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Population and environmental effects on the size-fecundity relationship in a common grasshopper across an aridity gradient

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Abstract

Body size is of primary interest to biologists because of its often positive correlation with fitness, in particular fecundity. The size-fecundity relationship is well established both within and among species. However, little is known about how the size-fecundity relationship differs among populations of the same species or whether it differs in response to environmental conditions experienced by a single population. This study examines the size-fecundity relationship in the pallid-winged grasshopper (*Trimerotropis pallidipennis*: Acrididae, Oedipodinae) among seven populations that extend along an aridity gradient in the southwestern United States. Results showed a positive relationship between body size of field-caught females and precipitation along the gradient, but only among those populations that receive less than 12 cm rainfall a year. There was a positive relationship between body size and the number of mature oocyte in the ovaries and with the number of hatchlings. Potential fecundity, measured as the number of ovarioles, was not correlated with body size in any analysis. All analyses showed that populations differ in their size-fecundity relationships. This relationship was also examined in laboratory conditions that mimic years of high,versus low, food abundance. Results indicate that across the whole aridity gradient, the size-fecundity relationship is largely a function of available resources. The populations at the xeric end of the gradient however, change their reproductive strategy in years of low food abundance and invest more into reproduction per unit size than they do in years of high food abundance. Together, these results caution against assuming, *a priori*, a positive relationship between size and fecundity; results indicate this relationship depends on the measure of fecundity used, that populations can differ in this relationship and that this relationship can change with changes in environmental conditions. Last, when examined among individuals, body size explained less than 20% of the variation in fecundity, suggesting that body size is not the main determinant of reproductive success in this species.

Key words

Acrididae, aridity gradient, Oedipodinae, size-fecundity relationship, *Trimerotropis pallidipennis*, grasshopper

Introduction

Body size is an important component of fitness in almost all organisms. Larger males typically experience greater mating success (Kosal & Niedzlek-Feaver 1997), and in females, larger body size is often positively correlated with fecundity (Roff 1992). These relationships are well established across species (Calder 1984), and are prevalent within species as well (Honek 1993).

It is well known that body size in insects is plastic (Schlichting & Pigliucci 1998, Nijhout & Davidowitz 2008): in general, insects grow to be larger on higher quality diets and at colder temperatures (Davidowitz *et al*. 2003, 2004). Grasshoppers inhabit a wide range of habitats (Davidowitz & Rosenzweig 1998, Capinera *et al*. 2004) that differ in environmental conditions such as temperature and diet quality. Populations across and within these habitats are likely to experience different environmental conditions, as well as differences in the variability of those conditions (Davidowitz 2002). Such differences are likely to affect body size and potentially alter the size-fecundity relationship (Joern & Behmer 1997). Thus, it is possible, or even likely, that in grasshoppers, the size-fecundity relationship may differ among populations, or across seasons or habitats within a population. However, although the size-fecundity relationship is well established within species (Honek 1993), it remains unclear whether this relationship does in fact differ among populations, or between different environmental conditions experienced by a population.

In this study I address the relationship between size and fecundity in a common oedipodine grasshopper. I examine this relationship at three levels: across field-caught individuals irrespective of their population of origin, across seven populations located at different points along an aridity gradient in the southwestern US, and among individuals raised under laboratory conditions that mimic across-year variation in above-ground plant biomass. Individual populations along this gradient may experience high variation in plant biomass across years or across seasons (Davidowitz 2002), depending on the rainfall. It is well documented that above-ground plant biomass is positively correlated with rainfall (Rosenzweig 1968, Leith 1973), and that grasshopper population dynamics are largely determined by the effects of rainfall on above-ground plant biomass (Nearney 1961, Nearney & Hamilton 1969, Capinera & Horton 1989, Joern & Gaines 1990, Kohler *et al*. 1999). Thus, we may expect populations along a gradient of increasing aridity to experience decreasing plant biomass. This study examines how the size-fecundity relationship may change across such an aridity gradient.

Methods

Trimerotropis pallidipennis (Oedipodinae) is the most widely dispersed banded-winged grasshopper in the New World: it inhabits the western prairies and desert scrubs from southwestern Canada to central Argentina (with large gaps in the tropics of Central America, Otte 1984). *T. pallidipennis* is polyphagous, feeding on a wide variety of shrubs and herbs, but prefers grasses (Otte & Joern 1977). This species is considered a strong flier and is known to occasionally swarm, at which times it can be an agricultural pest (Otte 1984). *T. pallidipennis* weighs, 0.64 ± 0.02 g (wet weight, $\bar{x} \pm s_{\bar{x}}$, n=31) with females about 25% heavier than males. Adult females are 27-33 mm in length and adult males 21-24 mm. Female femur lengths are 14.8 ± 0.05 mm ($\bar{x} \pm s_{\bar{x}}$, n=230) and those of

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Fig. 1. Map of grasshopper collecting sites and weather stations (see text).

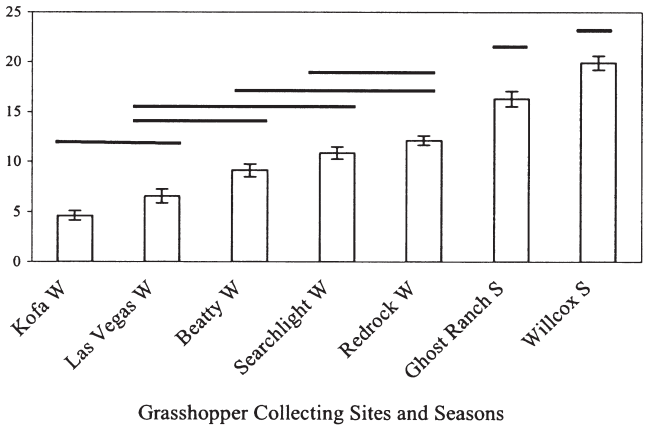


Fig. 2. Mean precipitation during grasshopper season at grasshopper collecting sites. W- winter (December to March), S – summer (July to October). Horizontal bars indicate sites that are significantly different at ∝= 0.05, with a Tukey post-hoc pair-wise comparison in a one-way ANOVA. Data obtained from NOAA through the Tree-Ring Laboratory at the University of Arizona

males 12.6 ± 0.04 mm ($\bar{x} \pm s_{\bar{x}}$, n = 255). Under laboratory rearing temperatures of 38°C day and 27°C night (12L:12D), the grasshoppers take 24.2±0.1 ($\bar{x} \pm s_{\bar{x}}$, n=217) days from hatch to adult. There are 32 ± 3 ($\bar{x} \pm s_{\bar{x}}$, n=304) eggs per pod and females can lay > 7 pods, at 2.6±0.04 ($\bar{x} \pm s_{\bar{x}}$, n=669)-day intervals. A single female was able to lay 955 eggs in 27 eggpods (Barnes 1963).

Adult grasshoppers were collected from seven populations in the southwestern United States (Fig. 1), located along a gradient of seasonal precipitation (Fig. 2): Beatty, Las Vegas, and Searchlight (Nevada) are in the Mojave Desert; Kofa and Redrock (Arizona) are in the Lower Colorado subdivision of the Sonoran Desert; Willcox (Arizona) is in a semidesert grassland; Ghost Ranch (New Mexico) is in a pine-juniper woodland (Brown and Lowe 1980, Brown 1982). The collecting sites of Beatty (n = 65 y of weather data), Ghost Ranch (n = 45 y) and Searchlight (n = 75 y), were all within 1 km of the nearest weather station. Distances to the nearest weather station for other collecting sites were: Kofa, 80 km; Las Vegas, 24 km (n = 53 y); Redrock 62 km; Willcox 14 km (n = 58 y). Weather data for Redrock and Kofa were from Tucson (n = 122 y) and Yuma (Arizona) (n = 120 y), respectively. NOAA weather data were obtained through the tree-ring laboratory at the University of Arizona. Weather data were used to identify the aridity gradient and the seasonal precipitation, averaged across all years, and used as a proxy for above-ground plant biomass (see above).

There is an unequal distribution of winter and summer rains in the southwestern US. The Mojave Desert receives predominantly winter rains, whereas the remaining biomes receive most of their rainfall in the summer (Davidowitz 2002). Grasshoppers reach their peak abundances in the rainiest season (*i.e.*, winter in the Mohave Desert and summer elsewhere). The summer rainy season was defined as July to October and the winter season as December to March (see Davidowitz 2002 for further details): during these months, nymphs and adults can be found (Otte 1984, Davidowitz pers. obs.). To minimize seasonal bias, only rainfall data for the season in which the grasshoppers were collected in each location were used (see Fig. 2).

In order to measure the size-fecundity relationship, grasshoppers were collected at the seven study populations and brought back to the laboratory. Male-female pairs from the same population were placed in individual cages and fed romaine lettuce (*Lactuca* spp.) and wheat bran *ad libitum* and the females allowed to oviposit. The bottom of the cages consisted of 473-ml plastic drinking cups, filled with moist sand to about 2 cm from the top. The upper half of the cage consisted of a cylinder of wire mosquito netting (15 cm tall, 9 cm diameter). A plastic petri dish was glued to the top. The sand provided an oviposition substrate, was replaced daily, and the eggpods allowed to hatch.

Upon hatching, an average of six randomly chosen nymphs from each family were placed in an individually marked cage. These resembled the adult cages described above, but were about one-third the size. The cages were kept on tables, over which were suspended 55, 100-watt indoor floodlights as a source of light and radiant heat. The lights were suspended 60 cm above the tables at 40-cm intervals. The nymphs were kept on a 12L/12D photoperiod with average day and night temperatures of 38.2±2 ($\bar{x} \pm s_{\bar{x}}$)°C and 26.9±1°C respectively.

Nymphs were placed in one of two treatments designed to mimic years of high and low food abundance. Nymphs in the high-food-abundance treatment were provided with an *ad libitum* diet of romaine lettuce and wheat bran, replenished daily. Nymphs in the low-food-abundance treatment received 6-mm diameter disks of romaine lettuce, given fresh daily, in the following design: 1st instar-1 disk, 2nd instar- 2 disks, 3rd instar-3 disks, 4th instar- 5 disks, 5th instar-6 disks, 6th instar- 7 disks, adults- 9 disks. In almost all cases, the lettuce in the low-food treatment was completely eaten in one or two meals. In no instance was the lettuce completely consumed in the high-food treatment. The nymphs in the low-food treatment were provided with unlimited amounts of wheat bran to prevent starvation. This mimics natural conditions, in which the grasshoppers have dried plant matter available as a food source even in the most extreme environments (MacMahon & Wagner 1985, G. Davidowitz pers. obs.). This diet was sufficient for the nymphs in both treatments to mature, develop fat bodies, and mature eggs (with the exception of the Redrock population in the low-food-abundance treatment).

Body size was measured as mean hind femur length (three measurements of each hind femur) using Optimus imaging software and analyzed with Image J (NIH). The number of mature oocytes in the ovarioles changes with time as the primary oocytes in the ovarioles are laid and the secondary oocytes mature: the time required for

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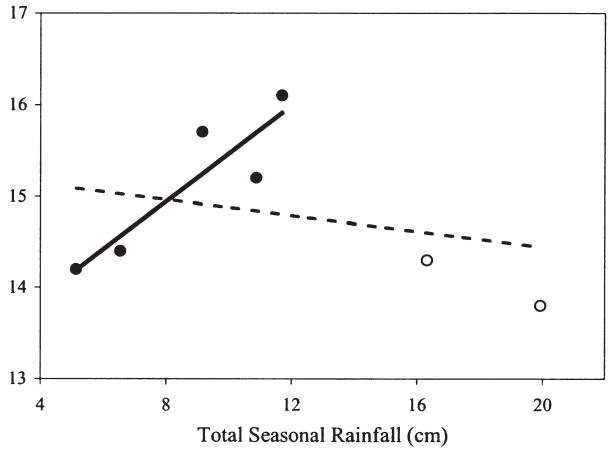


Fig. 3. Relationship between body size of field-caught females and rainfall. The five winter rainy-season populations below 12-cm rainfall (solid circles) show a significant positive relationship (female size = 0.003 × mean rainfall + 1.28, $r^2 = 0.81$, F = 12.49, p = 0.0385, N = 5). This relationship is no longer significant when the two summer rainy-season grassland populations (open circles) are added (female size = 0.0004 × mean rainfall + 1.53, $r^2 = 0.07$, F = 0.38, p = 0.5655, n = 7).

oocyte development is determined in part by available resources. In addition, grasshoppers may resorb immature oocytes depending on their nutritional status (Sundburg *et al.* 2001). For these reasons, only grasshoppers with mature oocytes, those with a visible micropyle on the chorion, were used to determine fecundity.

A subset of wild-caught females were dissected after they laid three eggpods, and number of ovarioles, number of mature oocytes, and oocyte size recorded as measures of fecundity. Similarly, a subset of offspring from each diet treatment were dissected 19 d postadult eclosion and number of ovarioles, number of mature oocytes, and oocyte size recorded as measures of fecundity. Oocyte size was measured as the mean length of six mature oocytes (those with a visible micropyle on the chorion) using a microscale (BioQuip) with a 0.1mm resolution and under appropriate magnification. For a subset of field-caught females, the number of nymphs that hatched from the first egg pods laid in captivity was counted as an additional measure of fecundity.

The number of ovarioles in a grasshopper is determined in the

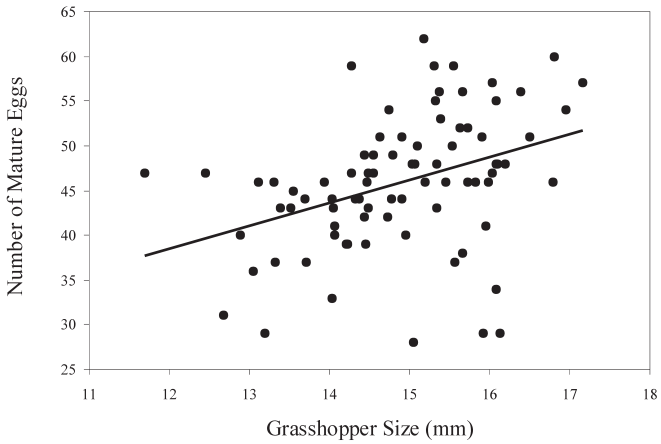


Fig. 4. Size-fecundity relationship of field-caught individuals. Fecundity is measured as the number of mature oocytes in ovarioles. Fecundity = 25.56 × size + 7.85, $r^2 = 0.14$, F = 13.29, p = 0.0005, n = 82.

Table 1. ANOVA of body size of field-caught females by collection site.

Source	df	MS	F	p
Site	6	26.75	57.13	<0.0001
Error	216	0.47		
Total	222			

embryo (Stauffer & Whitman 1997). In addition, the mother's condition and resulting egg size may, or may not, influence the number of ovarioles in their offspring. In some species, larger or better-fed, mothers apparently produce offspring with more ovarioles (Stauffer & Whitman 1997, Chapman 1998). We tested this using the field-caught females and their offspring.

Results

The aridity gradient.—A one-way ANOVA showed significant differences among sites in seasonal rainfall (Fig. 2), suggesting that grasshoppers along this gradient may experience differences in available above-ground plant biomass.

A regression of body size on the rainfall mean showed no significant relationship across the aridity gradient. However, among the five arid winter rainy-season populations (those receiving less than 12 cm rainfall in the season in which the grasshoppers were collected, Fig. 2), there was a significant and positive relationship between precipitation and grasshopper body size (Fig. 3). A one-way ANOVA of field-caught adult female grasshoppers revealed significant differences in body size among populations (Table 1).

The individual-level size-fecundity relationship.—The individual-level size-fecundity relationship was measured across all grasshoppers irrespective of their genetic background (*i.e.*, all populations were pooled). Larger field-caught females tended to have more eggs, although adult size explained only 14% of the variation in egg number (Fig 4). Ovariole number was not related to grasshopper size (ovariole number = 6.51 × size + 45.82, $r^2 = 0.03$, F = 2.26, p = 0.1371, n = 82). Grasshoppers with more ovarioles tended to have more eggs (Fig. 5). More hatchlings emerged from eggpods laid by larger females (hatchlings = 3.29 × size – 16.71, $r^2 = 0.11$, F = 24.18, p < 0.0001, n = 202).

The among-population size-fecundity relationship.—I asked whether the size-fecundity relationship changed across the gradient, using population means of field-caught females. If the size-fecundity relationship were constant across all populations along the gradient, the slope of the population mean regression would be zero (the intercept would change with the strength of the relationship). There was no significant difference between populations in the number of ovarioles in the wild-caught grasshoppers (ANOVA, F = 1.98, p = 0.0775, n = 95), and when the number of ovarioles was used as the measure of fecundity, the size-fecundity relationship across populations was not different from zero ($r^2 = 0.17$, p = 0.3543, F = 1.04, n = 7). When fecundity was measured as the number of mature oocytes however, body size explained over 61% of the variation in fecundity (Fig. 6). This relationship was also significant when the number of hatched nymphs was used as the measure of fecundity and size explained 56% of the variation in hatchling number (Fig 7). These two latter results indicate that populations across the gradient differ in their size-fecundity relationship.

Using these same field-caught females, I tested whether there

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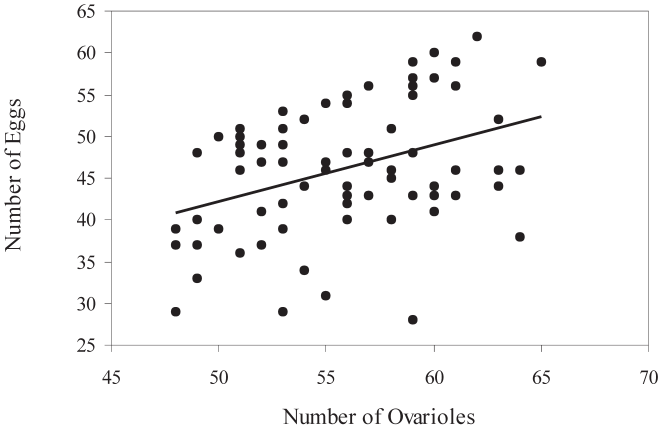


Fig. 5. Relationship between the number of ovarioles and the number of mature oocytes in field-caught individuals. Mature oocytes = 0.68 × ovarioles + 8.12, $r^2 = 0.16$, F = 14.76, p = 0.0002, n = 82.

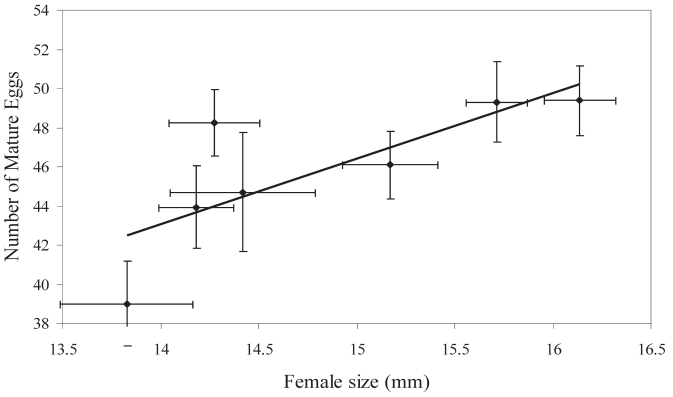


Fig. 6. Size-fecundity relationship of number of mature oocytes in field-caught grasshoppers. Each data point represents 8-16 females ($\bar{x} \pm s_{\bar{x}}$). Mature oocytes = 33.27 × size -0.3.49, $r^2 = 0.616$, F = 7.74, p = 0.0388, n=7.

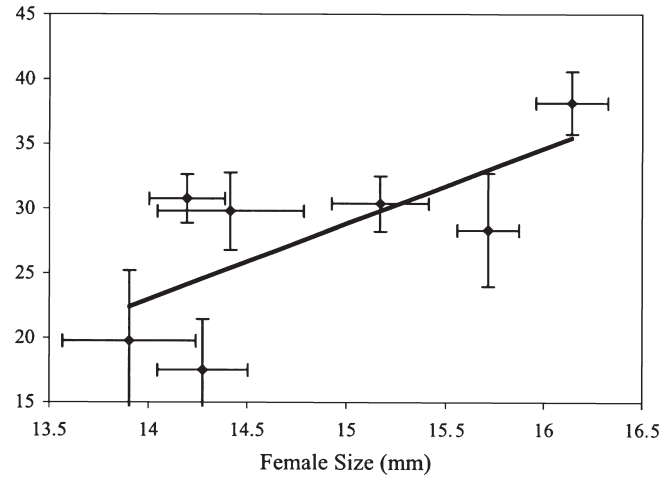


Fig. 7. Size-hatchling relationship from eggpods of field-caught females, comparing mean size of wild females from each population versus mean number of eggs hatching from each eggpod. Each data point represents 16-46 eggpods ($\bar{x} \pm s_{\bar{x}}$, n= 222 total). Hatchlings = 3.74 × size – 23.9, $r^2 = 0.56$, F = 6.32, p = 0.0535, n = 7.

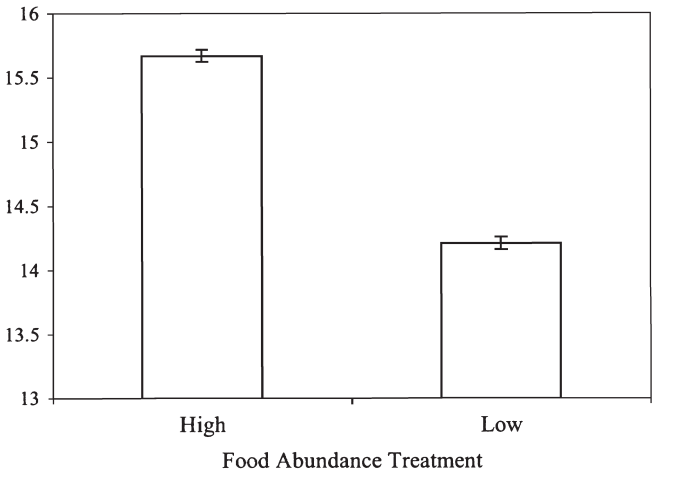


Fig. 8. Grasshopper body size in the two diet-abundance treatments (t = 21.75, p < 0.0001, n = 402).

were differences in the size-fecundity relationship within each population. In only one of the seven populations (Kofa, $r^2 = 0.57$, F = 18.7, p = 0.0001, n=16) was this relationship significant (after applying a Bonferroni correction). In the six other populations, the coefficients of determination ranged between 0.1% to 10% but were not significant. These results indicate that populations differ in their relationship between size and fecundity.

Does food abundance affect the size-fecundity relationship?— I tested whether plasticity in body size in response to food abundance could affect the relationship between size and fecundity. Before I could address this question, I first needed to determine whether there was a difference in size and fecundity between the two food-abundance treatments. Grasshoppers reared on unlimited amounts of food were significantly larger than those reared on a low food-abundance diet (Fig. 8). This result was significant within each of the seven populations individually as well (data not shown). Grasshoppers fed unlimited diet also matured more eggs than those reared on a limited diet (Fig 9), although there was no difference in the size of these eggs (t = 0.66, p = 0.5099, n = 70).

There was no significant difference in the number of ovarioles between the two diet treatments (t = -0.567, p = 0.5712, n = 408), nor were there any differences in ovariole number among populations within each treatment (ANOVA, high food: F = 1.87, p = 0.0864, n = 217; low food: F = 1.583, p = 0.1711, n = 191). Nor was the size-fecundity relationship with ovarioles as the measure of fecundity and including nymphs from both diet abundance treatments significant ($r^2 = 0.0001$, p = 0.8161, n=402). This relationship remained not significant for each treatment individually (high food abundance: $r^2 = 0.0096$, p = 0.1524, n = 215; low food abundance: $r^2 = 0.0005$, p = 0.7710, n=187). There was no relationship between the size of the field-caught mother and the number of ovarioles in the mother (F = 2.63, p = 0.1131, $r^2 = 0.07$, n = 39), nor between the size of the mother and the number of ovarioles in the offspring (F = 2.35, $r^2 = 0.017$, p = 0.1272, n = 135).

When the number of mature oocytes was used as the measure of fecundity, the size-fecundity relationship across both diet treatments was significant, although size explained only 9% of the variation in mature oocyte number in both food-abundance treatments together (Fig. 10). This relationship was not significant within each treatment

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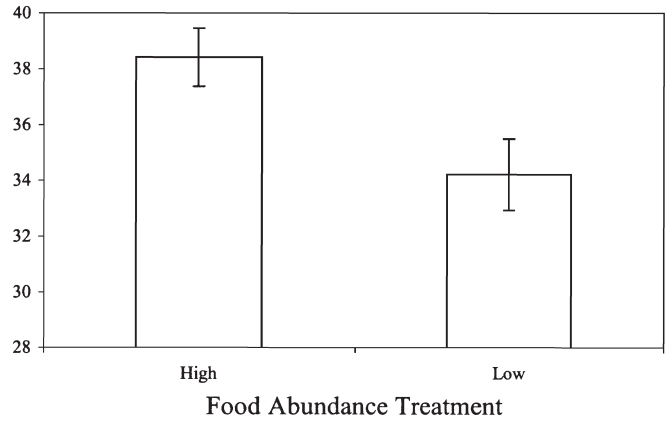


Fig. 9. Number of mature oocytes in ovaries in the two diet-abundance treatments ($\bar{x} \pm s_{\bar{x}}$, t = 2.558, p = 0.0117, n = 127).

primary reason for this interest is the often positive relationship between body size and reproductive output: larger females produce more offspring. Although there is ample evidence for a positive correlation between size and fecundity in individual populations (Honek 1993), it is not clear how this relationship changes among populations or among different growth conditions across habitats within populations.

T. pallidipennis is a polyphagous species with a very large geographic range (Otte 1984). As such, it encounters diverse habitats, fluctuating abundances of food (Davidowitz 2002) and foods of varying nutritional value (Otte & Joern 1977, Bernays & Simpson 1990, Bernays & Chapman 1994, Joern & Behmer 1998). The ability to plastically change the size-fecundity relationship in response to rainfall (and above-ground plant biomass) would provide a selective advantage to this generalist species.

It is well established that grasshopper population dynamics are tightly correlated with rainfall and subsequent above-ground

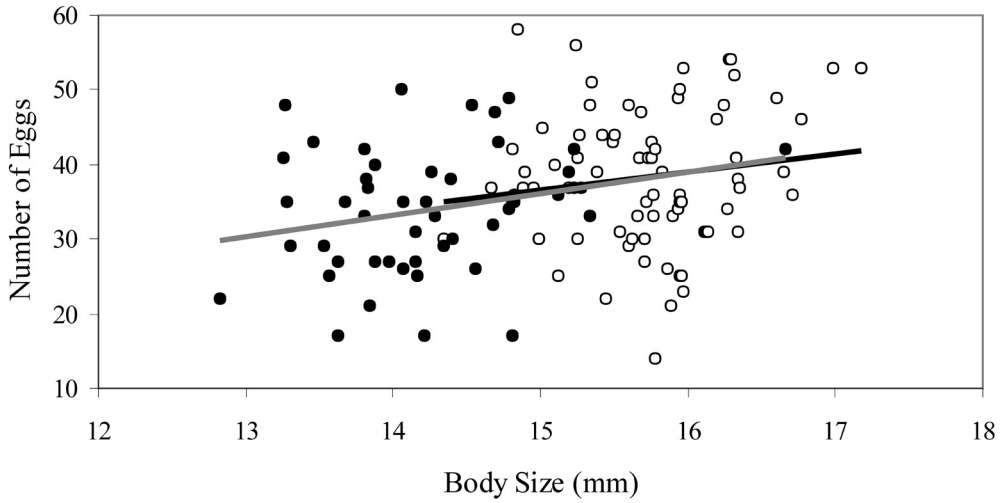


Fig. 10. The size-fecundity relationship comparing number of mature oocytes in females as the measure of fecundity within and between the high and low-food-abundance treatments. The open circles represent grasshoppers reared on a high-food-abundance diet and the closed circles represent grasshoppers reared on a low-food-abundance diet. The grey line represents the regression within the low food abundance diet treatment (mature oocytes = 0.28 × size – 6.56, $r^2 = 0.06$, F = 2.76, p = 0.1037, n = 48) and the black line represents the regression on the high-food abundance diet (mature oocytes = 0.24 × size + 0.6, $r^2 = 0.02$, F = 1.6, p = 0.2098, n = 75). These regression lines are almost completely overlapped by the regression line for both diet treatments together (for clarity this line is not shown, mature oocytes = 0.28 × size – 6.42, $r^2 = 0.088$, F = 11.63, p = 0.0009).

individually.

Although there was no relationship between adult size and ovariole number, there was a significant positive relationship between the number of ovarioles and the number of mature oocytes in field-caught females (number of mature oocytes = 9.32 + 0.66 × ovarioles, $r^2 = 0.15$, F = 15.15, p = 0.0002, n = 91). This positive relationship was significant within the diet treatments as well (high food abundance: mature oocytes = 0.93 × ovariole – 14.5, $r^2 = 0.19$, F = 12.6, p = 0.0008, n = 57; low food abundance mature oocytes = 1.02 × ovariole – 23.14, $r^2 = 0.25$, F = 14.2, p = 0.0005, n = 44).

Discussion

Body size is arguably one of the most important targets of selection and has long been the focus of ecological and evolutionary research (Calder 1984, Stearns 1992, Roff 1992, Bonner 2006). The vegetation (Nearney 1961, Nearney & Hamilton 1969, Capinera & Horton 1989, Joern & Gaines 1990, Kohler *et al*. 1999): the higher the rainfall, the more vegetation and the more resources available for grasshopper growth. Of the seven study populations across the aridity gradient, the five arid populations exhibited a significant positive relationship between rainfall and the body size of field-caught females (Fig. 3). This suggests the potential for differences in the size-fecundity relationship among populations. It also implies that grasshoppers will likely be larger in years of abundant rainfall and smaller in drier years within individual populations.

Across the entire gradient, there was a significant size-fecundity relationship (Figs 6,7). These nonzero slopes show that populations differ in their size-fecundity relationship. However, within populations, only one (Kofa), exhibited a significant size-fecundity relationship. Other studies have shown a similar positive size-fecundity relationship along a gradient, but not within individual populations

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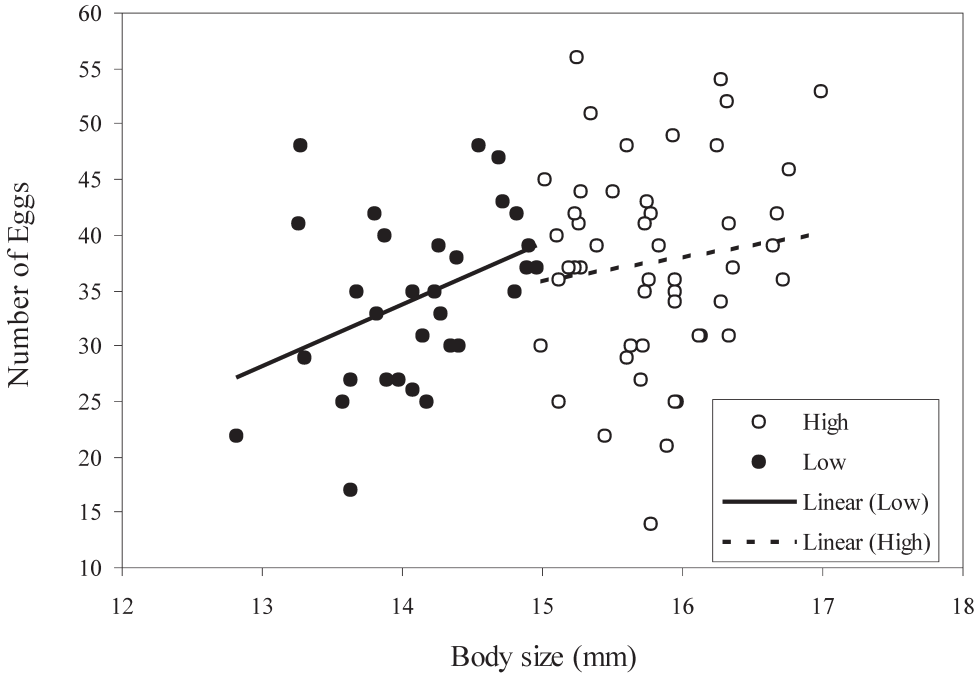


Fig. 11. Size-fecundity relationship of four xeric populations (Beatty, Kofa, Las Vegas, Searchlight) in the two food abundance treatments (see text). High food abundance (open circles): mature oocyte number = 6.53 + 1.96 × size, $r^2 = 0.015$, F = 0.70, p = 0.4075, n = 49. Low food abundance (filled circles): mature oocyte number = 24.2 + 4.13 × size, $r^2 = 0.16$, F = 5.71, p = 0.0236, n = 31.

(Orr 1996, Ashby 1998, Fischer *et al*. 2002). Both the gradient-level analyses and the within-population analyses show that populations differ from one another in their relationship between adult body size and fecundity. This is an important point, as it is often assumed in the literature that a positive size-fecundity relationship exists or that this relationship is consistent across populations.

One of the primary changes along an aridity gradient is the amount of vegetation available as food to the grasshoppers. It is not clear how such differences in food abundance influence the size-fecundity relationship. For example, in years of abundant rainfall grasshoppers may be bigger than grasshoppers growing in years of low rainfall (Fig. 8) and may lay more eggs (Fig. 9), but the relationship between adult size and fecundity can be isometric, indicating that fecundity is largely due to available resources. By contrast, the size-fecundity relationship may differ between high and low rainfall years, indicating a change in reproductive life history strategy. Such a difference would be evident as differences in the slope of the size-fecundity relationship between the two diet treatments. In this study, the size-fecundity relationship was significant across both diet treatments together, but not when examined within each treatment (Fig. 10). These results indicate that across the aridity gradient the size-fecundity relationship in this species, is largely a function of available resources.

However, at the xeric end of the gradient, but not the mesic, body size increased with an increase in rainfall (Fig. 3), suggesting that the pattern of the size-fecundity relationship shown in Fig. 10 may differ if only the five xeric populations were analyzed. We therefore reanalyzed the data in Fig. 10, excluding the two mesic populations (Ghost Ranch and Willcox). Redrock was excluded as well from the xeric populations, as no grasshoppers matured eggs in the low-food treatment. These results (Fig. 11) show that populations from habitats that receive < 12 cm rainfall differ in the size-fecundity relationship between years of high and low rainfall (high and low abundances of food). In high-rainfall years, there is sufficient food to produce eggs, irrespective of the body size of the mother. In years of low rainfall and limited food however, fecundity is positively correlated with body size. The greater slope in the low-food-abundance treatment indicates that in years of low plant productivity, grasshoppers change reproductive life history strategies and invest more into reproduction per unit size, than in years of high food abundance. This is further evidence that populations differ in their size-fecundity relationship and that this relationship can change with environmental conditions.

From the data presented here it is evident that the ability to identify a relationship between body size and fecundity depends on the metric used to measure fecundity. This point has been raised previously (Leather 1988, 1994) and was supported by the data in this study. The number of ovarioles was not correlated with size in any population or treatment. This is not surprising, because the number of ovarioles is presumably genetically or maternally determined before hatching, whereas body size is strongly influenced by environmental conditions during nymphal development. Also, insects rarely achieve their realized reproductive potential, because females often resorb some developing oocytes, even under optimal conditions (Wheeler 1996, Papaj 2000, Sundberg *et al*. 2001). The number of mature oocytes, eggs laid, and hatchlings were much better estimates of fecundity when determining the size-fecundity relationship (Figs 4-7, 10, 11). It is curious that individuals with more ovarioles produced more mature oocytes, because while ovariole number was not correlated with body size, the number of mature oocytes was. The mechanism for this is unclear.

Body size is often assumed to have a positive relationship with fecundity. Along a gradient of decreasing resources, this relationship differs among populations and among years or habitats within populations. Even though resource abundance is predictive of body size across the gradient, only the populations at the arid end of the gradient exhibited a significant relationship between body size and fecundity, under variable food treatments in the laboratory (Fig. 11). This suggests that *T. pallidipennis* in arid environments

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has evolved a plastic response in reproductive output to the highly variable rainfall patterns in the arid southwestern US (Davidowitz 2002). Even so, only 16% of the variation in fecundity could be explained by an individual's body size. Clearly, body size is not the main determinant of reproductive success in this species.

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