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ARE REPRODUCTIVE TACTICS DETERMINED BY LOCAL ECOLOGY IN *ROMALEA MICROPTERA* (ORTHOPTERA: ACRIDIDAE)?

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ABSTRACT

We tested whether reproductive tactics of a univoltine insect can be predicted by local ecology, specifically mean length of the frost free period (FFP) as a measure of the potential active season. We measured reproductive tactics and longevity for populations of the lubber grasshopper *Romalea microptera* (Beauvois) from Miami, Florida (FL; 365 days FFP), Lydia, Louisiana (LA; 280 days FFP), and Athens, Georgia (GA; 224 days FFP). Differences in local climate led us to predict that GA grasshoppers will have shorter interclutch intervals, fewer clutches, and shorter lifespan than FL grasshoppers, with LA grasshoppers intermediate in these traits. When reared in a common laboratory environment, longevity, total reproductive period, and number of clutches produced were not clearly related to FFP. Longevity and reproductive period of LA grasshoppers were significantly less than those of FL grasshoppers, and number of clutches produced by LA grasshoppers was less than that for the FL or GA grasshoppers. First interclutch interval was significantly greater for LA than for GA grasshoppers. Our data suggest that phylogenetic relationships among populations may be a better predictor of reproductive tactics in this species.

Key Words: age at reproduction; climate; clutch size; grasshopper; life history; longevity; seasonality

RESUMEN

Probamos si las táctica reproductivas de un insecto del univoltine se pueden predecir por ecología local, específicamente longitud del período libremente mala de la helada (FFP) como medida de la estación activa potencial. Medimos táctica y la longevidad reproductivas para tres poblaciones del saltamontes, *Romalea microptera* (Beauvois), Miami, Florida (FL; 365 días FFP), Lydia, Louisiana (LA; 280 días FFP), y Athens, Georgia (GA; 224 días FFP). Estas diferencias en clima local conducen a la predicción que los saltamontes de GA tendrán período entre las hornadas del huevos más cortos, pocos hornadas del huevos, y esperanza de vida más corta que saltamontes del FL, con los saltamontes del LA intermedios en estos rasgos. Cuando estaba alzada en un ambiente común del laboratorio, la longevidad, el período reproductivo del total, y el número de los hornadas del huevos producidos no fueron relacionados claramente con FFP. La longevidad y el período reproductivo de los saltamontes del LA eran perceptiblemente menos que los de los saltamontes del FL, y el número de los hornadas producidos por los saltamontes de LA era menos que eso para los saltamontes del FL o de GA. El primer intervalo del hornadas era perceptiblemente mayor para el LA que para los saltamontes de GA. Nuestros datos sugieren que las relaciones phylogenetic entre poblaciones puedan ser un predictor mejor de estos aspectos de táctica reproductivas en esta especie.

Translation provided by the author.

Latitudinal variation in life histories can be related to adaptation to local climate (Rowe & Ludwig 1991; Temte 1993; Hemborg et al. 1998; Johansson & Rowe 1999; Berkenbusch & Rowden 2000; Hatle et al. 2002). For a univoltine organism, age at first reproduction and duration of interclutch intervals are likely to be positively related to the duration of the active season (Roff 1992; Forsman 2001), because of time-constraints in areas with shorter active seasons. There is often a tradeoff between early reproduction and longevity (e.g., De Souza Santos & Begon 1987; Rowe & Scudder 1990; Kaitala 1991; Stearns 1992; Leroi et al. 1994; Rowe et al. 1994; Miyatake 1997; Frankino & Juliano 1999). This trade-off yields a prediction of reduced longevity and late-life reproduction in populations from areas with short active seasons, where early reproduction is advantageous.

Hatle et al. (2002) examined latitudinal variation and trade-offs in reproductive tactics during the first oviposition cycle for three populations of the univoltine Eastern lubber grasshopper, *Romalea microptera* (Beauvois), testing for the joint

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relationships of latitude to age at first reproduction, somatic storage (body mass immediately after oviposition relative to initial mass), and clutch mass. All three populations differed in their multivariate responses for the three reproductive tactics we studied. This difference across populations was due primarily to age at first reproduction, secondarily to somatic storage, and less so to clutch mass. Age at first reproduction was least in Georgia (GA) (34.5 ± 1.2 days; mean ± SE), and significantly greater for Louisiana (LA) (38.5 ± 1.4 days) and Florida (FL) (41.5 ± 1.4 days) grasshoppers. Estimated somatic storage was greatest in FL and LA, and least in GA grasshoppers. Clutch mass was greatest in LA and GA, and least in FL grasshoppers. Thus, allocation of resources among these reproductive tactics is different across populations, in ways that could be adaptive for each local climate.

In the present study, we investigate interpopulation differences in number of egg clutches, interclutch intervals, period of reproduction, and longevity using the same lubber grasshopper populations used by Hatle et al. (2002). Differences in climate and potential active season duration for these populations are indicated by the differences in mean duration of the frost free period (FFP) for these locations: Miami, Florida (FL, 365 days FFP); Lydia, Louisiana (LA, 280 days FFP); and Athens, Georgia (GA, 224 days FFP) (Koss et al. 1988). Because of the shorter period potentially suitable for reproduction, we predict GA grasshoppers will produce clutches faster, with shorter interclutch intervals than FL grasshoppers. Because of the putative tradeoff of longevity and early reproduction, we also predict that GA grasshoppers should have a shorter lifespan. Based on climate, the number of clutches and longevity for LA grasshoppers should be intermediate between those for GA and FL grasshoppers.

Materials and Methods

Grasshoppers were shipped as young nymphs from our three source populations to our laboratory at Illinois State University (Normal, IL, USA). Each population was reared on a 14L:10D photoperiod and a corresponding 32:24°C thermocycle. This photoperiod was chosen to approximate those observed at each of the sites in mid-active season for the adult grasshoppers. Photophases of 14 h occur at Athens at approximately 25 July, at Lydia at approximately 7 July, and at Miami at approximately 26 June (the longest photophase observed at Miami is 13.75 h) (US Naval Observatory 2003). A 14-h photophase was used by Hatle et al. (2002) in a previous comparison of reproductive tactics of these same populations. Photoperiod affects reproduction in *R. microptera*, with females from south Florida (Luker et al. 2002) and north Georgia (R. Homeny & S. Juliano, unpubl.) altering reproductive tactics in response to short photoperiods (11.5 and 12.0 h, respectively) associated with autumn. Thus, a 14 h photophase, typical of mid-summer at all sites, provides a reasonable point of comparison. All grasshoppers were offered Romaine lettuce and oatmeal *ad libitum* throughout the experiment. For a laboratory colony of lubbers from south Florida, the first oviposition cycle (~35 d) involves first somatic growth and then reproductive growth. During the first ~10 d the primary oocytes are not vitellogenic, despite a ~50% increase in somatic mass (Sundberg et al. 2001). Hence, the nymphal stages appear to be relatively unimportant for acquiring nutritional resources for egg production, and we are justified in conducting a common garden experiment beginning with newly molted adult females.

After adult eclosion, males and females were reared separately. Every other day, males and females were randomly paired for mating. Mated females were placed on 1.0 kg of sand with ~7% water (by mass) for oviposition. The calendar date of first oviposition, and all subsequent ovipositions, was recorded for each female. We maintained mated females until death or until 25 September 2002, when we terminated the experiment.

Data on interclutch interval, number of clutches, and period of reproduction were analyzed by one-way ANOVA with multiple comparisons (REGWQ method PROC GLM, SAS Inst., Inc. 1990a) among population means when the overall ANOVA test was significant. Assumptions of normality and homogeneity of variances were met. Proportions of experimental females in the three populations remaining alive at the end of the experiment were compared by Fisher's exact test (PROC FREQ, SAS Inst., Inc. 1990b). Longevity for the three populations was analyzed by nonparametric survival analysis (PROC LIFETEST, SAS Inst. Inc. 1990b, Allison 1995). Pairs of populations were compared for proportions alive and for survival time distributions with two-group Fisher's exact tests and two-group nonparametric survival analyses, respectively, with a sequential Bonferroni correction at experimentwise $\alpha = 0.05$ (Rice 1989).

Results

Clutch Production

Mean number of clutches produced differed significantly among populations ($F_{2,54} = 13.50, P = 0.0001$). LA grasshoppers produced significantly fewer clutches than did GA or FL grasshoppers, whereas GA and FL grasshoppers produced similar numbers of clutches (Fig. 1A).

The interclutch intervals between first and second, second and third, and third and fourth ovipositions were determined for each population

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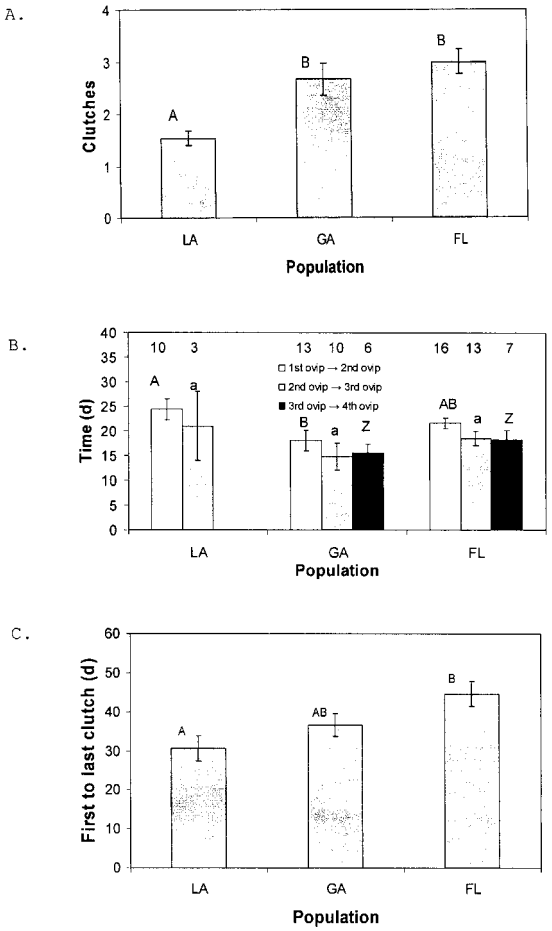


Fig. 1. Reproductive tactics of three populations of lubber grasshoppers, reared in a common environment. A. Number of clutches produced by each population. Means (± SE) for LA (N = 24), GA (N = 15), and FL (N = 18) grasshoppers associated with the same letters are not significantly different at $\alpha = 0.05$. B. Clutch intervals for three populations. Sample sizes are given at the top of the graph, above the corresponding mean. Within each interval, means (± SE) associated with the same letters are not significantly different at $\alpha = 0.05$. C. Time from each grasshopper's 1st clutch until its last clutch. Means (± SE) for LA (N = 10), GA (N = 13), and FL (N = 16) grasshoppers associated with different letters are significantly different at $\alpha = 0.05$.

(Fig. 1B). None of the interclutch intervals was significantly different at $P = 0.05$, but the interval from first to second oviposition for the LA vs. GA grasshoppers came close ($F_{2,36} = 3.12, P = 0.0564$).

Reproductive Period and Longevity

Reproductive period was quantified as the time from the first clutch until the last clutch (Fig. 1C). This period differed significantly among populations ($F_{2,36} = 4.86, P = 0.0136$) and was significantly less for LA grasshoppers than for FL grasshoppers. GA grasshoppers were intermediate and statistically indistinguishable from the other two populations.

The proportion alive at the end of the experiment differed significantly among the three populations ($P < 0.0001$). Pairwise tests indicated that the proportion alive for FL (0.63, N = 19) was significantly greater than that for LA (0.12, N = 25) and for GA (0.24, N = 17). Proportions alive for GA and LA did not differ significantly.

Survival distributions were quantified as the time from first clutch until death or the end of the experiment on 25 September. Individuals alive at the end of the experiment yielded censored observations, which are accounted for by PROC LIFETEST (see Allison 1995 for details). Survival analysis indicated significant differences in longevity among populations (Fig. 2). Pairwise tests indicated that longevity for FL was significantly greater than that for LA, and that GA was intermediate, and statistically indistinguishable from both FL and LA (Fig. 2). The majority of the FL individuals were still alive at the end of the experiment (Fig. 2). The early survivorship curves for FL and GA were very similar, indicating lower mortality than that for LA (Fig. 2), but later, mortality for GA accelerated and was more similar to that for LA (Fig. 2).

Discussion

Our prediction, based on local climate, that GA grasshoppers should have quicker clutch production and shorter lifespan than FL grasshoppers, and that LA grasshoppers would be intermediate, was not supported. Most reproductive tactics were roughly equal for FL and GA populations and longevity did not differ significantly. The most striking result in the data is the difference in reproductive tactics (number of clutches, reproductive period) and longevity between FL and LA grasshoppers.

We used the period from first clutch until death to estimate longevity. Hatle et al. (2002) found that these populations varied in the period from adult molt to first oviposition in a pattern partially consistent with variation of the frost-free interval (i.e., GA < LA = FL; see Introduction for means). In the present experiment, our measure of longevity did not include the period from adult molt to first clutch. Because of this, we have underestimated the difference in longevity between GA grasshoppers and LA and especially FL grasshoppers, and we have also underestimated the difference in longevity between LA grasshoppers and FL grasshoppers. Although the estimate of longevity we used is incomplete, the fact that it underestimates the difference between FL and LA grasshoppers strengthens our inference that these two populations differ in longevity.

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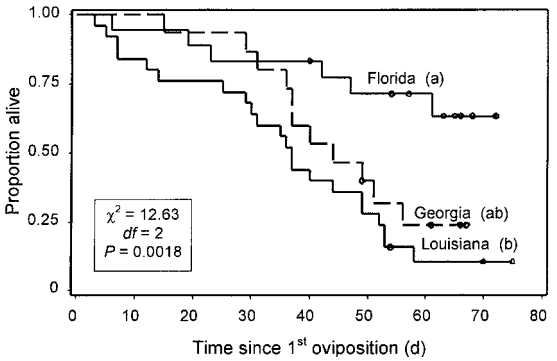


Fig. 2. Survivorship curves for three populations, beginning at first oviposition. Open points on the curves represent one or more censored observations. Overall χ^2 is for a nonparametric log-rank test of the null hypothesis of equivalent survivorship curves for FL (N = 18), GA (N = 15), and LA (N = 25). Curves associated with the same letters are not significantly different by pairwise log-rank tests (α = 0.05).

An estimate of total longevity for these three populations can be obtained by adding mean times to produce the first clutch reported by Hatle et al. (2002, see Introduction for values) and mean longevities from first oviposition recorded in the present study. Because of censoring, these mean longevities underestimate actual longevity, particularly for FL. Mean longevities from first oviposition for FL, GA, and LA are 51.5, 43.2, and 35.2 days, respectively, which yield estimates of longevities from eclosion of 93.0, 77.7, and 73.7 days, respectively. Thus, these estimates suggest it is FL that is unusual in its longevity and that despite a considerably greater apparent active season, LA grasshoppers have a lifespan as short as that for GA. These differences in longevity appear to be correlated with differences in first clutch mass (FL < GA = LA, Hatle et al. 2002), suggesting that longevity is indeed negatively related to early reproductive effort across populations.

Five years of field observations suggest that this population of LA grasshoppers senesces during the first week of September (J.D. Hatle, pers. obs.). Senescence occurs despite the fact that the mean temperature in Lydia, LA for 07 September is 27°C and mean rainfall for September is 144 mm (Weather.com 2003). Indeed, conditions seem to be ideal for lubbers during September in LA, and vegetation is still lush at this season. The mean temperature in Miami, FL for 07 September is 28°C and the mean rainfall is 160 mm. In Athens, GA the mean temperature on 07 September is 24°C and the mean rainfall is 98 mm. In contrast to their September senescence in LA, lubbers are present nearly the entire year in south FL, and all but the coldest months in north FL (Capinera et al. 2001), which has a climate very similar to south LA. In north GA, lubbers may be present into September (D. W. Whitman, pers. comm.), but are clearly declining in abundance during August (M. Brown, pers. comm.). It is unclear why this LA population of lubbers senesces in September, but based on our laboratory data, we propose that decreased survivorship of LA grasshoppers in September is a result of intrinsic factors that bring on senescence, rather than a result of increased disease or predation in this natural environment.

We find no evidence that interpopulation differences in interclutch intervals correlate with the duration of the FFP at these sites. The time required to produce the first clutch seems likely to be the most critical period with respect to laying multiple clutches before the end of the favorable season. The calendar dates of laying the second and third clutches are likely to be earlier if the first clutch is shorter. This may explain why we failed to find interpopulation differences interclutch intervals that correlate with the FFP, whereas Hatle et al. (2002) found interpopulation differences in the time required to produce the first clutch that did correlate with the FFP.

If local climate is not strongly related to these reproductive tactics, what does determine these fitness-related traits? Sequence analysis of mitochondrial DNA yielded a 69% probability that GA and FL populations are more closely related to each other than either is to the LA population (Mutun and Borst 2004). Thus, if reproductive tactics in this grasshopper are primarily associated with phylogenetic lineage, and not readily modified by local climate-driven natural selection (e.g., because genetic variation for these reproductive tactics is limited) we obtain alternative predictions: GA and FL grasshoppers will have similar reproductive tactics and longevity, and LA grasshoppers will differ from GA and FL grasshoppers. One of our results is consistent with this hypothesis. Grasshoppers from GA and FL produced a similar number of clutches, whereas LA grasshoppers produced a smaller number of clutches. Differences in interclutch intervals, time from first to last clutch, and longevity are not obviously consistent with either of these hypotheses.

Our results suggest that if these life history tactics are related to ecological conditions at each site, those conditions must involve more than active season duration, at least as it can be quantified by a crude measure like FFP. Alternatively, some differences in these life history tactics may in fact not reflect current adaptation, but rather, the phylogenetic constraints derived from the histories of different lineages. Because we have only examined three populations, our ability to correlate reproductive tactics with phylogeny is quite limited. Thus, at present we cannot distinguish between the hypotheses of more complex ecological determinants of reproductive tactics or phylogenetic constraints on reproductive tactics.

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