall per month from November to April (based on nearby Everglades City, FL; the pattern of precipitation is similar for several sites in south central and southwest Florida, Fernald and Patton 1984). At Copeland, hatching is in March, and adults appear in May. The adult population typically begins to decline in September, but adults may be found as late as November (D. W. Whitman, personal communication). Thus, at this site the unfavorable season is a cool, dry winter with low risk of freezing.

Experimental Methods. Newly eclosed adult females were isolated and then housed in 500 cm³, individual, ventilated plastic containers that were placed in environmental chambers. We had four treatments defined by combinations of photoperiod and food quantity, respectively: short-low, short-high, long-low, and long-high. Short photoperiod (11.50:12.50 [L:D] h) corresponded to the daylength at Everglades City, FL during the second week of October, whereas long photoperiod (13.75:10.25 [L:D] h) corresponded to the daylength at Everglades City, FL, during the second week of June (U.S. Naval Observatory 2001). Thus, our short and long photoperiods simulate, respectively, conditions at the end of, and in the middle of, the favorable season for adult feeding and development. For both photoperiods, we maintained females on a 12:12 hours, 32:24°C thermocycle (Fig. 1).

Food quantity was adjusted for grasshopper size at eclosion. Size was quantified by the length at eclosion of each individual's right femur. Individuals on the high food diet received $0.300 \times$ femur length (mm) g/d of Romaine lettuce and $3.000 \times$ femur length (mm) mg/d of dry oats, whereas individuals on the low food diet received $0.075 \times$ femur length (mm) g/d of Romaine lettuce and $0.750 \times$ femur length (mm) mg/d of dry oats. Based on other studies (Moehrlin and Juliano 1998, Hatle et al. 2000) our high food treatment represented ad libitum feeding, whereas our low food treatment was sufficiently low that animals should have prolonged reproductive development. Each group was fed once per day between 1100 and 1400 hours.

Reproductive tactics. Females remained unmated throughout the experiment. At age 28 d, each animal was placed in a 1-liter plastic container with moist sand for at least 1 h each day. *Romalea microptera* readily oviposits under these conditions (Stauffer et al. 1998). This procedure was repeated daily until each grass-

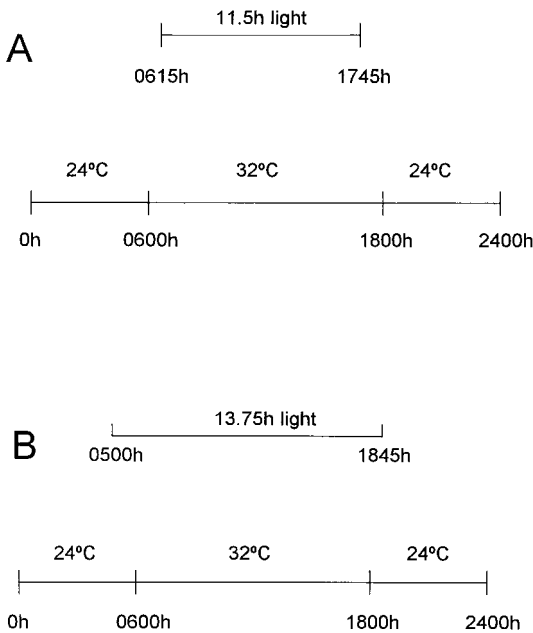


Fig. 1. Short-day (A) and long-day (B) photoperiods and thermocycles used in this study.

hopper oviposited. Upon oviposition, the age of the female, the number of eggs laid, and dry mass (60°C , >24 h) of a sample of 10 eggs were recorded. The grasshoppers were frozen and later dissected to count fully developed eggs that may not have been laid with the pod. Thus, total eggs = eggs laid + full size eggs remaining in the carcass. One third of the grasshoppers had hemolymph sampled every third day for analysis of hemolymph proteins, the results of which will be reported elsewhere.

Statistical Analysis. We tested whether food availability and photoperiod affected age at oviposition, number of eggs, and egg dry mass using multivariate analysis of variance (MANOVA). MANOVA is preferable to univariate analysis of variance (ANOVA) for data like these because the three reproductive variables we examine are expected to be correlated, and MANOVA provides both a test for overall treatment effects on the set of variables, and a quantification of which variables contribute most to any significant effects (Scheiner 2001). We first tested whether female size (femur length at eclosion) as a covariate accounted for significant variation in the response variables. Significant effects in MANOVA were further analyzed using standardized canonical coefficients (SCC-SAS Institute 1989). The magnitudes of SCCs indicate the relative contributions of each of the dependent variables to significant multivariate effects (Scheiner 2001). In addition, the signs of SCCs indicate the directions of the response of dependent variables, so that two variables with SCCs of opposite sign are responding to treatments in opposite directions (that is, means for those variables are negatively correlated across treatments, Scheiner 2001). All vari-

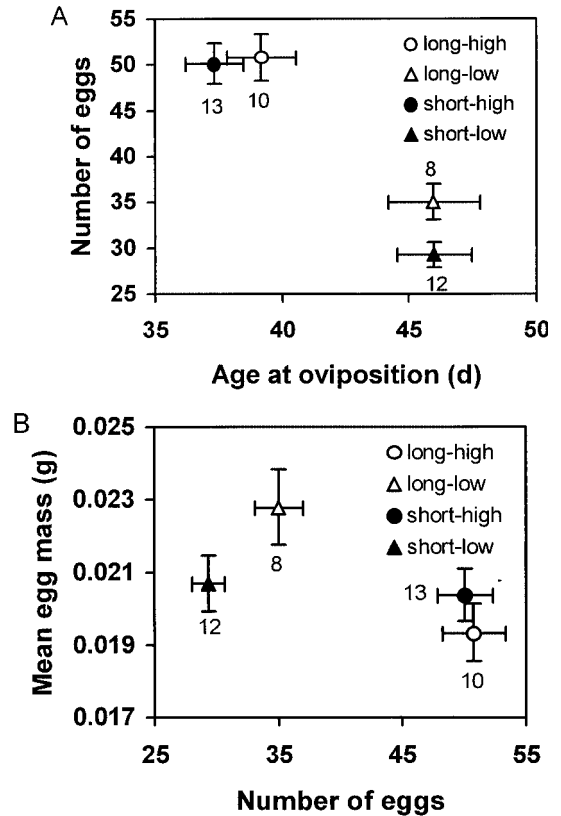


Fig. 2. Reproductive tactics (mean \pm SE) of experimental female lubber grasshoppers. (A) Number of eggs and age at oviposition. (B) Mean egg dry mass and egg number. Sample sizes for each group are indicated near the error bars. See Fig. 1 for explanation of short and long day photoperiods. See text for explanation of low and high diet treatments.

ables were log transformed to meet assumptions of homogeneous variances and normality.

Results

Femur length did not have a significant effect on age at oviposition, egg number, or egg dry mass (MANCOVA; Pillai's Trace; $F = 1.63$; $df = 3, 35$; $P = 0.2007$). Thus, the analyses were conducted without femur length as a covariate. Whether hemolymph was sampled also did not have a significant effect on the dependent variables (MANOVA; $F = 0.37$; $df = 3, 31$; $P = 0.7756$).

Food treatment had a significant effect (MANOVA; $F = 34.07$; $df = 3, 37$; $P = 0.0001$). This effect resulted primarily from effects on number of eggs (SCC = 1.6080), and secondarily from effects on age at oviposition (SCC = 0.6146; Fig. 2A). Egg dry mass contributed very little to the food effect (SCC = -0.1446 ; Fig. 2B). The opposite signs of the SCCs for egg number and age at oviposition indicate that these variables responded to food treatments in opposite directions. In the high-food group, egg number was greater and

age at oviposition was less (Fig. 2A, compare circles versus triangles).

Photoperiod did not have a significant main effect on reproductive tactics (MANOVA; $F = 1.76$; $df = 3, 37$; $P = 0.1720$). However, the interaction of food treatment and photoperiod was significant (MANOVA; $F = 3.16$; $df = 3, 37$; $P = 0.0359$). The interaction effect resulted primarily from number of eggs (SCC = 1.3643) and mean egg dry mass (SCC = 0.9292), whereas age at oviposition contributed relatively little to this effect (SCC = -0.4590). Low food and short photoperiod yielded lower egg number and lower egg dry mass (Fig. 2B, triangles), and thus overall lower investment in the first clutch. In contrast, under the high food regime, short and long photoperiods did not affect reproductive tactics (Fig. 2B, circles). Fig. 2B clearly shows that the response to low food and short photoperiod is only evident when viewed as a multivariate response. For all three variables, differences between long and short days under the low food regime were not large and indeed the food and photoperiod interactions were not significant in univariate analysis (Age: $F = 0.52$; $df = 1, 39$; $P = 0.4773$; Egg number: $F = 2.81$; $df = 1, 39$; $P = 0.1018$; Mean egg mass: $F = 3.50$; $df = 1, 39$; $P = 0.0687$). However, the differentiation between these two groups becomes much more distinct in the two-dimensional space represented in Fig. 2B. It seems clear that these two reproductive traits, which together quantify reproductive allotment (=mass committed to egg production), responded to treatments in a correlated fashion and thus are best evaluated via multivariate analysis.

Discussion

We have shown that the combination of photoperiod and food affects reproductive tactics of *R. microptera*. However, our data only weakly support our primary prediction, based on the hypothesis of adaptive responses to seasonal constraints on reproductive tactics. The variable we predicted to be most affected—age at oviposition—was largely unaffected by late-season photoperiod, regardless of food quantity (Fig. 2A). Also, age at oviposition did not appear to make a major contribution to the significant interaction between food and photoperiod. Photoperiod did not affect overall reproductive tactics ($P > 0.05$ by MANOVA) nor did it affect any of the variables individually ($P > 0.05$ by ANOVA; analyses not shown). Thus, it is clear that any impact of photoperiod on reproduction in this species is dependent on food availability, as predicted by Leimar (1996) and Johansson and Rowe (1999). The significant interaction of food and photoperiod is superficially consistent, at least in part, with our prediction that reproductive output should be reduced by late-season photoperiods. However, under our hypothesis, and that outlined by Johansson and Rowe (1999), such a reduction in investment with low photoperiod represents the cost of early oviposition. In the absence of a change in timing of oviposition, the change in reproductive in-

vestment cannot readily be interpreted as a cost. However, these hypotheses are all from studies of insects inhabiting areas with freezing winters rather than a cool, dry inactive season. The difference in life history response to late-season photoperiods between *R. microptera* and insects such as *Megalurothrips sjostedti* (Ekesi et al. 1999) and a northern population of *Locusta migratoria* (Tanaka et al. 1993) may derive from the different kinds of unfavorable seasons these insects encounter.

The biological significance of reduced egg number and egg size, but no change in age at oviposition, in late-season photoperiods under low-food conditions (Fig. 2B) could be interpreted in at least two ways. First, lack of a photoperiod effect on reproductive timing may indicate that our treatments were not sufficiently extreme, even though they reflect natural photoperiods for this population (see Materials and Methods). However, we also tested lubber grasshoppers on a more extreme photoperiod (9.25:13.75 [L:D] h; 3 g lettuce per day); even this extreme photoperiod did not affect the age at oviposition (S. Drakousis, J.D.H., and D. Borst, unpublished data). There are other seasonal cues that remain to be tested, including change in photoperiod (Tauber et al. 1986), temperature (Taub-Montemayor and Rankin 1997; Olvido and Mousseau 1998), crowding (Tanaka et al. 1993), and food quality (Tauber et al. 1986). Declining (as opposed to short but static) photoperiod, in particular, seems a likely cue to seasonal change for a long-lived insect like *R. microptera*. The oviposition cycle for these females lasted 35–50 d, and during that period, *R. microptera* near Everglades City, FL, could experience a decline of as much as 1 h in daylength (U.S. Naval Observatory 2001). Another experiment will be required to determine if a changing photoperiod would induce the predicted response to seasonal cues. Nevertheless, the treatments used in this experiment did produce a life history response, and it is that response we seek to understand.

A second, more interesting, interpretation is that reduced egg number and egg size in late-season photoperiods under low-food conditions may be an adaptive response to declining resource availability and the associated decline in growth rate (i.e., accumulation of mass) that would be attainable by a feeding grasshopper as the dry season advances. The dry season may lead to decreased quantity and quality of food due to drought stress of plants (e.g., English-Loeb et al. 1997) or due to ontogenetic changes in the plant tissue itself (reviewed by Scriber and Slansky 1981). Importantly, by either of these mechanisms, plant condition would continue to deteriorate until the following spring. Adjusting reproductive investment downward as the dry season approaches may reduce a female's risk of mortality (e.g., due to energy demands that cannot be met) or complete failure to produce a clutch due to food limitation. The impact of the dry season on growth and survival of adults and the probability of successful oviposition by *R. microptera* in the field is not known. However, laboratory experiments show that limiting food quantity does not usually cause

reduced survival of *R. microptera*, but does cause reduced mass of reproductive output and increased time to oviposition (Moehrlin and Juliano 1998; Hatle et al. 2000; food effect in the current study). If the dry season in south Florida reduces food quality or quantity for *R. microptera*, this does not necessarily mean that survival rate of these grasshoppers will be reduced. Instead, it may mean that the food resources needed to produce a full clutch will not be readily available. Short photoperiod and limiting food availability would thus be cues to these seasonal changes, and those cues were mimicked by our short-low treatment. A further effect of the subtropical winter season is low (but rarely freezing) temperature. Although unlikely to be lethal, winter temperatures are likely to have negative impacts on these grasshoppers, which appear to grow and to develop best at relatively high body temperatures. Lubber grasshoppers thermoregulate behaviorally to maintain a high body temperature (Whitman 1987; 1988 for the western lubber grasshopper; unpublished data for *R. microptera*).

Thus, based on our results, we propose a variant of the seasonal constraint hypothesis for insects like *R. microptera* that experience unfavorable growth seasons that are not likely to be lethal in the short run. We propose that to cope with seasonal declines in growth and development rate, insects respond to late-season cues by reducing demands for reproductive investment to match current resource storage and anticipated resource acquisition. In our experiment, the combination short days and low food resulted in no change in reproductive timing (Fig. 2A), but a reduction in the mass of reproductive output (Fig. 2B). The best interpretation of our data are that the combination of short days and low food availability serves as a cue to lubber grasshoppers indicating the oncoming cool, dry season, and associated poor growth conditions. These grasshoppers appear to respond to this cue by reducing the mass of reproductive output but not by accelerating reproductive timing.

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