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Geographic variation of reproductive tactics in lubber grasshoppers

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Abstract We investigate plastic and interpopulation variation of trade-offs among reproductive tactics. There is a potential three-way trade-off among timing of reproduction, somatic storage, and investment in reproduction. We tested whether this trade-off shows latitudinal interpopulation variation. We studied populations of the lubber grasshopper, *Romalea microptera*, from Florida (FL; lowest latitude), Louisiana (LA; intermediate latitude), and Georgia (GA; highest latitude), each tested at three diet levels. All three populations differed in their multivariate responses of 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 GA, intermediate in LA, and greatest in FL grasshoppers. 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. Diet levels also differed in this suite of reproductive tactics, primarily due to variation in age at reproduction. In contrast to significant, independent effects of population and diet, we find no evidence that the trade-off itself varies across populations (as indicated by the non-significant interaction of population and diet level). Thus, we show that the innate allocation of resources among reproductive tactics is different across populations, but all three populations responded similarly to a range of diet levels.

Keywords Phenotypic plasticity · Lubber grasshoppers · Reaction norm · Latitudinal variation

Introduction

For many organisms, trade-offs exist among reproductive traits (Roff 1992; Stearns 1992; Glazier 1999). One of the most common trade-offs in insects is between early fecundity and longevity (e.g., Rose 1984; Kaitala 1991; Miyatake 1997; Frankino and Juliano 1999). For species inhabiting a range of climates, early onset of reproduction could increase fitness for individuals in areas subject to seasonal constraints, such as onset of an unfavorable climate (Rowe and Ludwig 1991). Early reproduction has costs, such as reduced investment in offspring, reduced somatic storage, or reduced longevity (De Souza Santos and Begon 1987; Rowe and Scudder 1990; Kaitala 1991; Leroi et al. 1994; Djawdan et al. 1996; Frankino and Juliano 1999; Forsman 2001). Although advantages of early reproduction may outweigh these costs when seasonal constraints are severe, such costs could diminish fitness in environments in which constraints are minimal (Rowe et al. 1994; Glazier 1998, 2000; Johansson and Rowe 1999). Thus, there may be a three-way trade-off among onset of reproduction (which may influence potential number of clutches in a season), investment in reproduction (which may influence investment per offspring or number of offspring), and somatic storage (which may influence future reproduction or adult survival).

In concert with this trade-off, latitudinal variation in the onset of reproduction is known for several organisms. Latitudinal variation has often been attributed to microevolutionary adaptation to climates, in both plants (e.g., Lacey 1988; Winn and Evans 1991; Li et al. 1998) and animals (Temte 1993; Hemborg et al. 1998; Berkenbusch and Rowden 2000). In addition, there have been several studies on reproductive trade-offs (Dearn 1977; Kaitala 1991; Frankino and Juliano 1999; Seigel and Ford 2001), but few of these have examined timing of reproduction. Most recently, Forsman (2001) investigated trade-offs among morphs (i.e., not latitudinally distinct populations) of pygmy grasshoppers, and he found a trade-off of clutch timing and clutch size, but no evidence that

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stored fat was also involved in the trade-off. To our knowledge, geographic variation in a trade-off between age at reproduction and somatic storage has been shown only for pied flycatchers (Hemborg et al. 1998), and never for insects.

Latitudinal variation in reproductive tactics would be particularly likely in species with low vagility and gene flow, resulting in a high potential for local adaptation (Mopper 1996). Eastern lubber grasshoppers [*Romalea microptera* (=guttata)] are univoltine, flightless, and exhibit low vagility. Lifetime dispersal of individuals has been estimated at 50 m (D.W. Whitman, unpublished data). Hence, lubber grasshopper populations are nearly isolated both in time and space. The geographic range of lubbers includes climates that differ distinctly (see Methods, animal collection and care). Populations of lubbers vary in their hatching dates, whereas most populations (and all three used in this study) seem to die in September (D.W. Whitman and J.D. Hatle, personal observations). Over their range, lubber populations exhibit dramatic color and size variation. Florida lubbers are mostly yellow; Louisiana lubbers are larger and black, and Georgia lubbers are almost one-third smaller in mass and intermediate in color. All three of these populations are distinguishable by their mtDNA cytochrome-b gene sequences, and Florida and Georgia grasshoppers appear to be more closely related to each other than to Louisiana grasshoppers (Mutun 1999). Finally, lubber nymphs have a lengthy development period (60–100 days), potentially limiting the time available for adult growth and reproduction (Flanagin et al. 2001).

Reproductive tactics of lubber grasshopper females are plastic in response to food availability (Moehrli and Juliano 1998; Hatle et al. 2000). Females offered lower amounts of food during the first 2 weeks of adulthood both delayed oviposition and produced fewer eggs when compared to females fed ad libitum. Reductions in clutch size due to low amounts of food appear to be the result of facultative oocyte resorption (Moehrli and Juliano 1998; Sundberg et al. 2001). Moehrli and Juliano (1998) observed no variation in egg size, in contrast to nearly twofold variation in egg number, in response to different diet levels. This suggested that in the physiological trade-off between egg size and egg number, lubbers adjust the number of eggs. This study did not examine somatic storage.

The interpopulation morphological variation in lubber grasshoppers suggests that life-history characteristics might also vary among populations. We tested the hypothesis that there is interpopulation variation for the trade-off among age at first reproduction, somatic storage, and investment in the first clutch (see Djawdan et al. 1996; Hemborg et al. 1998; Glazier 2000; Forsman 2001). We also examined how reproductive output was packaged, to investigate the trade-off between egg size and egg number. We used populations of *R. microptera* from Florida (FL), Louisiana (LA), and Georgia (GA). Specifically, we predicted that:

1. age at first reproduction (=oviposition) is directly related to length of the active season, so that for age at oviposition, FL>LA>GA;
2. age at first reproduction is part of a three-way trade-off involving somatic storage and clutch mass; because of this trade-off, we predict positive correlations of age at first reproduction with:
 - a. clutch mass, such that FL>LA>GA, or;
 - b. somatic mass after the first oviposition cycle, so that for storage, FL>LA>GA;
3. food availability will affect the three-way trade-off differently in the three populations (i.e., a significant interaction of diet and population), implying that *plasticity* of reproductive tactics varies among these populations.

Materials and methods

Animal collection and care

Grasshoppers from all three populations were field-collected as nymphs and shipped to our laboratory in Illinois. The three populations were from locations in the southeast United States of America: 17000 block of SW 119th Ave., Miami (FL); highway 83 about 6 km east of Lydia (LA); the Boulevard neighborhood in Athens (GA). These locations were chosen in part because they fall along a latitudinal cline with different climates. Their latitude-longitude locations are: FL, 25.8°N, 80.3°W; LA, 29.9°N, 91.8°W; GA, 34.0°N, 83.4°W. The 10-year average periods between first and last frost at each location are: FL, 0 days; LA, 85 days; GA, 116 days. Each location is about 1,100 km from each of the other two locations. We raised nymphs from each population to adulthood in communal cages on ad libitum Romaine lettuce and oats, at 25±2°C and a 14L:10D photoperiod. On the day of adult eclosion, we transferred each female to an individual, 500-ml ventilated cage at a 14L:10D photoperiod and a corresponding 32:24°C thermocycle. We assigned newly eclosed females to one of three feeding treatments that were adjusted for the individual's size (as estimated by femur length). Low-fed grasshoppers were offered [femur length (mm)*0.075] g Romaine lettuce and [femur length (mm)*0.75] mg oats daily. Medium-fed grasshoppers were offered twice the low-fed ration; high-fed grasshoppers were offered twice the medium-fed ration. Grasshoppers on the low-food treatment nearly always consumed their entire daily ration, whereas grasshoppers on the high-food treatment never consumed their entire daily ration (i.e., it served as an ad libitum diet). Each grasshopper was weighed at adult eclosion.

After age 25 days, we placed each grasshopper in a 1-liter plastic oviposition cup with 1,000 g sand plus ~7% water for at least 1 hr each day. We repeated this daily until the individual oviposited. Upon oviposition, we weighed the grasshopper, recorded her age, and counted the number of eggs laid. We then froze the grasshopper and later counted the number of full-sized eggs retained in the calyx and the number of oocyte resorption bodies. In the remainder of the paper, we report the number of total eggs produced by each grasshopper (eggs laid+full-sized eggs in the carcass). Finally, we selected ten laid eggs, dried them at 60°C for at least 24 h, and recorded their dry mass.

Statistical analysis

We analyzed the data using two, two-way MANCOVAs and one, two-way ANOVA. For both MANCOVAs, we used mass at eclosion as a covariate. All variables were log-transformed to meet assumptions of normality, homogeneity of variances, and linearity and homogeneity of slopes relative to the covariate (which was

also log-transformed). Our first MANCOVA examined allocation of resources to current reproduction, somatic storage, and the onset of reproduction. We tested for effects of diet, population, and the interaction of population and diet on: (1) age at oviposition; (2) somatic mass immediately after oviposition (=mass after laying-mass of unlaidd, full-size eggs retained in the calyx); and (3) clutch mass (=number of eggs*average mass of a single egg). We determined that full-size, unlaidd eggs have the same length as laidd eggs. Our second MANCOVA addressed how the reproductive output was packaged, to test for a trade-off between egg size and egg number. We tested for effects of diet, population, and the interaction of population and diet on: (1) average mass of one egg; and (2) number of eggs produced. For both MANCOVAs, we used *F* statistics derived from Pillai's Trace (SAS 1989; Scheiner 2001). We tested any significant MANCOVA effects using multivariate pairwise contrasts (Scheiner 2001), with sequential Bonferroni correction for multiple tests within each MANCOVA at experimentwise $\alpha=0.05$ (Rice 1989). We interpreted the contributions of individual dependent variables to significant effects using standardized canonical coefficients as outlined by Scheiner (2001). Finally, we tested for effects of diet, population, and the interaction of population and diet on the number of egg resorption bodies with an ANOVA, because this response variable was not affected by body size (see Results). We used SAS PROC GLM for all analyses (SAS 1989).

Results

Timing of reproduction and allocation of mass

Diet strongly affected age at oviposition, moderately affected clutch mass, and did not affect the mass after oviposition (see standardized conical coefficients in Table 1; Fig. 1A, B). The first MANCOVA showed significant effects of diet level and population, but the interaction of diet and population was not significant (Table 1). Because we used mass at adult eclosion as a covariate, mass after oviposition indicates the somatic mass gained during the egg-production cycle. Canonical coefficients for age at oviposition and clutch mass were of opposite signs (Table 1), indicating that diet treatments that increased age at oviposition also decreased clutch mass (Fig. 1B). Multivariate pairwise contrasts for diet groups showed that low food differed significantly from high and medium food, which did not differ from each other (Table 1; Fig. 1A, B). The clearest effect of diet was that low-fed individuals produced smaller

clutches much later than medium- and high-fed individuals (Fig. 1B).

Population strongly affected age at oviposition, and secondarily affected both clutch mass and mass after oviposition (Table 1; Fig. 1C, D). Multivariate pairwise comparisons showed that each population differed from the other two, but that the variables that contributed most to the pairwise differences were not the same for each pair of populations (Table 1). Comparing females from FL and LA, FL females laidd smaller clutches and laidd somewhat later, whereas mass after oviposition differed little (Table 1; Fig. 1C, D). Comparing females from FL and GA, FL females laidd much later, retained more mass after oviposition, and produced smaller clutches. Comparing females from LA and GA, LA females laidd significantly later and retained more mass after oviposition, but clutches differed little in mass. Louisiana females were, in some ways, intermediate between FL and GA females in pattern of investment; they were intermediate in age at oviposition, similar to FL in mass retained after the cycle (Fig. 1C), and similar to GA in clutch mass (Fig. 1D).

Packaging of reproductive output

Diet strongly affected the number of eggs and only weakly affected egg size (Table 2; Fig. 2A). The second MANCOVA showed significant effects of diet level and population, but the interaction of diet and population was not significant (Table 2). Eclosion mass was significant as a covariate. For significant pairwise comparisons, the coefficient for egg number was opposite in sign from the coefficient for egg size, indicating that diets that yielded high numbers of eggs also yielded relatively small eggs (Table 2; Fig. 2A).

The population effect on the packaging of reproductive output was not as strong as the diet affect, but was still significant. The number of eggs was the primary source of interpopulation differences (Table 2; Fig. 2B). In pairwise comparisons, only FL and LA grasshoppers differed significantly in the packaging of reproductive output, with FL grasshoppers producing fewer eggs than LA grasshoppers (i.e., opposite of our prediction).

Table 1 MANCOVA results and standardized canonical coefficients for the investment of reproductive output. For significant main effects, multivariate pairwise contrasts of factor levels are included. Effects significant in MANCOVA are highlighted in **bold face**. For multivariate pairwise comparisons, comparisons significant at experimentwise $\alpha=0.05$ are indicated also in **bold** (Sequential Bonferroni correction, six comparisons)

Source	Pillai's Trace (<i>F</i>)	<i>df</i>	<i>P</i>	Standardized canonical coefficients		
				Age at oviposition	Mass after oviposition	Clutch mass
Diet treatment	9.65	6, 106	0.0001	1.59	0.03	-0.66
H vs M	0.92	3, 52	0.4357	1.60	0.33	0.12
H vs L	29.78	3, 52	0.0001	1.62	0.06	-0.61
M vs L	24.78	3, 52	0.0001	1.54	-0.00	-0.73
Population	7.07	6, 106	0.0001	1.17	0.96	-0.62
FL vs LA	4.24	3, 52	0.0094	1.00	0.52	-1.11
FL vs GA	16.86	3, 52	0.0001	1.17	0.96	-0.61
LA vs GA	5.15	3, 52	0.0034	1.03	1.10	-0.04
Interaction	1.30	12, 162	0.2235	1.23	0.16	0.67
Eclosion mass	6.34	3, 52	0.0010	0.43	1.00	0.64

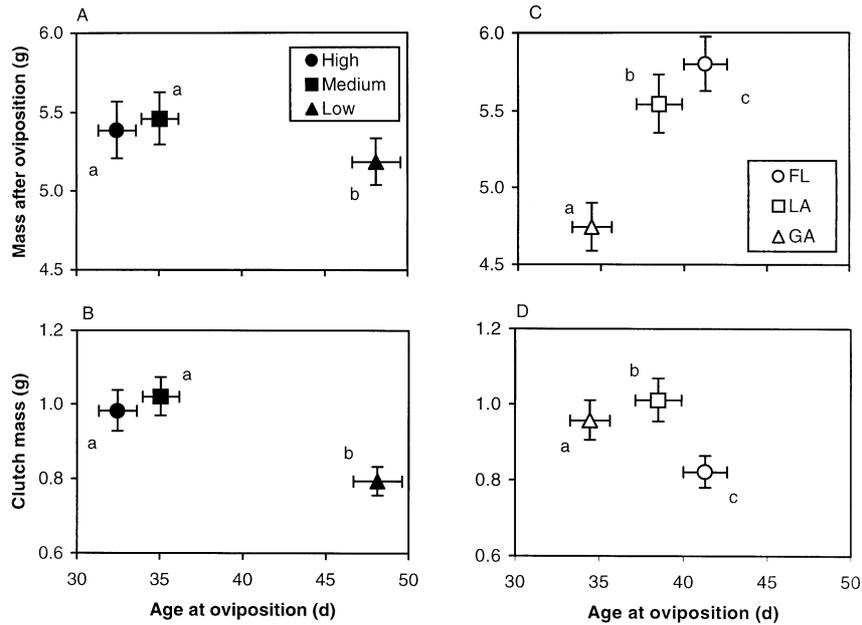


Fig. 1 Bi-variate plots of reproductive tactics by diet treatments (**A** and **B**) or populations (**C** and **D**). Data were statistically tested using a two-way MANCOVA. The interactions of diet and population for age at oviposition, mass after oviposition, and clutch mass were not significant. Hence, we combined the data from all three populations for the diet treatment plots, and we combined the data from all three diets for the population plots. Data sets with different

letters are significantly different. Error bars are ± 1 SE. Mass after oviposition indicates the somatic storage retained after laying the first clutch. All three populations lie at different points on the three-way trade-off among age at reproduction, somatic storage, and clutch mass. Importantly, the age at reproduction versus somatic storage trade-off for each population (**C**) is correlated with its latitude of origin

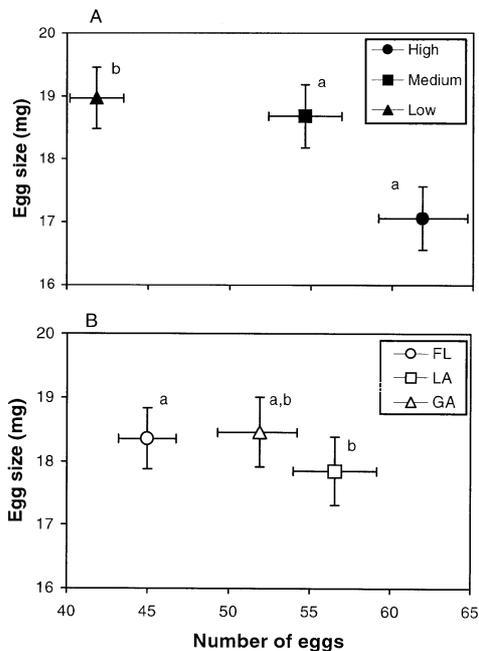


Fig. 2 Trade-off between egg size and egg number for diet treatments and populations. Data were statistically tested using a two-way MANCOVA. The interactions of diet and population for egg size and egg number were not significant. Hence, we combined the data from all three populations for the diet treatment plots (**A**), and we combined the data from all three diets for the population plots (**B**). Data sets with different letters are significantly different. Error bars are ± 1 SE. Both diet and population affected egg number more than egg size

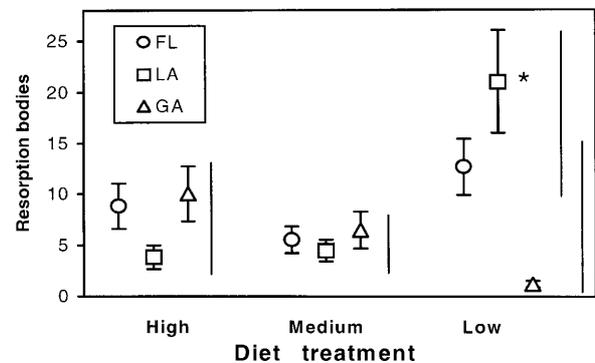


Fig. 3 Effects of diet treatment and population on number of oocyte resorption bodies. Data were statistically tested using a two-way ANOVA. Within a diet treatment, means associated with the same vertical line are not significantly different. Within each population, means marked with an asterisk are significantly different from all other means for that population. Error bars are ± 1 SE

Resorption bodies

There was a significant effect of diet ($F_{2,55}=9.06$; $P=0.0004$), no effect of population ($F_{2,55}=0.27$; $P=0.7677$), and a significant effect of the interaction of diet and population ($F_{4,55}=4.63$; $P=0.0027$) on the number of oocyte resorption bodies. Eclosion mass was not a significant covariate when testing the number of resorption bodies ($F_{1,54}=1.22$; $P=0.2740$), so we used ANOVA for this analysis. Low-fed LA grasshoppers resorbed more eggs

Table 2 MANCOVA results and standardized canonical coefficients for the packaging of reproductive output. Effects significant in MANCOVA are highlighted in **bold face**. For multivariate pairwise comparisons, comparisons significant at experimentwise $\alpha=0.05$ are indicated also in **bold** (Sequential Bonferroni correction, six comparisons)

Source	Pillai's Trace (<i>F</i>)	<i>df</i>	<i>P</i>	Standardized canonical coefficients	
				Egg mass	Number of eggs
Diet treatment	8.95	4, 110	0.0001	-0.42	1.35
H vs M	3.07	2, 54	0.0544	0.96	-0.61
H vs L	19.04	2, 54	0.0001	-0.50	1.30
M vs L	11.04	2, 54	0.0001	-0.14	1.44
Population	3.56	4, 110	0.0091	-0.20	1.43
FL vs LA	7.23	2, 54	0.0017	-0.24	1.42
FL vs GA	2.93	2, 54	0.0617	0.01	1.44
LA vs GA	1.15	2, 54	0.3254	-0.56	1.26
Interaction	1.28	8, 110	0.2618	0.64	1.08
Eclosion mass	5.76	2, 54	0.0054	-0.01	1.44

than high- and medium-fed LA grasshoppers and low-fed GA grasshoppers (Fig. 3). No other pairwise comparisons within diets or within populations were significant.

Discussion

Our data show innate differences across populations in the allocation of resources among age at first reproduction, somatic storage, and clutch mass (Fig. 1C, D). All three populations exhibit similar trade-offs of age at oviposition with somatic storage. We show no differences across populations in trade-offs (i.e., no significant interaction of diet and population). Hence our third prediction, implying that low-fed FL grasshoppers would produce more eggs later relative to low-fed GA grasshoppers, was not supported. Instead of differing in their plastic responses, these grasshopper populations appear to differ in their innate patterns of allocation of resources to reproductive tactics. Populations differ in life-histories averaged over environments, rather than in multivariate reaction norms. We believe this is one of the clearest demonstrations of geographic variation within a trade-off involving reproductive tactics. To our knowledge, this is the first demonstration of geographic variation within a trade-off of age at first reproduction versus somatic storage for an insect.

Timing of reproduction and allocation of mass vary across populations

The allocation of resources among age at reproduction, somatic storage, and mass of reproductive output differed among all three populations in ways that make sense in light of their respective local climates. Contrary to prediction, populations that showed delayed reproduction did not produce larger clutches, but instead produced smaller clutches (Fig. 1D) and had a greater gain in somatic mass (Fig. 1C) than did grasshoppers that showed early reproduction. Hence, lubber grasshopper populations that reproduce more slowly do not allocate the additional resources to the present clutch. Instead, most additional resources acquired by slower reproduction during the egg-production cycle are allocated to so-

matic mass. It seems probable that this stored mass would then be directed toward reproduction during subsequent clutches. These results are different from those for pygmy grasshoppers, which show a trade-off of clutch size with clutch rate, but not storage (Forsman 2001). This may reflect interspecific differences in allocation to current reproduction (i.e., clutch size) versus future reproduction (i.e., somatic storage).

The three-way trade-off across diet levels is not structured in the same way as the three-way trade-off across populations. The difference in the diet trade-off versus the population trade-off is clearest when comparing age at oviposition and mass after oviposition (Fig. 2A, C). Among diets, age at oviposition is only weakly and negatively related to mass after oviposition (=storage). In contrast, among populations, age at oviposition and mass after oviposition are strongly and positively related. The low-latitude population (i.e., FL) allocated more resources to somatic mass, but reproduced later and produced a smaller clutch than did the high-latitude population (i.e., GA). These traits were intermediate in a population from an intermediate latitude (i.e., LA).

We have now shown that reproductive tactics of lubber grasshoppers can vary due to both plasticity (Moehrli and Juliano 1998; Hatle et al. 2000; this study) and interpopulation variation (this study). This allows testing of hypotheses on the evolution of this phenotypic plasticity, by comparing the ranges of responses exhibited by the three populations. Some evolutionary biologists have hypothesized that plasticity is evolutionarily flexible (West-Eberhard 1989; Hodin 2000; Hodin and Riddiford 2000). This leads to the prediction that population variation in plasticity will be common. Our results suggest that this is not the case for egg production in lubber grasshoppers. We found no evidence of variation in plasticity across populations, and therefore no direct evidence that plasticity in egg production has evolved in lubber grasshoppers. Instead, we demonstrate simultaneous, but separate, plastic and population variation in egg production. Winn and Evans (1991) obtained similar results for plastic responses to light for the perennial weed *Prunella vulgaris*. The developmental physiology underlying aspects of plastic and population variation in reproductive tactics of lubber grasshoppers will be a focus of future studies (see Hatle et al. 2001).

Variation in packaging of reproductive output is largely due to the number of eggs

Examining the packaging of reproductive output can shed light on the evolutionary mechanisms by which populations have adapted to local conditions. Our results suggest that populations varied primarily in the numbers of eggs rather than egg size (Fig. 2), and this appears to explain most of the interpopulation variation in clutch mass (Fig. 1D). Lubber grasshoppers on limiting diet levels also responded primarily by reducing the number of eggs, and not by adjusting the size of eggs (Fig. 2). Thus, the diet-induced variation in clutch mass (Fig. 1B) is largely explained by the number of eggs laid. This agrees with a previous study in which lubber grasshoppers from south Florida responded to a range of diet levels by producing different numbers of eggs, but not different sizes of eggs (Moehrli and Juliano 1998).

Many reproductive trade-offs have been demonstrated in insects (Roff 1992; Stearns 1992), such as longevity versus early reproduction (e.g., Rose 1984; Miyatake 1997). Effects on longevity in this trade-off may be caused by greater somatic storage (Djawdan et al. 1996). If somatic storage is a general mechanism for longevity, then our results suggest an early fecundity versus longevity trade-off in lubber grasshoppers. In addition, changing somatic storage may be the mechanism behind some previously documented trade-offs between early fecundity and longevity in other insects. That we observed an interpopulation trade-off in early fecundity versus somatic storage, rather than egg number, suggests that the early fecundity versus somatic storage trade-off may be more evolutionarily labile than the early fecundity versus egg number trade-off (but see Forsman 2001).

Interpopulation variation in reproductive tactics is important because it implies adjustment to local conditions (Bradshaw and Holzapfel 1989; Kaitala 1991; Reznick et al. 1996a, b; Frankino and Juliano 1999; Glazier 2000; Forsman 2001). This variation might be particularly important when the populations are geographically isolated, as is the case for lubber grasshoppers. Such isolated populations are primed for adaptive evolution. Microevolutionary trade-offs in reproductive tactics, typically demonstrated by laboratory selection experiments, are evidence of pleiotropy involving two traits important to fitness (Stearns 1992). Many laboratory experiments have demonstrated both that such linkages exist and that they are subject to artificial selection. We now have evidence, via a natural experiment, that the linkage of age at reproduction and somatic storage may be subject to natural selection in insects. This is important for the evolution of life-history traits. It serves as evidence that suites of reproductive tactics might evolve in concert to maximize fitness in response to environmental variation.

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