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Influence of individual body size on reproductive traits in melanopline grasshoppers (Orthoptera: Acrididae)

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Abstract

Body size affects many aspects of an organism's performance, including reproduction. Ecologists have shown an increased interest in linkages between body size variation and population dynamics. Fecundity in a number of insect orders is often positively correlated with body weight or structural size, but reproductive characteristics and body size are not always positively correlated, particularly in field studies. Numerous biotic and environmental factors can influence individual body size and reproduction in grasshoppers under field conditions. Intraspecific relationships between reproductive traits and individual body size in melanopline grasshoppers were examined using data from four field experiments. Significant positive correlations between body size and reproductive traits occurred in three of four field experiments involving *Melanoplus sanguinipes* (Fabricius) and *Phoetaliotes nebrascensis* (Thomas) where *per capita* resource availability was manipulated, with a highly significant relationship between femur length and functional ovarian follicles when statistical results were combined from all correlations. In addition, individual femur length was a significant covariate for at least one reproductive trait in three experiments. Biotic factors such as food availability and predation could be more important than body size in determining reproductive output under field conditions, but further work is required to examine under what conditions individual body size affects reproduction in grasshoppers.

Key words

body size, individual variation, reproduction, grasshopper, Melanoplinae, *Melanoplus sanguinipes*, *Phoetaliotes nebrascensis*

Introduction

Body size is a fundamental trait of an organism that affects many aspects of its performance (Filin & Ovadia 2007, White *et al.* 2007). Ecologists have shown an increased interest in linkages between body-size variation and population dynamics (Uchamanski 2000, de Roos *et al.* 2003, Filin & Ovadia 2007, Gothard *et al.* 2007), with both empirical and theoretical work indicating that body-size variation has important implications for understanding insect population dynamics (Ovadia & Schmitz 2002, Ovadia *et al.* 2007, Filin & Ovadia 2007). Individual variation in body size can also be related to individual differences in exploitative competitive ability (Branson 2003a, Filin & Ovadia 2007). When larger adults are competitively superior, they should acquire more resources and have greater reproduction (Wall & Begon 1987, Belovsky *et al.* 1996). Filin and Ovadia (2007) argued that if later-maturing females were smaller, the poorer quality resources typically available later in the growing season should magnify size-based differences in reproduction (also see Belovsky & Slade 1995, Oedekoven & Joern 2000).

Body size is an important component of life-history theory in ectotherms, with particular relevance for reproductive effort (Roff 1992). A trade-off is often assumed between the presumed fecundity benefits from growing larger prior to adulthood and the benefits of reproducing earlier in a seasonal environment (Roff 1992). As predicted, fecundity in a number of insect orders is positively correlated with body weight or structural size, based largely on laboratory studies (Leather 1988, Honěk 1993, Tammaru *et al.* 1996). Positive correlations between reproductive characteristics and body size have not been found in all studies (Klingenberg & Spence 1997, Sokolovska *et al.* 2000), particularly in field studies where environmental factors such as food availability and predation may play a more important role in determining fecundity (Leather 1988, Branson 2003a, Gotthard *et al.* 2007). A further complication in extrapolating laboratory-derived fecundity-body size relationships to the field, is that relationships between fecundity and body size can change as environmental factors are manipulated (Carroll & Hoyt 1986, Honěk 1993). Positive correlations between body size and fecundity are expected to be weaker in insects that acquire resources for reproduction as adults, where environmental constraints are likely more important in determining fecundity, than in insects that acquire resources as nymphs for subsequent reproduction (Honěk 1993, Tammaru *et al.* 1996).

Grasshoppers acquire and allocate resources for reproduction primarily as adults (Moehrlin & Juliano 1998, Branson 2004, Hatle *et al.* 2004). Grasshopper ovaries consist of a series of ovarian follicles that are capable of developing eggs, with the number of ovarian follicles apparently fixed before birth (Uvarov 1977, Bellinger *et al.* 1987, Stauffer & Whitman 1997). Potential fecundity, as measured by the total number of ovarian follicles, provides the upper limit for egg pod size and varies widely (2 to >100) among grasshopper species (Bellinger & Pienkowski 1985, Joern & Gaines 1990). The number of eggs in a given egg pod is typically less than the number of ovarian follicles, because not all ovarian follicles are functional, or developing an egg (Bellinger *et al.* 1987), particularly when resources are limited (Branson 2003a, 2004). Reductions in the number of functional ovarian follicles occur through oosorption, when a developing ovarian follicle stops development and resources are reabsorbed (Joern & Klucas 1993, Chapman 1998, Branson 2003a, Danner & Joern 2004). The number of functional ovarian follicles, and thus egg pod size, varies in response to biotic factors including resource availability, exploitative competition, and parasitism (Joern & Gaines 1990; Branson 2003 a,b, 2004). Grasshoppers can reduce allocation to reproduction when resources are limiting by reducing the rate of egg pod production and increasing oosorption (Chapman 1998; Branson 2003a, 2006; Danner & Joern 2004).

Intra- and interspecific correlations between individual body size and life-history variation in grasshoppers have been inconsistent (*e.g.*, Atkinson & Begon 1987, Wall & Begon 1987, Sanchez *et al.* 1988). Adult hind femur length has been widely used to assess exoskeleton size (*e.g.*, Monk 1985, Wall & Begon 1987, de Souza Santos & Begon 1988, Danner & Joern 2004) and is assumed to reflect nymphal environmental conditions, with body weight representative of a combination of adult and nymphal conditions (Wall & Begon 1987, Danner & Joern 2004). Ovariole number was highly positively correlated with femur length in an interspecific comparison of *Melanoplus* species (Bellinger & Pienkowski 1985, Joern & Gaines 1990), with 93% of variation between 10 species explained by femur length (Bellinger & Pienkowski 1985). However, this strong interspecific relationship does not hold among all grasshopper taxa (Joern & Gaines 1990). Intraspecific correlations between individual body size and the number of functional ovarian follicles or egg pod size are often weak (Dearn 1977, Sanchez *et al.* 1988), although positive relationships have been found when comparing individuals across an environmental gradient (Atkinson & Begon 1987, Berner & Blankenhorn 2006).

In this paper, relationships between reproductive traits and individual body size in melanopline grasshoppers were examined by utilizing individual-based data collected previously in four manipulative experiments. Specifically, the strength of the relationships between reproductive traits and either femur length or body weight was examined. Numerous biotic and environmental factors can influence body size and reproduction in grasshoppers (references in Stauffer & Whitman 1997). It is important to ascertain the relative influence biotic factors and body size have on fecundity, to aid in the understanding of grasshopper population dynamics and outbreaks (Branson *et al.* 2006, Filin & Ovadia 2007).

Methods

Biology of the insects.— Two species of melanopline grasshoppers were examined in the experiments. *Melanoplus sanguinipes* (Fabricius) is a midsized grasshopper and one of the most common species of rangeland grasshopper in western North America (Pfadt 2002). *M. sanguinipes* is polyphagous and reproductively plastic (Branson 2003a,b, 2004), laying egg pods ranging from 1 to 36 eggs (D. Branson unpub. data). *Phoetaliotes nebrascensis* (Thomas) is a later-hatching, slightly smaller species, that feeds nearly entirely on grasses (Pfadt 2002). It can be a dominant member of grasshopper communities in tallgrass and northern mixed-grass prairie (Pfadt 2002, Branson 2008). Although relatively little is known about the reproductive ecology of *P. nebrascensis*, Pfadt (2002) reported a typical ovariole number of 28. Both species overwinter as eggs and are univoltine in the northern U.S.

Experiments.—To assess correlations between individual female body size and reproductive traits, data were utilized from four previous manipulative experiments that examined treatment effects on mean *per capita* reproductive traits. Individual-based data from those experiments were used to examine the relationship between individual body-size variation and reproductive traits. Although traits measured differed between experiments, the proportion of functional ovarian follicles and femur length was recorded for all experiments.

Experiment 1 was conducted in Palouse prairie on the National Bison Range in northwestern Montana, USA, and is described in Branson (2004). The experiment was designed to examine the effects of nymphal resource availability and increased *per capita* adult resource availability on life history variation in *M. sanguinipes*. The experiment consisted of a 2 × 2 factorial design with *ad libitum* and reduced food-rearing regimes for nymphs in outdoor rearing cages, followed by natural and watered vegetation treatments with adult grasshoppers in 0.1-m^2 field cages. The density of adult grasshoppers used for both vegetation treatments was chosen to minimize strong density-dependent effects on survival and reproduction. Body weight and femur length were measured on adult females prior to initiating the adult experiment, with the number of follicular relicts (eggs laid) and the proportion of functional ovarian follicles measured on females at the end of the experiment. The number of functional ovarian follicles determines the size of the next egg pod to be laid.

Experiment 2 is described in Branson (2003a) and was also conducted on the National Bison Range. The experiment examined the effects of *per capita* resource availability and the importance of exploitative resource competition on survival and reproductive allocation in *M. sanguinipes*. The experiment consisted of a 2 × 2 fully factorial design with two natural and fertilized vegetation treatments and five grasshopper density levels in 0.36-m^2 cages. The experiment was initiated with 4th instar nymphal *M. sanguinipes* at an even sex ratio. At the end of the experiment, all surviving females were collected and femur length, the number of follicular relicts (eggs laid), and the proportion of functional ovarian follicles determined.

Experiment 3 is described in Branson (2008). The effects of differing grasshopper densities on population dynamics and reproductive correlates were examined at a northern mixed-grass prairie site on the USDA-ARS Livestock and Range Research Lab in eastern Montana. The experiment consisted of four grasshopper density treatments in 10-m^2 cages and was initiated with early to mid-instar grasshoppers. Grasshoppers added to cages were randomly caught at the site, with *M. sanguinipes* and *P. nebrascensis* the two most common species. High-quality grass growth occurred following a mid-August rain, reducing food limitation. At the end of the experiment, femur length, body weight, ovary weight, and the percentage of functional ovarian follicles were measured on females.

Experiment 4 was also conducted on the USDA-ARS Livestock and Range Research Lab (Branson & Haferkamp, in prep.) and examined the effects of the timing of sheep grazing and grasshopper densities on grasshopper population dynamics. The study was conducted during a severe grasshopper outbreak, with densities in outside controls reaching ~130 per m^2. The study was initiated with early to late-instar nymphal grasshoppers in 10-m^2 cages at densities of 40 and ~120 per m^2. *P. nebrascensis* and *M. sanguinipes* were the two most common grasshopper species. At the end of the experiment, femur length, body weight, ovary weight, and the percentage of functional ovarian follicles were measured.

Statistics.— For each experiment, Pearson product-moment correlations were used to assess the strength of the relationship between female body-size traits and reproductive traits for all females in a given experiment (Quinn & Keough 2002). As a fully developed egg pod can be a significant portion of a females' body weight, correlations between body weight and ovary mass were not assessed. Correlations between femur length and functional follicles were assessed for each species in all experiments. Because each of the six correlations examine the relationship between femur length and the proportion of functional ovarian follicles, a meta-analytic technique was used. Fisher's combination of significance test (Sokal & Rohlf 1995) assessed the overall significance of the correlation between body size and functional ovarian follicles across experiments. ANOVA models were used to examine if the experimental treatments affected femur length. When correlations between femur length and the proportion of functional follicles were significant, ANCOVA models with femur

Table 1. Pearson correlations (r) between body size traits (femur length, body weight) and reproductive traits (proportion of functional ovarian follicles, number of follicular relicts, ovary weight) for each experiment. p values less than 0.05 are in bold.

	Species	Body size trait	Reproductive trait	Correlation	p
Experiment 1	*M. sanguinipes*	Femur length	Functional follicles	-0.05	0.639
		Femur length	Follicular relicts	-0.06	0.608
		Body weight	Functional follicles	0.06	0.587
		Body weight	Follicular relicts	-0.04	0.711
Experiment 2	*M. sanguinipes*	Femur length	Functional follicles	0.52	**<0.001**
		Femur length	Follicular relicts	0.31	**0.011**
Experiment 3	*M. sanguinipes*	Femur length	Functional follicles	0.28	**0.001**
		Femur length	Ovary weight	0.26	**0.009**
		Body weight	Functional follicles	0.19	0.055
	P. nebrascensis	Femur length	Functional follicles	0.46	**0.003**
		Femur length	Ovary weight	0.50	**0.001**
		Body weight	Functional follicles	0.34	**0.031**
Experiment 4	*M. sanguinipes*	Femur length	Functional follicles	0.25	**0.016**
		Femur length	Ovary weight	0.30	**0.004**
		Body weight	Functional follicles	0.39	**<0.001**
	P. nebrascensis	Femur length	Functional follicles	0.21	**0.008**
		Femur length	Ovary weight	0.24	**0.002**
		Body weight	Functional follicles	0.45	**<0.001**

length as a covariate were used to examine if individual body size explained significant variation in reproductive traits in relation to treatment effects. Treatment effects on mean *per capita* reproductive traits were assessed previously. Proportion of functional ovarian follicle data was arcsine-square root transformed when needed, to meet normality assumptions. Systat 12 (Systat Software Inc. 2007) was used for all statistical analyses.

Results and Discussion

Experiment 1.—Body size and weight were not significantly correlated with either the proportion of functional ovarian follicles or the number of follicular relicts (eggs laid) (Table 1), with all correlations < ± 0.1. Females reared under lower nymphal resource conditions had shorter femur lengths ($t = 2.389$, $p = 0.02$) and lower body weights ($t = 6.13$, $p < 0.001$) than those reared with *ad libitum* food. There was no indication that the smaller structural size of females reared with lower resource availability as nymphs was associated with reduced reproductive allocation, either on an individual (Table 1) or cage-mean basis (Branson 2004). Increased food availability for adults resulted in a higher average *per capita* number of functional ovarian follicles and follicular relicts (eggs laid) (Branson 2004).

Experiment 2.— Femur length was positively correlated with the percentage of functional ovarian follicles and with the number of follicular relicts or eggs laid (Table 1). Both vegetation and density treatments significantly affected femur length in the direction expected with resource availability (ANOVA: Density, $F_{4, 72} = 5.18$, $p < 0.001$; Vegetation, $F_{1,72} = 13.1$, $p < 0.001$). When analyzed using an ANCOVA model with femur length as a covariate, femur length explained a significant amount of variation in the proportion of functional ovarian follicles ($F_{1,71} = 4.51$, $p = 0.04$), but not for the number of follicular relicts ($F_{1, 66} = 1.47$, $p = 0.228$). The analyses indicate a stronger relationship between femur length and the proportion of functional follicles than for follicular relicts. Assessed on a cage-mean basis, grasshopper density and resource treatments each influenced the average *per capita* number of follicular relicts, with *per capita* digestible plant biomass explaining over half of the variation in functional ovarian follicles (Branson 2003a). However, it appears that individual body-size variation also contributes to the observed variation in reproductive traits.

Experiment 3.— Femur length was positively correlated with the percentage of functional ovarian follicles in both *M. sanguinipes* and *P. nebrascensis* (Table 1). Femur length was also positively correlated with grasshopper ovary weight for both species, particularly for the later-developing *P. nebrascensis* (Table 1). Body weight was positively related to the proportion of functional ovarian follicles in *P. nebrascensis*, and marginally for *M. sanguinipes* (Table 1). Increasing grasshopper densities negatively affected femur length in *M. sanguinipes* (ANOVA: $F_{3,71} = 3.78$, $p = 0.01$), with a marginal effect on the later-hatching *P. nebrascensis* (ANOVA: $F_{3,70} = 2.35$, $p = 0.08$). The availability of high quality food increased in late summer, while *P. nebrascensis* were still nymphs, reducing food limitation and enhancing reproduction (Branson 2008). When the proportion of functional ovarian follicles in each density treatment was analyzed using an ANCOVA model, femur length was significant as a covariate in both *M. sanguinipes* ($F_{1,70} = 5.60$, $p = 0.02$) and *P. nebrascensis* ($F_{1,60} = 5.117$, $p = 0.02$).

Experiment 4.— Femur length was positively correlated with the percentage of functional ovarian follicles and with ovary weight in both *M. sanguinipes* and *P. nebrascensis* (Table 1) at a site where the density of grasshoppers reached ~130 per m^2. Correlations between femur length and proportion of functional ovarian follicles were < 0.3 in both species, indicative of a weak relationship. Body weight was positively related to the proportion of functional ovarian follicles in both species (Table 1). Both treatments negatively affected femur length in *P. nebrascensis* (ANOVA: Density, $F_{1,151} = 56.1$, $p < 0.001$; Grazing, $F_{3,151} = 5.78$, $p = 0.001$) and *M. sanguinipes* (ANOVA: Density, $F_{1,80} = 21.2$, $p < 0.001$; Grazing, $F_{3,80} = 5.43$, $p = 0.002$). When analyzed with an ANCOVA, femur length contributed to the proportion of functional ovarian follicles in *P. nebrascensis* ($F_{1,150} = 11.8$, $P = 0.001$), but not in *M. sanguinipes* ($F_{1,79} = 0.573$, $p = 0.45$). Therefore, body size explained variation in future egg-pod size in the later-hatching *P. nebrascensis* under the conditions of strong food limitation and exploitative competition that occurred during the study.

Fisher's combination of significance test (Sokal & Rohlf 1995), used to assess the overall significance of the six correlations between femur length and functional ovarian follicles, revealed a strong positive effect of femur length on the proportion of functional follicles ($\chi 2= 67.3$, d.f. = 12, $p < 0.0001$). Although femur length and functional ovarian follicles were not significantly correlated in Experiment 1, this analysis indicates the overall relationship was highly significant when results from the six correlations were combined. The nonsignificant relationship between female body size and reproductive traits in Experiment 1 could be biologically important, but is not obviously explained. In Experiment 1 nymphal grasshoppers were reared in an outdoor laboratory before females were placed in field cages (Branson 2004), while the resource manipulations in the other experiments affected conditions for both nymphal and adult grasshoppers. Density and vegetation treatments in the other three experiments also resulted in a larger range of *per capita* resource availabilities than in Experiment 1.

In a study with *Chorthippus brunneus* varying food availability, Wall and Begon (1987) found a positive relationship between egg-pod size and femur length. By contrast, de Souza Santos and Begon (1988) found a negative correlation between body weight and reproductive effort in *C. brunneus*. Femur length is a more straightforward measure of body size when examining correlations between body size and functional ovarian follicles, as total body weight is potentially confounded by the inclusion of ovary mass. Nevertheless, correlations between body weight and the percentage of functional ovarian follicles exhibited largely similar patterns compared to femur length in the three experiments with body weight data (Table 1). Given the results of this study and other published studies, additional research is needed to assess if food availability influences the nature of the relationship between structural size, body weight and reproductive traits.

Food limitation and exploitative competition can strongly affect reproduction in grasshoppers (Belovsky & Joern 1995, Belovsky & Slade 1995, Branson 2004, Branson 2006), but few studies have examined correlations between reproductive traits and body size when food availability and exploitative competition are manipulated at a single site. Given the strength of the relationship between *per capita* resource availability and reproduction (Branson 2003a, 2006), relationships between body size and reproductive traits could be more difficult to detect in experiments manipulating the *per capita* availability of plant resources. However, positive relationships between body size and reproductive traits were apparent in three of four experiments manipulating resource availability. In addition, Fisher's combination of significance test was highly significant for the correlation between femur length and functional ovarian follicles. Host plant quality is another key determinant of fecundity in herbivorous insects (Awmack & Leather 2002; Branson 2003a, 2006) and was manipulated simultaneously with plant biomass in Experiment 2. In a lab study manipulating only diet quality, Joern and Behmer (1998) found no effect of body weight as a covariate in explaining reproduction in *M. sanguinipes* and *P. nebrascensis*.

Body size can impact other important aspects of grasshopper performance in seasonal environments (Filin & Ovadia 2007) including optimal thermoregulation (Chappell & Whitman 1990). Body size can also affect competitive outcomes when resources are limiting (Wall & Begon 1987), with Ovadia and Schmitz (2002) finding larger *Melanoplus femurrubrum* had higher survival. Body size is often an important determinant of susceptibility to predation, with both birds and hunting spiders size-selective predators, but in opposite directions (Belovsky & Slade 1993, Ovadia & Schmitz 2002, Danner & Joern 2004, Branson 2005). Predators can also indirectly reduce body size by modifying foraging behavior and thus development (Danner & Joern 2004). *Ageneotettix deorum* reared with spiders were smaller, but there were no body-size effects on reproduction (Danner & Joern 2004). Because *A. deorum* has five or six ovarian follicles, potential variation in egg-pod size would be constrained relative to *M. sanguinipes* or *P. nebrascensis*.

Conclusion.— Relationships between body size and fecundity are predicted to be weaker when fecundity is determined by adult resources (Honěk 1993, Tammaru *et al.* 1996), as with grasshoppers. Positive correlations between body size and reproductive traits were evident in three of four field experiments, with a positive highly significant overall correlation between femur length and functional ovarian follicles. Furthermore, individual femur length was significant as a covariate in explaining variation for at least one reproductive trait in three experiments.

Additional research is needed before generalizations can be made regarding the relative roles of biotic factors and individual body size on reproductive allocation in grasshoppers. As correlation coefficients were less than 0.52 in all cases, a maximum of ~ 27% of the variance was shared between body size and reproductive traits. Importantly, biotic treatments explained a significant amount of variation in reproductive traits on a mean *per capita* basis in all four experiments — even in Experiment 1, where no significant correlations between body size and reproductive traits were evident. As a result, factors such as food availability and predation may be more important than body size in determining reproductive output under field conditions (Joern & Behmer 1998, Branson 2003a, Danner & Joern 2004).

Further work is required to understand the range of conditions where individual body size affects reproduction in grasshoppers, and how relationships between body size and reproductive traits may change with food availability. Models indicate that body size variation contributes to population stability in seasonal environments (Filin & Ovadia 2007) and may be a key factor in predicting the strength of plant-herbivore interactions (Ovadia *et al.* 2007). Thus, body-size variation likely has a wide range of important effects on grasshopper population dynamics and grasshopper-plant interactions.

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