Linzer biol. Beitr.	48/2	1823-1834	19.12.2016

Relationship between body size and reproductive capacity in females of the black field cricket (Orthoptera, Gryllidae)

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A b s t r a c t : According to general ecological theories, reproduction of insects is among other controlled by the fitness of male and female individuals. Since only few data are available with regard to the relationship between fitness and reproductive capacity in female crickets, respective investigations were carried out for females of the black field cricket *Teleogryllus commodus* WALKER, 1869 (Gryllidae, Gryllini). As found by statistical analyses, mean daily fecundity, expressed by the number of eggs deposited into the substrate, correlates significantly ($P = 0.02$) with female body mass ($b_0 = -19.91$, $b_1 = 0.135$, $R^2 = 0.538$). Positive correlations could also be found between the number of eggs stored in the ovaries and body mass ($P < 0.05$; $b_0 = -78.45$, $b_1 = 0.208$, $R^2 = 0.426$) as well as the mass of the female gonads after drying and body mass ($P < 0.05$; $b_0 = -8.01$, $b_1 = 0.118$, $R^2 = 0.460$). Ovariole number exhibited a positive correlation with female body mass according to the equation $y = 0.104\ x - 14.15$ ($P < 0.05$; $R^2 = 0.411$). The study strongly suggests that large (heavy) females produce a higher offspring than small females. Further, the investigation confirms the hypothesis that body mass represents a principal determinant with regard to female fecundity.

K e y   w o r d s : Fecundity, body mass, oviposition, ovary mass, black field cricket, Orthoptera.

Introduction

Size and mass of animals are key components that are known to correlate strongly with fitness and to influence directly or indirectly a great number of biological phenomena. Among insects, size and body mass represent determinants of physiology, function, ecological performance, and behaviour (DIAL et al. 2008; WHITMAN 2008). Larger insect species are thought to be more metabolically efficient than small species (BOSWELL et al. 2008; DEBANO 2008; FIELDING & DEFOLIART 2008). Additionally, larger individuals are often characterized by greater food reserves and starvation resistance (SLANSKY 1985). From an ecological point of view, larger individuals often have more success in intra- and interspecific competition (JOERN & KLUCAS 1993; CHASE 1996; BRANSON 2008). Although they run, swim, and fly faster than small individuals (DUDLEY 2000), they are typically marked by lower mobility and agility with respect to their small competitors (SLANSKY 1985; KELLY et al. 2008).

Concerning life-history features and fecundity of insects, body size and mass often occur as important controlling factors, both between and within single species (ROFF 1992, 2002; STEARNS 1992; NYLIN & GOTTHARD 1998; BRANSON 2008; HODIN 2009). In the Orthoptera, development correlates negatively with adult body size in numerous cases

(FRONSTIN & HATLE 2008; LEHMANN & LEHMANN 2008), and larger species often show a tendency for higher survival and longer life spans (UVAROV 1977). These characteristics, however, have important consequences for fecundity because longer-lived females may be able to oviposit higher amounts of eggs. As summarized in the reviews of REISS (1989) and HONĚK (1993), fecundity of insects is commonly positively correlated with body size and mass. In the past, this phenomenon was, among other, reported for grasshoppers. Within this insect group, larger species show the tendency to possess ovaries consisting of more ovarioles and to lay larger clutches of larger eggs, whereby egg-laying takes place at longer intervals than in smaller species (STAUFFER & WHITMAN 1997; BRANSON 2008). Regarding the individuals of a single species, larger animals usually deposit larger clutches and sometimes more clutches and larger eggs (LEWIS 1984; STAUFFER & WHITMAN 1997; BERNER & BLANCKENHORN 2006). On the other hand, they may show the ability to resorb fewer oocytes (AKMAN & WHITMAN 2008; DEBANO 2008).

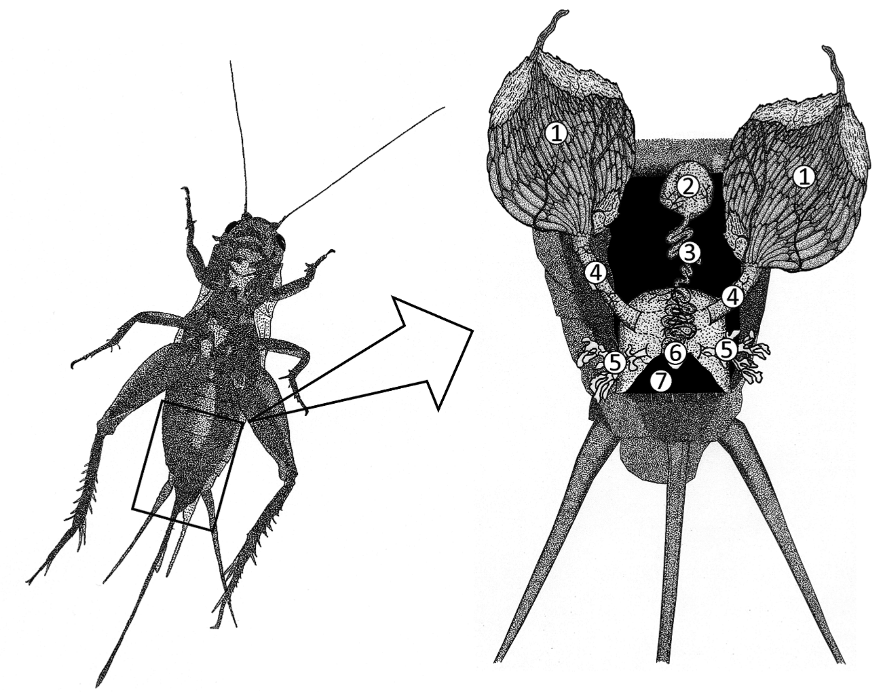

Fig. 1: Anatomic organization of the female reproductive system in the black field cricket: (**1**) ovary with eggs, (**2**) receptaculum seminis, (**3**) ductus receptaculi, (**4**) oviduct, (**5**) accessory glands, (**6**) terminal papilla, (**7**) genital chamber.

Statistical investigations of several oviparous and larviparous insect orders demonstrated that slopes b_1 of the regression line expressing the correlation between fecundity (i.e., the total number of eggs delivered during the adult period) and body mass commonly range from 0.88 to 1.22 (HONĚK 1993). This indicates a partly dramatic increase of produced egg numbers per time with growing body size. Most remarkable values for b_1 could be determined for the Homopteran *Nephotettix* which varied between 3.95 and 5.15 (VALLE et al. 1987). As a main result being derived from a common regression for all oviparous and larviparous insects that have been investigated in this way so far, a 0.95% increase in median fecundity is predicted for each 1% increase in body weight (HONĚK 1993). The unequivocal results presented above suggest that female size is a principal determinant controlling the potential of insect fecundity. In the Orthoptera, such a regression analysis is among other available for *Calliptamus barbarus* ($b_1 = 0.425$; HUGUENY & LOUVEAUX 1986), whereas similar information for crickets and grasshoppers may be evaluated as rather scarce hitherto.

In the contribution presented here, body mass-fecundity relationships are provided for the black field cricket *Teleogryllus commodus* and are confronted with respective data for other insect species available from the literature. The study aims to increase or knowledge on reproductive biology in insects and especially in orthopterans which frequently occur as major pasture pests in farm lands, increasing the demand for controlling their reproductive cycles. The contribution is based on the hypotheses that (1) there is a significant positive correlation between reproductive capacity and body size (expressed by body mass) in females of the black field cricket, (2) the amount of produced offspring is strongly related to female fitness, and (3) small and large females follow different strategies in order to maximize their reproductive success. Since these questions are largely solved with regard to males of the black field cricket (e.g., STURM 2011, 2014), the present work has to be understood as another contribution to the solution of an essential ecological question.

Materials and Methods

Animals

All crickets used for the study were reared under identical conditions (constant temperature of 25°C, light:dark = 12h:12h, relative humidity of c. 60%) in a climate chamber at the former Institute of Zoology, University of Salzburg. Adult animals were separated by gender, and females were kept individually in 5 L glass vessels filled with crumpled paper. They were provided with food *ad libitum*, thereby offering standard diet for laboratory animals (Altromin© 1222), lettuce leaves as well as water that was contained in small dishes plugged with cotton wicks (STURM & POHLHAMMER 2000; STURM 2002, 2003).

Adult females (age: 10 days, N = 50) used for experiments were subjected to a preceding measurement procedure, where body length (i.e., the total length of the three body segments without antennae and cerci, measured from the front of the head to the end of the abdomen) was determined by using a high precision (0.01 mm) slide caliper, whilst body weight was analyzed with a Satorius© balance (precision: 0.0001 g). In order to guarantee an undisturbed analysis of the size parameters, animals were anaesthetized in a carbon dioxide stream prior to the measurements. Besides the mass of living females also their dry mass was estimated according to the formula of JAROŠIK (1989): Dry weight = $0.0305 \times \text{length}^{2.62}$.

Oviposition

Female crickets (age: 10 days, previously unmated) were transferred together with mature males into glass vessels with a volume of 500 ml. After transfer of the spermatophore by the male, animals were separated again and females were transferred into specific oviposition vessels, filled with a 3-4 cm thick layer of sterilized sand, food, and water. After an oviposition period of 24 hours, females were transferred back to their glass vessels. For a statistical evaluation of oviposition, 50 animals were investigated according to this method. The content of the oviposition vessels was evacuated into a large glass dish (diameter: 30 cm) and carefully spread out. Afterwards, the substrate was dried, using a desk lamp, and sieved (grid size: 0.5 mm) to eliminate the fine sand fractions. From the remaining coarse fraction, eggs were separated with feather tweezers, transferred into an embryo vessel, and counted.

Dissection of the ovaries

Alternatively to the egg-counting procedure stated above, the ovaries of 10-day old females used for oviposition experiments were dissected, analyzed for their content of mature eggs, and weighed using the Satorius© balance (precision: 0.0001 g). For that, females (N = 50) were anaesthetized in a carbon dioxide stream, decapitated, and transferred into a dish filled with specific insect Ringer's solution (STURM & POHLHAMMER 2000). After complete opening of the abdomen by one transversal and two cranio-caudal sections (Fig. 1) and maceration of fatty tissue, one of the two ovaries was carefully isolated and dried on filter paper. Subsequently, the ovary was transferred on the balance for measurement of its mass. Numbers of ovarioles and mature oocytes (i.e., eggs with similar size as those deposited into the substrate) contained in the single ovarioles were determined without destroying the integrity of the organ.

Statistical analysis

Physiological parameters (body size and body mass), daily fecundities, ovary contents, and ovary masses were analyzed statistically by computing means and standard errors for all the measurements. For the determination of possible correlations between body mass and those traits expressing female fecundity, respective scatter plots were drawn and least-squares regression analyses were carried out. Constants b_1 and intersects b_0 of the regression lines following the general equation $y = b_0 + b_1x$ were tested for significance by using a suitable Student's t-test. Statistical analysis was conducted with the help of MS-EXCEL© (v. 2007) and the specialized application statistiXL© (v. 1.x).

Results

Descriptive statistics

Results of descriptive statistics are summarized in Tab. 1. Whilst mean body mass of the females analyzed in this study amounts to 842.5 $\pm$ 78.9 mg (range: 632.7 – 1039.1 mg), body length of the animals, measured from the front of the head to the end of the abdomen, takes an average value of 22.2 $\pm$ 1.4 mm (range: 18.0 – 24.3 mm). According to the egg-counting experiments, one female of given age deposits 94.6 $\pm$ 14.6 oocytes into the substrate within 24 hours (range: 53 – 124 oocytes). The mean number of mature oocytes stored in the ovaries amounts to 97.0 $\pm$ 25.2 (range: 51 – 173 oocytes). For ovary mass a mean of 92.1 ± 13.8 mg could be determined (range: 61.5 – 123.2 mg), whereas the number of ovarioles composing a single ovary is 73.8 ± 12.7 (range: 49 – 97). Dry mass, calculated for the sake of completeness, amounts to 119.4 ± 18.5 mg (range: 67.6 – 148.7 mg).

Tab. 1: Results of descriptive statistics concerning diverse physiological traits of the black field cricket (SD...standard deviation, MIN...minimum, MAX...maximum).

	Body mass (mg)	Body length (mm)	Daily fecund.	Eggs in ovary	Ovary mass (mg)	Dry mass (mg)	Ovarioles
Mean	842.5	22.2	94.6	97.0	92.1	119.4	73.5
SD	78.9	1.4	14.6	25.2	13.8	18.5	12.8
MIN	631.7	18.0	53	51	61.5	67.6	49
MAX	1039.1	24.3	124	173	123.2	148.7	97

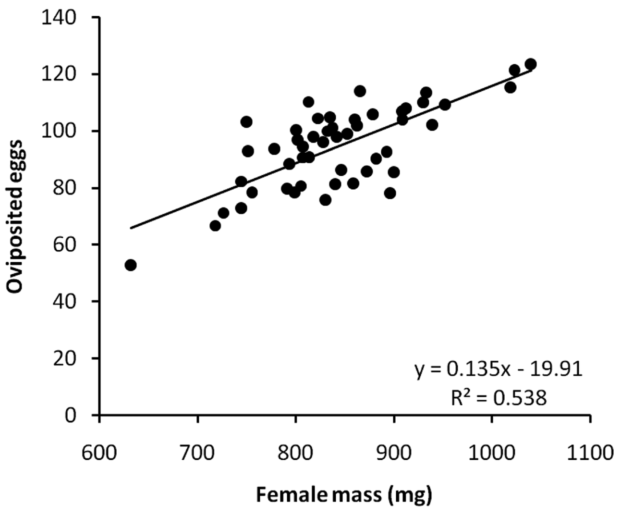

Fig. 2: Relationship between the daily number of eggs oviposited in the substrate and female body mass (N = 50).

Relationship between daily fecundity and female mass

As clearly demonstrated by the regression analyses exhibited in Figs. 2 and 3, daily fecundity of female *T. commodus* positively correlates with body mass. Concerning the daily number of oocytes deposited into the substrate, a regression line following the equation $y = 0.135x - 19.91$ ($R^2 = 0.538$) could be determined. Significance of the constant b_1 ($P = 0.02$) and the intersect b_0 ($P < 0.01$) was attested. As suggested by the linear function, each additional mg of female body mass results in an increase of daily fecundity by 0.135 eggs.

The number of mature eggs stored in a single ovary of the female black field cricket depends on body mass according to the linear regression formula y = 0.208x – 78.45 (R^2 = 0.426). Both regression parameters were classified as highly significant ($P < 0.01$). In the case given here, each increase of female's body mass by 1 mg results in an increase of the content of mature eggs in the ovaries by 0.208.

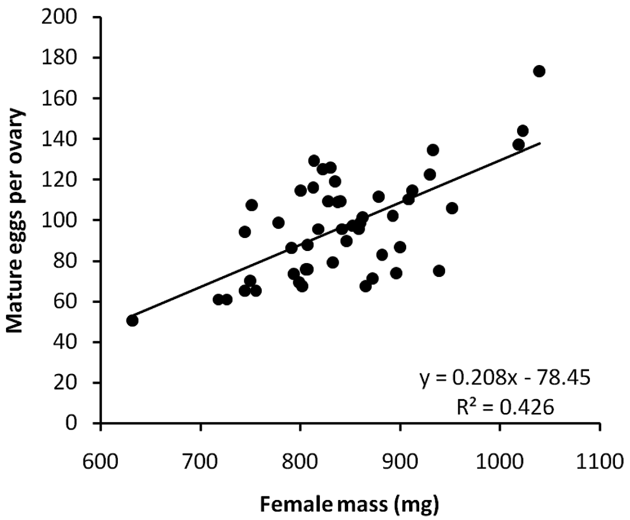

Fig. 3: Relationship between the number of mature eggs stored in the ovary and female body mass (N = 50).

Relationship between ovary mass/ovariole number and female mass

Similar to daily fecundity, also ovary mass exhibits a clearly positive correlation with female body mass (Fig. 4). Based upon statistical computations, a regression line with the formula y = 0.118x – 8.01 (R^2 = 0.460) was obtained. Whilst the constant b_1 was categorized as significant ($P = 0.02$), for the intersect b_0 high significance ($P < 0.01$) could be found. According to the linear regression equation ovary mass interrelates with female body mass insofar as each additional mg of body mass causes an increase of ovary mass by 0.12 mg.

Regarding the interrelationship between the number of ovarioles per ovary and female body mass, the respective correlation found by experimental work takes the form y = 0.104x – 14.5 (R^2 = 0.411). For the constant b_1 a probability of significance of 0.034 was computed, whereas the intersect b_0 was evaluated as highly significant ($P < 0.01$). The data commonly suggest an increase of the ovariole number by 0.10 for each additional mg of female mass (Fig. 5).

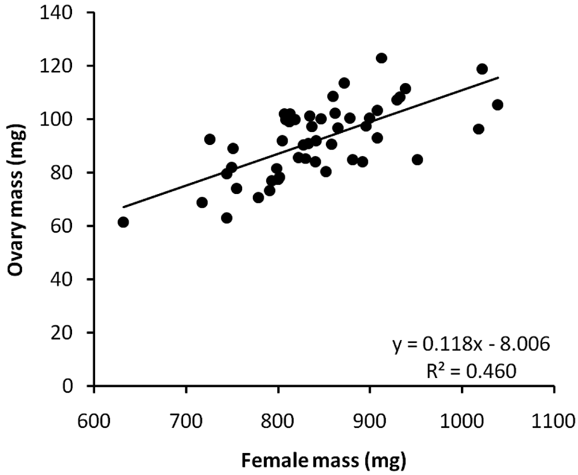

Fig. 4: Relationship between ovary mass and female body mass (N = 50).

Discussion

The present study yields clear evidence that size of female *T. commodus*, expressed by its body mass, represents a principal determinant with regards to female fecundity. As demonstrated by linear regression analysis, each trait describing female's fecundity (egg number oviposited within 24 hours, eggs stored in the ovaries, ovary mass, etc.) exhibits a positive correlation with body mass, whereby regression coefficients b_0 and b_1 were tested as significant or even highly significant in all cases.

Concerning the interrelationship between egg number and body size, similar linear functions or more complex allometries are frequently discussed in literature (LABARBERA 1989; HONĚK 1993; BROWN & WEST 2000; WHITMAN 2008) and are, among others, substantiated by the space available within the female's body and proportionality between this space and female mass. However, this assumption requires a constant egg size throughout the determined female size classes. In the case of *T. commodus*, variation of mature egg size could be determined as almost negligible, which is also observed in other insect species (e.g., KRAINACKER et al. 1989; SOLBRECK et al. 1989; FITT 1990). In insects exhibiting a positive correlation between egg size and female body size (e.g., KIMURA & TSUBAKI 1985; DIXON 1985; LARSSON 1990; MCLAIN 1991), respective regression coefficients are commonly characterized by lower significance compared to regression coefficients determined for the fecundity/size interrelationship (WIKLUND & KARLSSON 1984; PALMER 1985). Therefore, it may be concluded that any variation of egg size, as far as observable, only contributes to a limited extent to the main correlation between fecundity and female body mass (HONĚK 1993). Factors influencing egg size more remarkably than female body size are, among others, female age (WICKMAN & KARLSSON 1987; SVÄRD & WIKLUND 1988; KASULE 1991) and environmental temperature (BRITTAIN et al. 1984; WALL 1990), which were kept as constant as possible in the present investigation.

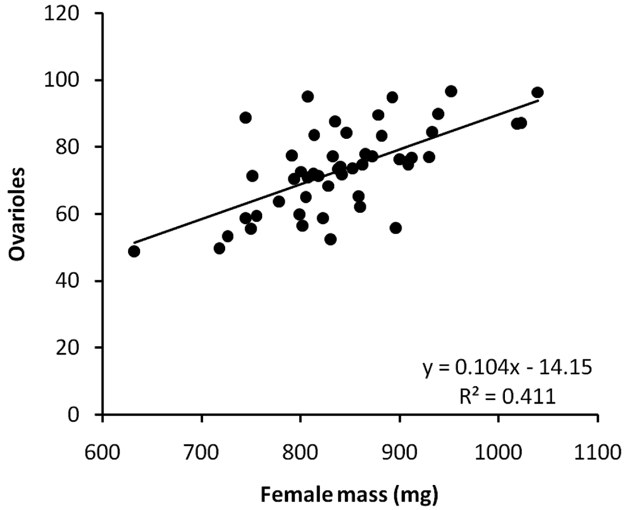

Fig. 5: Relationship between the number of ovarioles and female body mass (N = 50).

For reasons of a better comparison of the results presented here with the results of other similar studies, data obtained from the measurement procedures were standardized according to an algorithm that was originally introduced by HONĚK (1993): for each experimental line data transformation based on the formula (actual factor – median factor)/median factor was conducted and plotted in an XY-diagram (Fig. 6). Slopes of subsequent linear regression analyses applied to the data points were compared with respective regression slopes determined for other insects. As could be found by detailed comparison, *T. commodus* shows an interrelationship between fecundity and body size that is very similar to other insects, especially to that of many Hymenoptera (e.g., LIU 1985; TAKAGI 1985) and numerous Lepidoptera (e.g., MILLER et al. 1982; BANNO 1990). Slopes of standardized regressions computed for *T. commodus* are commonly greater than 1 which indicates that fecundity per unit body mass is greater in large females than in small ones (HONĚK 1993). For regression slopes being smaller than 1, an inverse relationship between fecundity and size becomes true (SIBLY & CALOW 1986).

It has to be strictly noted in this context that the fecundity/size regressions computed for females of the black field cricket are only valid for specific environmental conditions which prevailed during nymph development and adult life time. Modification of one or more environmental factors was shown to have a positive or negative effect on the growth of this cricket species (STURM 2008, 2010). This essential circumstance also limits the use of fecundity/size relationships determined in the laboratory for precise predictions in the field, where insect's life is controlled by a complex spectrum of biogenic and abiogenic factors (LEATHER & BURNAND 1987; LEATHER 1988). Future studies on this interesting topic should help to close the gap between ideal conditions offered in the laboratory and reality existing in nature.

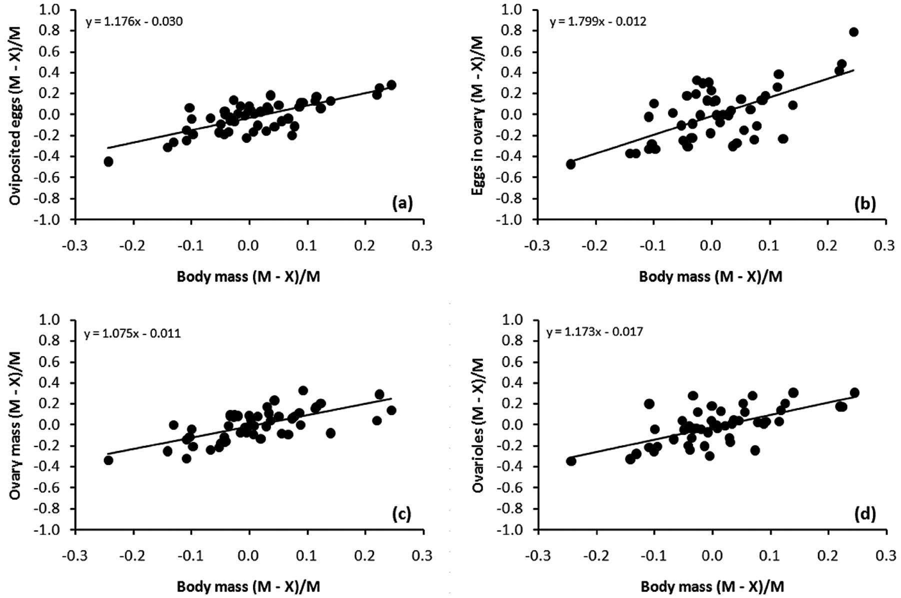

Fig. 6: Standardization of the data presented in Figs. 2 to 5 according to the algorithm presented by HONĚK (1993): (**a**) oviposited eggs vs body mass, (**b**) eggs stored in the ovary vs body mass, (**c**) ovary mass vs body mass, (**d**) number of ovarioles vs body mass. Abbreviations: M - median, X - investigated trait.

The results of this study lead to the conclusion that larger females producing a higher number of eggs and, thus, a larger offspring have important ecological and evolutionary advantages with respect to small females. A similar conclusion, however, was recently found for males of the black field cricket, where body size is positively correlated with spermatophore size and the amount of sperm stored in the ampulla (STURM 2011, 2014). From an ecological point of view, larger females provide better fitness with regard to the reproductive process. Due to their higher longevity (STURM 2008), they are additionally enabled to extend their oviposition period with respect to small females. In many insects, large females are subject to assortative mating insofar as they choose only large males as sexual partners (CUEVA DEL CASTILLO 2003; WHITMAN 2008). Large males are a better guarantee for a maximization of the offspring than small males. The evolutionary advantages of larger females compared to small females are mainly founded upon the circumstances that larger individuals often live longer, develop faster, and adapt better to any environmental changes of their habitats than small individuals (WHITMAN 2008 for review).

Although our knowledge concerning the fecundity/size relationship in animals and especially in insects has been continuously increased during the past decades, further studies dealing with this interesting topic have to be carried out in near future to confirm the predictive value of the experimental results.

Zusammenfassung

Gemäß allgemeiner ökologischer Theorien wird die Reproduktion von Insekten unter anderem durch die Fitness der männlichen und weiblichen Individuen gesteuert. Da es nur wenige Daten bezüglich des Zusammenhangs zwischen Fitness und reproduktiver Kapazität bei weiblichen Grillen gibt, wurden entsprechende Untersuchungen an Weibchen der Australischen Feldgrille *Teleogryllus commodus* WALKER, 1869 (Gryllidae, Gryllini) durchgeführt. Wie anhand statistischer Analysen festgestellt werden konnte, korreliert die mittlere tägliche Fekundität, welche durch die Anzahl der in das Substrat abgelegten Eier zum Ausdruck gelangt, mit der Körpermasse der Weibchen ($P = 0{,}02$; $b_0 = -19{,}91$, $b^1 = 0{,}135$, $R^2 = 0{,}538$). Positive Korrelationen konnten zudem zwischen der in den Ovarien gelagerten Eizahl und der Körpermasse ($P < 0{,}05$; $b_0 = -78{,}45$, $b_1 = 0{,}208$, $R^2 = 0{,}426$) sowie der Ovarienmasse (getrocknet) und der Körpermasse ($P < 0{,}05$; $b_0 = -8{,}01$, $b_1 = 0{,}118$, $R^2 = 0{,}460$) verzeichnet werden. Die Anzahl der Ovariolen zeichnete sich ebenfalls durch eine positive Korrelation mit der Körpermasse aus, wobei folgende Regressionsgerade ermittelt wurde: $y = 0{,}104\ x – 14{,}15$ ($P < 0{,}05$; $R^2 = 0{,}411$). Die Studie demonstriert sehr klar, dass große (schwere) Weibchen eine größere Anzahl an Nachkommen produzieren als kleine Weibchen. Zudem bestätigt die Untersuchung jene Hypothese, wonach die Körpermasse einen übergeordneten Einflussfaktor in Bezug auf die weibliche Fekundität darstellt.

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