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Parental size influence on offspring phenotype in *Schistocerca americana* (Orthoptera: Acrididae)

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Abstract

In order to test the hypothesis that parents influence offspring body size, crosses between male and female *Schistocerca americana* of various sizes were made in the laboratory. Measurements of the offsprings' body characteristics were made after every instar. No correlation was found between the mother's characteristics and that of her offspring; however, paternal size was positively correlated with adult offspring body size. Other studies have shown that variation in the size of both males and females significantly affects reproductive success. Thus, the current study is significant in that a father can influence his offsprings' adult size.

Key words

parental influence, inheritance, *Schistocerca americana*, size, offspring benefits

Introduction

Previous work has indicated that in many insect species females prefer to mate with large males (e.g., see Simmons 2001 for references) and in some species, the large size is correlated with nutritional investment that a male will give a female during copulation (e.g., Gwynne 1982, Thornhill 1983). Such direct benefits can positively influence a female's reproduction (e.g., Gwynne *et al.* 1984) such as when male products are absorbed and used by the female in egg production (Friedel & Gillott 1977, Bowen *et al.* 1984, Pitnick *et al.* 1991).

It would also pay a female to prefer a large mate if indirect benefits were offered to her offspring. For example, low-mass category females (categories based on weight) of *Agelenopsis aperta*, the desert spider, produce fewer fearful offspring of both genders when mated to high-mass males (Riechert & Johns 2003). Such behavior is important to the individual's competitive ability in a food-limited desert environment (Riechert 1979).

Thus, large mate size has the potential of influencing offspring morphology and behavior. Such body size phenotypic plasticity has been shown to be caused by genetic variation, as with the grasshopper *Melanoplus femurrubrum* (Thompson 1999). In other insects, male size has also been shown to be heritable and therefore selectable. For example, in male southern green stink bugs, *Nezara viridula*, heritable size is positively correlated with mating and sperm competition success, as well as with rate of development and fecundity (McLain 1991). Such size heritability studies have not been commonplace among Orthopteran species, with the exception of the size differences inherited with phase in locusts (Uvarov 1966).

The following study was conducted to examine if parental size influences offspring phenotype in *Schistocerca americana* (Orthoptera:

Acrididae). Previous work on this grasshopper species has shown that females choose large males as mates more often than small males in a seminatural cage situation (Kosal & Niedzlek-Feaver 1997).

Methods

Potential parents were collected from Farm Unit One of North Carolina State University in early April. Mating typically begins in late April or early May in the field. Animals were assumed to be virgin when as isolated females they failed to oviposit in the laboratory. Another group of adults were collected from the field in August. These individuals were the offspring of matings of field adults during the months of May through July. Upon collection, these late summer animals were subjected to shorter days and cooler temperatures to simulate a natural winter period, a precursor to successful mating (Kosal & Niedzlek-Feaver 1997).

In total, 40 matings were investigated with one female and one male placed in a cage to mate freely until death. Animals were reared under identical regimes of 12 h of light 12 h of dark and unlimited feeding of sprouted wheat and rye berries, Bermuda and fescue grass, wheat flakes, and ground cat and rabbit food. The parents were provided with sand cups for oviposition, checked for eggs every 4 days. If eggs were found, the sand cups were isolated until nymphs began to hatch. To avoid damaging the eggs, the weight of the eggs was not measured; however, the number of eggs in each pod was counted after the nymphs hatched. In this paper, *set* or *progeny* are used to refer to all the offspring that hatched from one egg pod. Upon hatching, each set was given its own cage for development, with a maximum of 40 nymphs allowed in any one cage. If there were more than 40 nymphs, individuals were divided into two (or more if necessary) cages. Development was monitored; the femur, body, tegmen and pronotum, as well as weight, were measured. Measurements of animals in a cage were made after all grasshoppers molted, an average number of 3 days after a molt. Measurements were repeated on newly molted adults.

The 40 mated parents produced a total of 30 egg pods and thus 30 sets of progeny; however, five of these were disregarded because the eggs were laid immediately prior to the death of the female (e.g., Uvarov 1966). From the remaining sets, 1083 offspring were obtained. Nonparametric analyses were used to examine data (Wilcoxon rank sum tests and Kendall Tau correlation). Different indicators of body size (e.g., femur, tegmen, body length) were examined and it was determined that chosen characteristics were correlated and so were good indicators of overall body size. For example, a male parent's body length and femur length were positively

correlated ($p < 0.0001$) as well as paternal femur length and weight ($p = 0.0007$). These data were factored into principal component analyses to obtain an overall estimate of body size, which allowed the selected size measurements of femur, tegmen, body length, and weight, to be treated as one variable.

Results

General: egg number, instar number and density effects.—No correlation was found between parental traits such as femur or body length or weight and the number of eggs produced. Correlations, however, were found between the number of eggs in a pod and the nymphal survivorship. A negative correlation was found between the number of hatchlings produced and survivorship (Fig. 1; $\text{Tau} = -0.6396$, $p = 0.0001$) when compared to the number of eggs in the egg pods. Thus, nymphs died sooner if they came from egg pods that contained more eggs, compared to egg pods with fewer eggs.

If there were more than 40 eggs in a pod as the nymphs hatched, they were randomly separated into different cages to reduce cage density. There were on average 25.4 grasshoppers in a cage, with a range of 3 to 40. When examining cage number in relation to survivorship, no correlation was found ($\text{Tau} = -0.2299$, $p = 0.3654$). When focusing on the numbers of grasshoppers in a cage, body traits were similarly not influenced. The femur, body, tegmen, and pronotum length, as well as the weight, did not correlate with the numbers of nymphs or adults in the cage.

The majority of the nymphs (63%) went through five instars before becoming adults; however, there was some variation among siblings. Two sets went through six instars, and four sets of egg pods produced individuals that went through either five or six instars before becoming adults. Regardless of the number of instars, all nymphs were pink in coloration.

There was no significant correlation found between the number of instars and the length of development time. On average, it took 44 ± 7.8 d to molt five times before becoming adults and 45 ± 8.7 d if animals molted six times before becoming adults. The number of instars did not influence the adult size of the animals. In general, a trend was found that as nymphs, those grasshoppers that went through five instars were larger than those individuals that molted six times; however, these averages were not statistically significant

from one another. If we compare the femur during the third instar of such animals, those that ultimately went through five instars had, on average, a femur length of 9.68 ± 1.59 mm compared to an average length of 8.01 ± 1.19 mm for those animals that ultimately molted six times. If we compare the average femur length of these animals during the fourth instar, it becomes 14.67 ± 1.70 mm and 12.53 ± 1.7 mm for animals that molted five and six times, respectively. By the fifth instar, these numbers were closer: 19.13 ± 0.92 mm and 19.17 ± 0.06 mm for animals that underwent five and six molts, respectively.

There was no correlation detected between any phenotypic characteristic of the father or the mother and average nymphal body measurement, or percentage of nymphs or adults that survived.

Parental size influence found on adult offspring.—There was no significant correlation found between any of the mother's phenotypic characteristics, her overall estimate of body size using principal components analysis, and that of her offspring. Similarly, there was no correlation detected between any phenotypic characteristics of the father and any nymphal body measurement. However, the father's traits were correlated to his offsprings' adult measurements. The best overall indicator of size combined femur, tegmen, body length, and weight as the principal components parameter. When using this estimate of size in a principal components analysis, a positive relationship was found between fathers and adult sons ($\text{Tau} = 0.42$, $p = 0.0037$). Upon closer examination of separate correlations, the strongest was between the femur length of the father and the mean femur length of his adult sons ($p = 0.0017$, Fig. 2) and between the tegminal lengths of the father and the mean tegminal lengths of the adult sons ($p = 0.0010$, Fig. 3).

To examine father and daughter relationships, an overall indicator of size was used that consisted of a combined parameter of femur, tegmen, body length and weight. Through a principal components analysis, this indicator of size showed a positive correlation between the father's phenotype and his daughters' adult phenotype. ($\text{Tau} = 0.2916$, $p = 0.0439$). As for sons, upon closer examination of separate correlations, the femur and tegminal lengths of fathers and adult daughters resulted in the strongest correlation ($p = 0.0392$ and $p = 0.005$, respectively).

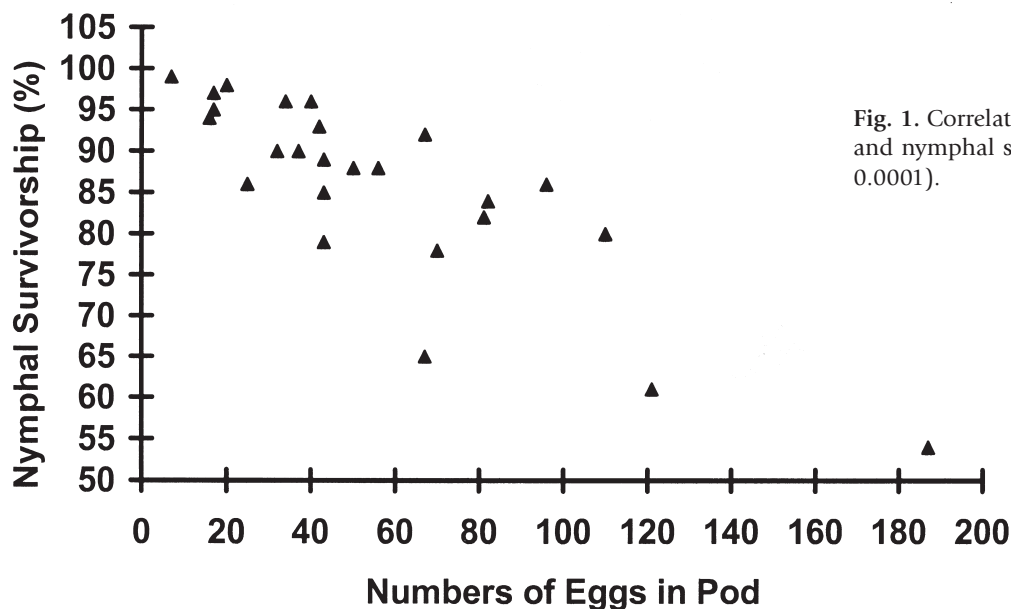


Fig. 1. Correlation between the number of eggs and nymphal survivorship ($\text{Tau} = -0.6396$, $p = 0.0001$).

Fig. 2. Correlation between the length of the femur of fathers and the mean femur length of their sons ($n = 25$; $\text{Tau} = 0.4543$, $p = 0.0017$). Measurements in mm.

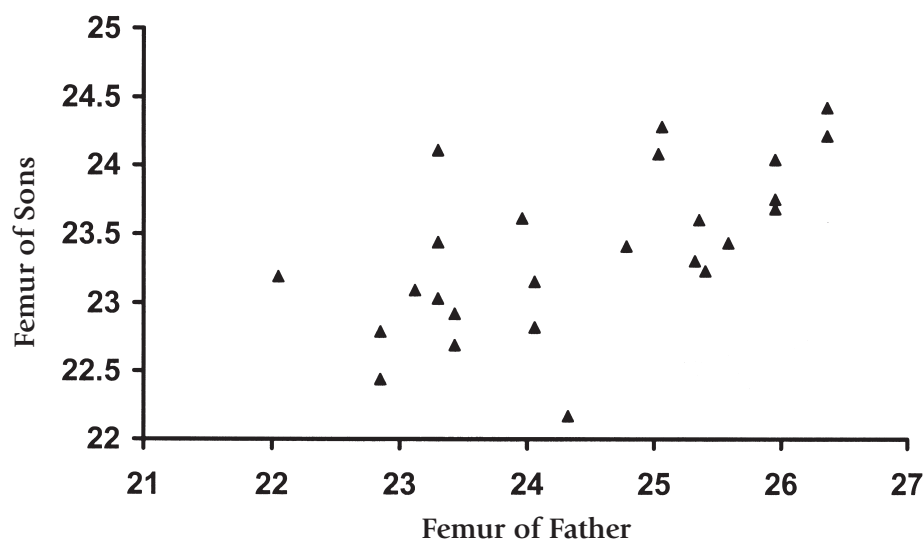
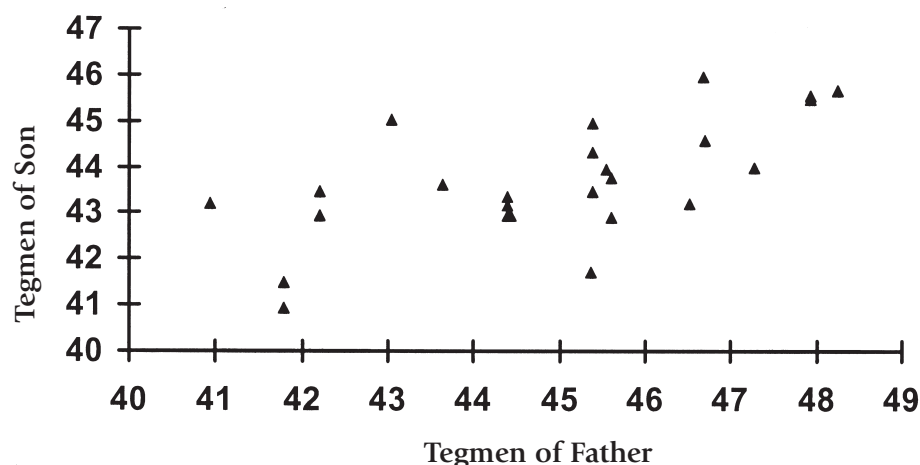


Fig. 3. Correlation between the length of the tegmen of fathers and the mean tegminal length of their sons ($n = 25$; $\text{Tau} = 0.4746$, $p = 0.0010$). Measurements in mm.



Discussion

Since all progeny obtained from mated pairs used in this study were reared under identical conditions, any significant size differences were expected to derive from the two types of variation that remain: egg size variation and parental size variation. Variation of offspring size may be correlated with a male's ability to provision a female and/or a female's ability to sequester excess nutrients to her eggs (Friedel & Gillott 1977, Bowen *et al.* 1984, Pitnick *et al.* 1991). Larger females may be able to lay more eggs of comparable size than smaller females or there may be a trade-off between numbers of eggs laid and egg size, which may result in pods with a greater number of eggs yielding less vigorous hatchlings (*e.g.*, Capinera 1979).

This potential type of variation was not under direct investigation in the current study, although it was taken into consideration as it was indirectly monitored. For example, the number of eggs, not the number of nymphs in a cage, influenced longevity of the nymphs. These data suggest that egg quality may be involved with ensuring nymphal survivorship. Interestingly, maternal size, paternal size or a combined variable of both were not correlated with numbers of eggs laid. It appears then that regardless of size, if a female lays an egg pod with more eggs, the overall quality of those eggs is less than an egg pod with fewer eggs. What could possibly

have caused this difference in egg number is unclear. Other studies have shown environmental influences, such as fluctuations in temperature (Hamilton 1950) and food (*e.g.*, Barnes 1955) affecting egg number. The females used in the current study were earlier exposed to different food plants in the field; however, once in the lab, all animals were exposed to the same food and in unlimited supply. Perhaps the early nutritional differences from the females accounted for some of the variation in the numbers of eggs laid per pod. Other researchers have noted that differences in feeding among females may affect egg size or numbers (Harvey 1983, Evans *et al.* 2004).

Because all females in the current study had access to the same food resources (in the laboratory), nutrient availability probably does not address most of the variation seen with production of the offspring, such as the number of eggs. For example, maternal age was a bigger factor in egg size than multiple mating in the beetle *Callosobruchus maculatus* (Fox 1993). Although the size of the eggs was not measured in the current study, it has been suggested that in order to package more in a pod, the eggs must be small in size (Atkinson & Begon 1987). If this is assumed with *S. americana*, smaller animals would result from larger egg pods (*e.g.*, Honek 1987). This trend was not found in the current study nor in some

other studies (e.g., Wiklund & Persson 1983).

Instar number may be related to egg quality. The protein donated by the father or the mother may play a role in regulating this number for offspring produced by the same set of parents that went through various numbers of instars. This behavioral plasticity is in contrast to the reported set number of six instars for *S. americana* (Capinera 1993). The male-donated protein may have been different for each copulation, thus resulting in different offspring development rates. Further studies would need to be conducted to examine this possibility.

The second type of variation to account for nymphal variation, parental size variation, was studied directly in this study with female and male parents influencing their offspring in different ways. These findings are discussed more fully below.

Cage number effects on offspring.—The data from the current study indicate that cage number had no effect on the phenotype or longevity of the nymphs. This was somewhat unexpected since there are ample instances where rearing density influences phenotype and life history characteristics (e.g., Chapman *et al.* 1979) through inducing phase changes primarily through visual contact in crowded conditions in some species (Ellis & Pearce 1962, Nolte 1963, Lohr 1990). Perhaps we did not record such differences because all nymphs appeared to be in the same phase, exhibiting the bright pink-to-red morph seen only in field conditions after field burns, where there is increased visual contact among nymphs. Such changes have also been noted in the lab. When one animal was reared alone, it remained green; with two animals, the red morph was seen (Niedzlek-Feaver, unpub. data). During the current study, red morphs were the norm and were assumed to be the gregarious phase. Still, there was no evidence of the number of nymphs per cage having an influence on nymphal phenotype or life span, perhaps due to direct or indirect competition.

The number of grasshoppers in a cage may have influenced parameters that we did not measure in this study. For example, fat body formation and the maturation of these animals may have been delayed. Norris (1962) found that crowded males are generally more active, which limits fat body and delays maturation. In the current study, activity and fat body were not measured; however, the weight of the animals was taken once per instar and no correlations with numbers were found. Additionally it is significant to note that weight was correlated with other characters measured, such as femur length and pronotum length, characters that do not change during instars in the way that weight might be expected to fluctuate. Such consistent phenotypic characters also did not correlate with cage number. Workers with *Locusta* and *Schistocerca* report similar findings. For example, a small sexual dimorphism was seen with hatchling weight (with females being heavier), but this weight was not influenced by density (Uvarov 1966). Thus, it is concluded from our study that body characters are not influenced by the number of grasshoppers in a cage.

Parental influence on adult offspring.—The father is definitely influencing the adult phenotype of his offspring. This finding is significant given that the environmental conditions and resources in the laboratory were identical for all animals. Quality of habitat is expected to play an important role in nature as illustrated with *Melanoplus femurrubrum*. Here, grasshoppers raised on a hard-plant diet had significantly smaller mean tibia length and greater mean residual articular width of their face, compared to their full siblings who were reared on a soft-plant diet (Thompson 1999). In nature,

such differential access to resources is expected since egg pods are oviposited in different microhabitats. Regardless of food quality, the current study shows that offspring fathered by larger males will have the potential advantage of becoming large in size.

The mechanism of such size inheritance in *S. americana* is still under investigation. It is possible that large males produce more protein or a higher quality protein, which they donate to the females during copulation, thus insuring larger offspring. This would allow females to allocate more resources to eggs, but would still constitute an indirect form of paternal investment. A similar finding has been shown with the sand cricket *Gryllus firmus* in relation to weight, head width and nymphal development time, where highly significant correlations between egg length and the growth parameters of weight and development time were seen. In this reciprocal-effects study, data pointed to maternal influences, probably in the form of extra-nuclear effects, which suggested that at least "part of the reciprocal effect observed in growth rate trait is because of maternal effects acting through egg size". (Roff & Sokolovska 2004) Another study of *Gryllus* showed paternal effects on nymphal traits, perhaps also through maternal provisioning (Weigensberg *et al.* 1998). In such cases, larger nymphs, and hence resulting larger adults, are expected. In the current study there was no significant correlation between mother or father size and offspring size during the nymphal stages. The fact that adult offspring phenotype is correlated with paternal phenotype is exciting in that there are relatively few studies that have shown parental effects persisting into adulthood (Mousseau & Dingle 1991, Cheverud & Moore 1994). In addition the fact that food and other resources were identical for the males points to a stronger role for genetics.

Whether the father's size influence is transmitted nutritionally or genetically, larger adults are expected as a result of larger nymphs. Yet, there was no significant correlation between the father's size and average nymph size. Perhaps any difference in average nymph size that was correlated with paternal size was obscured by the variation noted in the number of instars until molting to adulthood. For example, should a fifth instar nymph that will molt into the adult phase be compared to another fifth instar nymph that will molt into an adult only after its sixth instar? In order to make this comparison a larger sample size than available in the current study is needed.

Regardless of the mechanism, larger size for both males and females can be advantageous. Large female size may be advantageous if larger, heavier females produce more eggs or heavier eggs (Uvarov 1966, Atkinson & Begon 1987, Wall & Begon 1987). In addition, there has been some work showing that such large females receive more matings (Rutowski 1982, Rhainds *et al.* 1995). Large males are also preferred as mates in many orthopteran species. For example, female katydids *Conocephalus nigropleurum* (Gwynne 1982), female ground crickets of *Neonemobius* sp. (Forrest *et al.* 1991) and female field crickets *Gryllus bimaculatus* (Simmons 1986), all mate with larger males when exposed to males of varying size. In some cases, male size has been shown to correlate with nuptial gift size (e.g., Gwynne 1982, Thornhill 1983) and in other cases, large males are preferred as mates even when potential resource gifts are held constant (e.g., Thornhill 1983). For example, females of the whitespotted sawyer beetle *Monochamus scutellatus* lay eggs in areas of pine bark over which the males compete. Larger males were found at the more preferred oviposition sites; however, females still preferred these large males when the resource quality was held constant (Hughes & Hughes 1985).

For the current species, *S. americana*, large size has been shown to

be beneficial in that large males were found to receive more matings in a previous study (Kosal & Niedzlek-Feaver 1997). Furthermore, larger males obtained more nonsequential matings in that study: matings that are separated by at least one week from one another. Since females were found to oviposit on average two days after a mating, these large males probably enjoyed matings where there was no sperm competition for paternity (Kosal & Niedzlek-Feaver 1997).

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