Dependence of daily oviposition activity and total fecundity on body mass in the house cricket *Acheta domesticus* (L.) (Insecta: Orthoptera)

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A b s t r a c t : The contribution investigates the possible effect of body mass on daily and total fecundity for the exemplary case of the house cricket *Acheta domesticus* (L.). For this purpose, female crickets were assigned to three different body mass categories (600-800 mg, 801-1000 mg, 1001-1200 mg). Females of each category (N = 20) were studied with regard to their daily oviposition activity by application of a welldocumented experimental method. Climatic conditions were kept constant for all experimental lines (25°C, photoperiod of 12 h, relative humidity of 60%). Total fecundity of an individual was evaluated by summing up all eggs deposited into the substrate during the whole life-time. According to the results of this study daily fecundity significantly increases with body mass, with highest differences between the datasets being available between the 5th and 20th day of the adult lifespan. Also total fecundity is subject to significant discrepancies between the selected mass categories. The study strongly recommends body mass of female house crickets as essential trait concerning the reproductive capacity and, as consequence of that, the production of offspring.

K e y w o r d s : Oviposition, daily fecundity, total fecundity, reproductive fitness, crickets.

Introduction

As already reported in numerous previous studies (e.g., WHITMAN 2008, STURM 2011, 2014, 2016a), reproduction of female orthopteran insects is affected by a multitude of physical, chemical, and biological factors. Whilst among the physical control parameters environmental temperature has been crystallized out as highly essential with regard to the amount of produced eggs (e.g., UVAROV 1977, LABARBERA 1989, HONĚK 1993, STURM 1999, 2008, 2010, 2011), body size, expressed by body mass, has been evaluated as important biological parameter influencing reproductive fitness (STURM 2011, 2014, 2016a). According to the comprehensive scientific results summarized in the review of WHITMAN (2008) body mass is assumed to represent a trait with enormous biological consequences for the orthopteran insects (Fig. 1): Besides its valuable effect on reproduction in both female and male individuals, it also has a remarkable influence on the physiological efficiency, competitive capacity, and mating success of the animals.

Within the family of the crickets, lots of scientific investigations could already produce a direct relationship between body size of the individuals and reproductive output. Some male bush crickets and field crickets are characterized by a positive correlation between

spermatophore size, expressed by the diameter of the ampulla, on the one side and body size on the other (STURM 2011, 2014). The female Australian field cricket *Teleogryllus commodus* exhibits a positive correlation between ovary mass and body mass. In addition, the maximum fecundity per day, occurring between the 5th and 10th day of the adult lifespan, highly depends upon the mass of the females, with heavier (= larger) individuals ovipositing significantly more eggs than lighter (= smaller) individuals (STURM 2016a). Since many recently published results are limited to only few cricket species, ecophysiological studies dealing with the relationship between body traits and reproduction may not be considered as complete for a long time yet.

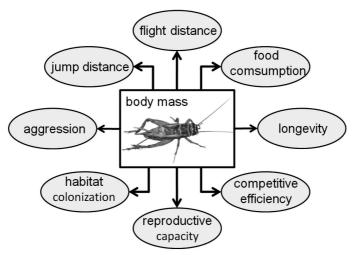


Fig. 1: Biological traits demonstrably influenced by body mass in orthopterans (WITHMAN 2008).

The present contribution pursues two main objectives: First, fecundity of female crickets and its possible dependence upon body mass is subjected to a detailed analysis. Here, the life-time egg production of single animals is measured with the help of large-scale experimental lines. Second, the probable effect of body size on total fecundity is evaluated statistically in order to obtain a firm foundation for critical argumentation. All experiments were conducted on the house cricket *Acheta domesticus*, which has been proved as worthwhile regarding its keeping and rearing in the past (STURM 1999, 2002b, 2003, 2008, 2011b).

Material and Methods

Culture and keeping of Acheta domesticus

A large population of the house cricket was reared by using the climate chamber at the former Institute of Zoology, University of Salzburg. Cricket nymphs belonging to early developmental stages were kept in small plastic boxes ($15 \times 10 \times 5 \text{ cm}$) filled with peat soil and food, whereas intermediate and late instars were transferred into larger plastic boxes ($50 \times 40 \times 30 \text{ cm}$) that contained a 3 cm thick layer of peat soil, an extended sup-

ply with food (lettuce, water, standard diet for laboratory animals), and egg cartons serving for shelter of the animals (Fig. 2a). After their imaginal molt, crickets were separated by gender and subsequently kept in glass vessels with a volume of 5 L, respectively (Fig. 2b). Each of these reservoirs contained a maximum of five animals and was additionally equipped with food (lettuce, water, standard diet) as well as wrinkled paper, in which single individuals could find shelter (STURM & POHLHAMMER 2000, STURM 2002a, 2002b, 2003, 2010, 2011, 2014, 2016a, 2016b). Culture of the house cricket was conducted by application of constant temperature conditions (25 °C), a photoperiod of 12 h and a relative humidity of 60%.

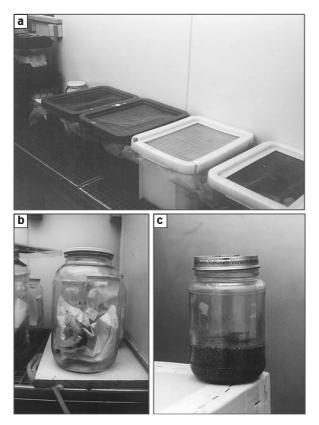


Fig. 2: Equipment for the culture of the house cricket *Acheta domesticus*: (**a**) climate chamber with plastic boxes containing cricket nymphs, (**b**) glass vessels containing adults separated by gender, (**c**) small oviposition vessels for the investigation of daily fecundity.

Analysis of daily and total fecundity

Measurement of reproductive capacity in females of *Acheta domesticus* was preceded by the mating process, where selected males and females were brought together in specific glass dishes (diameter: 30 cm). After completion of copulation, females were anesthe-

tized in a weak stream of carbon dioxide (CO₂) and weighed by using a high-precision balance. Animals were assigned to three different mass categories (600-800 mg, 801-1000 mg, 1001-1200 mg). Awakening from anesthesia was followed by the transfer of single animals into specific glass vessels (volume: 250 mL) especially serving for the oviposition of fertilized eggs (Fig. 2c). These glass containers were filled with a 5 cm thick layer of moistened sand and additionally contained some food for the crickets. After 24 h, females were transferred into a new set of oviposition vessels, where they again could deposit their eggs into the substrate. This process was carried out from the beginning of female oviposition activity, which can be committed with the 8th day of the adult phase at an environmental temperature of 25°C, till its end occurring between the 40^{th} and 45^{th} day (STURM 2003, 2008, 2011, 2016b).

Total fecundity of single females was determined by simply summing up the numbers of eggs oviposited into the substrate each day. Daily and total fecundity were analyzed by application of both descriptive and conclusive statistics, in the course of which the calculation software MS-Excel was used.

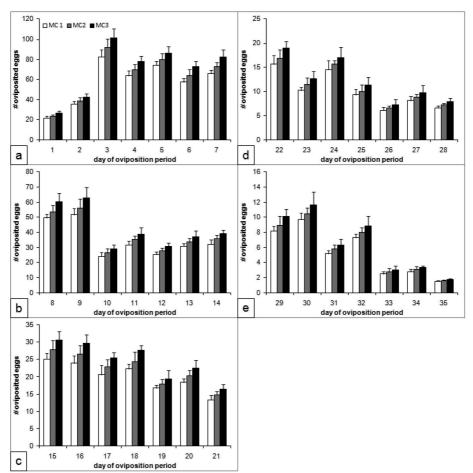
Results

Relationship between daily fecundity and mass

Detailed results of the large-scale analysis of daily fecundity and its dependence on body mass of the female house cricket are summarized in Fig. 3. For all mass categories a total fecundity period (i.e., the period, within which active oviposition takes place) of 35 d could be determined experimentally. Therefore, deposition of fertilized eggs into the substrate starts at the 8th day of the adult phase and ends at the 42nd day. Most females die immediately after the fecundity period. As demonstrated by the graphs of Fig. 3, highest oviposition activity may be recognized in the time interval ranging from the 3rd to the 9th day of oviposition. The maximum daily fecundity uniformly occurs on the 3rd day of the reproduction-active phase (Fig. 3a).

The graphs of Fig. 3 show that daily fecundity is subject to a valuable increase with body mass. Between mass category 1 containing females with a mass of 600-800 mg and mass category 2 including females with a mass of 801-1000 mg this increase in reproductive activity amounts to 5-10%. Between mass category 2 and mass category 3 comprising female crickets with a mass of 1001-1200 mg another enhancement of fecundity amounting to 7-12% can be observed. Whilst mass category 1 and mass category 2 are characterized by significant differences (p < 0.05) during the main phase of reproductive activity (1st to 20th day), at later stages of the adult phase respective discrepancies become more and more insignificant, indicating higher fluctuations of daily fecundity. A very similar observation can be made after comparison of mass category 2 with mass category 3. If reproduction of heaviest females (mass category 3) is directly compared with that of light-weights (mass category 1), highly significant differences (p < 0.001) can be computed throughout the entire period of experimental analysis.

Summing up the results a specific course of fecundity can be diagnosed for all mass categories of the female house cricket: Therefore, a very short phase with rapid increase in daily oviposition (1^{st} to 3^{rd} day) is succeeded by a much longer phase with continuous exponential decrease of daily reproductive activity (4^{th} to 35^{th} day). The half-width of the



computer-generated time-dependent fecundity function varies between 6 and 10 days and thus indicates high temporal limitation of reproductive top performance in *Acheta*.

Fig. 3: Temporal course of daily fecundity (mean + sd) in *Acheta domesticus* and its dependence on body mass. Three mass categories (MC) have been distinguished: MC1 - 600-800 mg, MC2 - 801-100 mg, MC3 - 1001-1200 mg; (a) 1st to 7th day of oviposition period; (b) 8th to 14th day; (c) 15th to 21st day, (d) 22nd to 28th day, (e) 29th to 35th day. Between most adjacent values significant differences (p < 0.05) could be determined.

Total fecundity of Acheta domesticus and its dependence on body mass

With regard to total fecundity the effect of body mass on reproductive capacity of single females becomes much better visible (Fig. 4). Therefore, individuals belonging to mass category 1 oviposit a total number of 893.7 ± 66.6 eggs into the substrate, whereas for crickets of mass category 2 the total amount of released eggs assumes a value of 978.8 ± 52.6 . Finally, the heaviest females belonging to mass category 3 are characterized by a total fecundity of 1088.6 ± 97.4 eggs. According to conclusive statistics (Student's t-test)

applied to the three datasets differences between mass category 1 and 2 as well as between mass category 2 and 3 have to be valued as highly significant with p < 0.001, respectively.

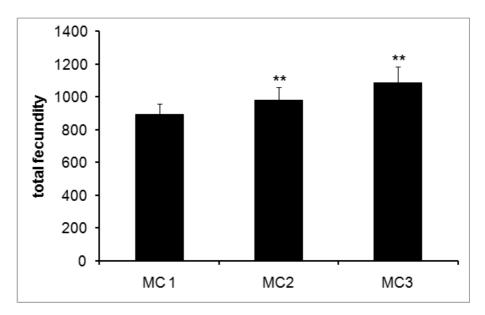


Fig. 4: Total fecundity (mean + sd) measured for female crickets belonging to mass category (MC) 1, 2, and 3. Asterisks indicate highly significant differences between adjacent mean values (p < 0.001).

Discussion

In the past, body length and body mass, both being representatives of insect size, have been identified as essential indicators with regard to physical efficiency and reproductive success (HONĚK 1993, WHITMAN 2008, STURM 2014). Among orthopteran insects, heavier individuals of a given species are able to develop numerous abilities, which are largely refused to their light-weight counterparts. For instance, large crickets can perform wider jumps and faster flights than smaller ones, so that greater distances can be overcome and, as consequence of that, a wider distribution of the population can be guaranteed (WHITMAN 2008). In reproductive regards, large orthopterans have higher mating success than small ones, because heavy males can copulate both large and small females, whereas males with reduced body mass can only copulate small females (WHITMAN 2008, STURM 2011a, 2014, 2016a).

The possible effect of body mass on daily fecundity was repeatedly stated in diverse publications (WHITMAN 2008), but was not proven by concrete experimental data. In the present contribution, respective experimental data are presented for the house cricket *Acheta domesticus*. As already mentioned above, collection of such data encounters

some difficulties, because animals used for the experimental lines have to be available in high numbers and have to be marked by rather constant and predictable behaviour with regard to their reproductive activity. These important frame conditions are only realized in professional long-term cultures taking place under precise environmental conditions (STURM & POHLHAMMER 2000, STURM 2002a, 2002b, 2003, 2008, 2010, 2011, 2014).

The results obtained from the experimental lines clearly demonstrate that body mass has a valuable and mostly significant effect on daily fecundity of the female house cricket. Therefore, large females deposit more eggs into the substrate than small ones, with highest differences between them occurring at phases of maximum reproductive activity. The results provided in this contribution are rather similar to those published for females of the Australian field cricket *Teleogryllus commodus*. In the case of this orthopteran, both ovary mass and maximum daily fecundity exhibit a linear correlation with body mass (STURM 2016a). This behaviour, however, may be observed for a multitude of insect orders and species summarized therein, but its intensity, expressed by the slope of the linear regression function, may be subject to high variations among the different insects (REISS 1989, HONĚK 1993, NYLIN & GOTTHARD 1999, AKMAN & WHITMAN 2008, BOSWELL et al. 2008, BANSON 2008, KELLY et al. 2008, HODIN 2009).

A much clearer picture of the situation may be drawn in the case of total fecundity, whose dependence on body mass of the female house cricket may be evaluated as highly significant. This circumstance unequivocally leads to the conclusion that large females of *Acheta domesticus* produce a much higher total number of eggs than small females, by which the hypothesis of a direct relationship between female reproductive activity and body mass is strongly confirmed. A similar relationship has already been proven for males of several field crickets, where larger individuals have the ability to produce larger spermatophores with higher numbers of spermatozoa stored therein (STURM 2011, 2013, 2014). Another interesting fact concerns the temporal course of female fecundity. Previous publications could demonstrate that the relationship between oviposition and time can be well approximated by a Weibull distribution (STURM 2008, 2010, 2011) with rather steep increase at early reproductive phases and slow decrease at intermediate and late phases.

The present contribution has to be understood as another small step concerning the study of possible factors controlling insect reproduction. Although the results presented here have to be evaluated as essential for the entire understanding of ecophysiological processes, further investigations have to follow in future.

Zusammenfassung

Abhängigkeit der täglichen Ovipositionsaktivität und totalen Fekundität von der Körpermasse beim Heimchen Acheta domesticus (L.) (Insecta: Orthoptera). Der Beitrag untersucht den möglichen Effekt der Körpermasse auf tägliche und totale Fekundität für den exemplarischen Fall des Heimchens Acheta domesticus (L.). Zu diesem Zweck wurden weibliche Grillen drei verschiedenen Massenkategorien (600-800 mg, 801-1000 mg, 1001-1200 mg) zugeordnet. Weibchen aus jeder Kategorie (N = 20) wurden in Bezug auf ihre tägliche Ovipositionsaktivität untersucht, wobei hierfür eine gut dokumentierte experimentelle Methode zur Anwendung gelangte. Die klimatischen Bedingungen wurden bei allen Versuchsreihen konstant gehalten (25°C, Fotoperiode von 12 h, Relative Luftfeuchtigkeit von 60%). Die totale Fekundität eines Individuums wurde durch Aufsummierung aller Eier, welche das Tier während seiner gesamten Lebensspanne in das Substrat

abgelegt hatte, ermittelt. Gemäß den gewonnenen Resultaten dieser Studie wächst die tägliche Fekundität signifikant mit der Körpermasse an, wobei maximale Diskrepanzen zwischen den jeweiligen Datensätzen zwischen dem fünften und zehnten Tag der adulten Lebensphase auftreten. Auch die totale Fekundität weist signifikante Unterschiede zwischen den ausgewählten Massenkategorien auf. Die Untersuchung deutet klar darauf hin, dass die Körpermasse des weiblichen Heimchens als essenzielles Merkmal bezüglich der reproduktiven Kapazität und der daraus resultierenden Produktion von Nachkommenschaft gilt.

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