Linzer biol. Beitr.	42/1	803-815	30.7.2010

Life Time Egg Production in Females of the Cricket *Teleogryllus commodus* WALKER 1869 (Insecta: Orthoptera): Experimental Results and Theoretical Predictions

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A b s t r a c t : Egg-laying activity of female *Teleogryllus commodus* was studied at four different environmental temperatures, namely 20 °C, 23 °C, 25 °C, and 30 °C, whereby the number of eggs oviposited per day and the total number of eggs oviposited during adult life time were determined. For recognizing the eggs stored in the female ovaries at the different environmental conditions, also ovary weights of 5-day old and 10-day old females were measured and compared. As the main result number of oviposited eggs increases with growing environmental temperature, with females reared at 30 °C laying four to five times as many eggs as females reared at 20 °C. Duration of the oviposition period is also enhanced with temperature, because females start earlier with their oviposition and continue the egg-laying process to higher ages. Besides the number of eggs oviposited, also the number of eggs stored in the ovaries increases with environmental temperature, whereby ovary weight of 10-day old females kept at 30 °C was three to four times higher than ovary weight of respective females kept at 20 °C. In addition to the experimental results also a computer model, named CRICKTHERM, is presented, which allows the generation of total fecundity functions for different cricket species and the prediction of oviposition efficiencies after variation of different environmental factors such as temperature, humidity, photoperiod, and population density. As a preliminary result, respective predictions are presented for four environmental factors.

K e y   w o r d s : *Teleogryllus commodus*, Orthoptera, environmental temperature, fecundity, photoperiod, population density, computer model.

Introduction

Under natural conditions, poikilotherms are subject to a combination of abiotic and biotic environmental influences determining the dispersal and abundance of a respective species to a certain extent (TAUBER et al. 1986). Within the class of the Insecta, speed of development, duration of life, and reproductive activity are mainly affected by the environmental temperature, resulting in a preferential temperature range for each insect species, out of which the mortality rate becomes strongly increased (HOFFMANN 1995). As exhibited by numerous experimental studies (HOFFMANN 1985 and references cited therein), the velocity of development and reproductive rate of most insects increase with rising temperature and, again, decline rapidly after exceeding of an upper temperature limit. Experiments investigating the positive correlation between reproductive activity and temperature have been so far carried out for members of various insect orders, including the Orthoptera (e.g. GHOURI & MCFARLANE 1958; HOFFMANN 1974; MERKEL 1977; BEHRENS et al. 1983; STURM 1999), Hemiptera (e.g. WELBERS 1975), and Lepidoptera (e.g. Barker & Herman 1976). Besides the general effect of environmental temperature on egg production in females, it could be successfully demonstrated by extensive laboratory work that a diurnal variation of temperature (i.e., a change of temperature between light and dark period) may result in a further increase of the reproductive activity. As an explanation of this phenomenon, insects living in a habitat with daily fluctuating temperatures are assumed to adapt their activities such as ingestion and resting to the rhythmic change of environmental temperature. This causes, on the one side, an increase in body weight due to an enhanced food intake per time (ADKISSON 1961) and, on the other side, a prolongation of the egg-laying period within adult's life time as well as a partly dramatic increase of the daily egg production. As described in the comprehensive study of BEHRENS et al. (1983), orthopteran insects like *Gryllus bimaculatus* show a positive reaction to diurnally changing temperatures, but exhibit a further increase of their reproductive activity (e.g. doubling of egg number with respect to constant temperatures), if the temperature regime is subject to quick oscillations (e.g. every 2 hours). However, the respective behaviour of other crickets as well as grasshoppers and mantids has not been worked out in detail until now.

Concerning mathematical models describing the relationship between insect ontogenesis or reproduction and environmental factors such as temperature, humidity, photoperiod, inter- and intraspecific competition, only few approaches have been published in the scientific literature until now. For the mathematical description of the relationship between duration of development and temperature, respective model functions were introduced by JANISCH (1925), which in the following decades were extended and improved by e.g. LOGAN et al. (1976) as well as HILBERT & LOGAN (1983). For a better understanding of the effect of fluctuating temperatures on insects KAUFMANN (1932) defined the so-called temperature sum role, based on the product of developmental period and effective environmental temperature. Applications of this role were more recently made by e.g. SHARPE & DEMICHELE (1977) as well as BEHRENS et al. (1983). A recently developed alternative to the temperature sum role of KAUFMANN was the concept introduced by EUBANK et al. (1973), including the addition of developmental rates and therefore representing insect development under rapidly oscillating temperatures in a better way. Influences of other environmental factors than temperature have only awakened marginal attention until now.

The contribution presented here has two main objectives: First, experimental data describing the relationship between life time egg production of the black field cricket *Teleogryllus commodus* and environmental temperature are presented and discussed. Second, a mathematical model, named CRICKTHERM, is introduced, which allows the computation of egg production functions and, more interesting, the prediction of cricket fecundity at variable environmental conditions.

Materials and Methods

Animals

Teleogryllus commodus was reared in a climate chamber at the Institute of Zoology, University of Salzburg. The animals were fed with fresh lettuce, dry food (Altromin 1222, protein content: 20-30 %), and water. While larval instars and subadults were kept in specific plastic boxes (L x W x H = 45 x 30 x 25 cm) filled with a three cm thick layer of peat soil, adults were separated by gender and transferred into glass vessels with a volume of 5 l, respectively. Reproductive behaviour of females was observed at four different temperatures: 20 °C, 23 °C, 25 °C, and 30 °C. For each of the four experimental lines, atmospheric humidity was kept at a constant value of 60 %, and the photoperiod was set to 12 hours.

Oviposition

Female crickets 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 three to four cm thick layer of sterilized sand, food, and water. To determine the amount of oviposited eggs within a pre-defined time span, females were moved into new oviposition vessels every 48 hours. For a statistical evaluation of oviposition, 25 animals were investigated according to this way. 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. The total number of oviposited eggs and development of oviposition activity was determined by transferring females in new oviposition vessels every two days during the whole period of fertility.

Dissection of the Ovaries

To determine the overall production of mature eggs during a pre-defined period, the ovaries had to be dissected and investigated on their content of fully developed eggs. Therefore, 5-day old and 10-day old females were anaesthetized in a carbon dioxide stream, decapitated, and transferred into a dish filled with specific insect Ringer's solution (MUSIOL et al. 1990; STURM & POHLHAMMER 2000). After complete opening of the abdomen by one transversal and two cranio-caudal sections and maceration of fatty tissue, the ovaries were carefully isolated and transferred into an embryo vessel (Fig. 4 A). Main interest was focused on the relationship between mass of single ovaries and the environmental temperature, following the observations of BARKER & HERMAN (1976) on *Danaus plexippus*. Prior to the quantification of mature eggs ovaries were freed from any surrounding fatty tissue, dried with filter paper and weighed. For statistical purposes, 20 ovaries from each experimental line were investigated.

Computer Model for the Prediction of Egg-laying Activities

The computer program CRICKTHERM with its main input and output features is shown in Fig. 1. As clearly recognizable from the input window (Fig. 1B), the theoretical computations enabled by the program are based on a rather large number of input variables. Thereby the selection of the cricket species has to be regarded as an essential parameter for all further calculations, since all mathematical regressions obtained from CRICKTHERM are dependent upon species-specific coefficients. At the moment, data of four cricket species, namely *Acheta domesticus*, *Gryllus bimaculatus*, *Gryllus assimilis*, and *Teleogryllus commodus*, are implemented in the program, because for these

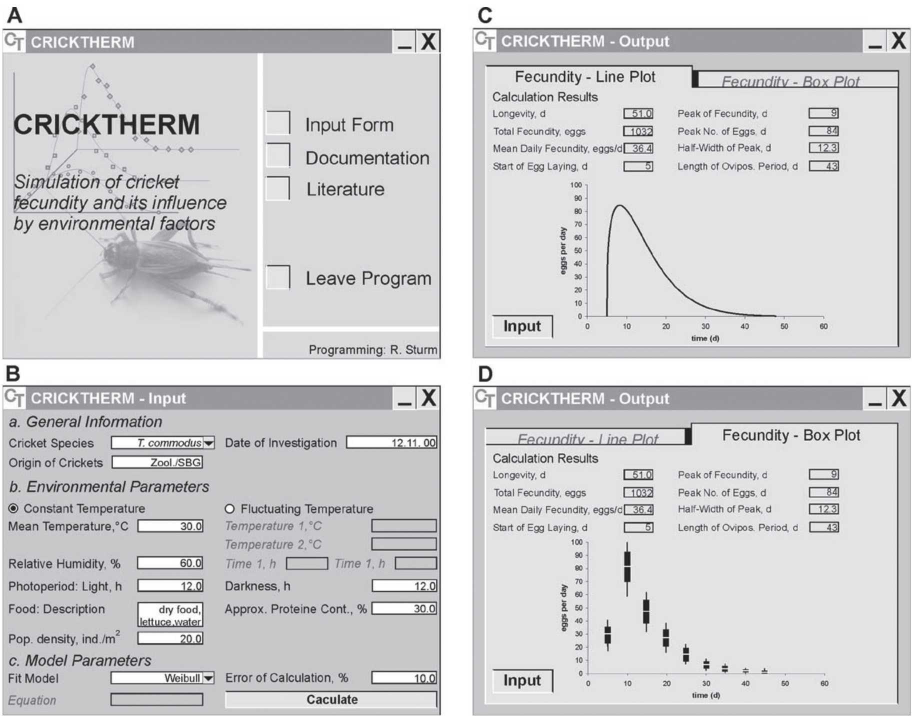

Fig. 1: Window design and function of the computer program CRICKTHERM calculating the fecundity of female crickets as a function of various environmental parameters. (**A**) Entrance window, (**B**) Input window including animal information and input parameters, (**C**) Output window presenting the fecundity-time-relationship as a line plot as well as specific output parameter, (**D**) Alternative output window presenting fecundity data as mean values and standard deviations.

orthopterans comprehensive ecophysiological data material is available from the literature (e.g. GHOURI & MCFARLANE 1958; HOFFMANN 1974, 1985; BEHRENS et al. 1983; RATTE 1985; STURM 1999, 2002). Input of external environmental factors includes a selection between constant as well as alternating temperature conditions, whereby in the first case a mean temperature has to be provided, while in the latter case frame temperatures and their respective durations have to be typed into the designated field (Fig. 1B). Further input parameters are relative humidity, duration of the photoperiod, estimated protein content of the supplied food, as well as population density, i.e., the extrapolated number of animals per m^2. For the presentation of the relationship between fecundity and time, the user is enabled to select from different distribution functions being most appropriate for these calculations (e.g. Weibull distribution or Log-Normal distribution) or to define an own function. Characteristic values of the distribution functions such as maximum fecundity, half width of the fecundity peak, and total fecundity (i.e. the area under the fecundity function) are determined by the application of linear regression models (Tab. 1). For the relationship between fecundity and environmental temperature, the temperature sum role is applied (KAUFMANN 1932), whereas also a respective increase of fecundity with rising duration of the photoperiod on the one hand and growing protein content of the food on the other hand is assumed (e.g. MERKEL 1977). The negative effect of population density on oviposition is mainly based on the assumption that the number of rivals positively correlates with the number of individuals per m^2, causing an enhanced frequency of interactions between individuals with reciprocal damage. This circumstance is accompanied by a continuous shortage of resources.

Tab. 1: Results of regression analysis forming the basis for the calculations with the computer program CRICKTHERM.

	Hour degrees, h*°C	Protein in food, %	Photoperiod, h	Population density, ind./m²	Intercept	R value
Longevity, d	-0.017	0.038	-0.915	-0.030	69.93	0.619
Oviposition period, d	-0.026	-0.115	-0.800	-0.037	69.43	0.865
Total fecundity, eggs	0.789	11.63	13.95	-0.653	13.43	0.481
Daily fecundity, eggs/d	0.200	1.394	1.850	-0.084	-94.25	0.853
Start of oviposition at day	-0.012	-0.049	-0.150	-0.007	18.33	0.936
Peak at day	-0.038	-0.144	-0.350	-0.014	46.12	0.851
Half total fecundity at day	-0.042	-0.165	-0.350	-0.021	53.11	0.866

The output of calculation results is given in numerical and graphical form (Fig. 1C, D), whereby in the latter case selection between a line diagram and a box plot is enabled. Numerical results being positioned above the graphs include longevity of the selected cricket species, total fecundity, mean daily fecundity, start of oviposition (days after imaginal moult), date of maximum fecundity with respective number of oviposited eggs, half width of the distribution, and duration of the oviposition period.

Experimental Results

Daily Fecundity of Female *Teleogryllus*

The relationship between female's fecundity and lifetime and its dependence upon environmental temperature is summarized in the graphs of Fig. 2. As can be clearly recognized, during the first half of the fertility period, daily fecundity significantly increases with rising temperature, while at the end of the oviposition period (i.e. between the 30th and 40th day after the imaginal moult) thermal influences continuously lose their importance. Regarding the start of oviposition, values range from 8 days (20 °C - 23 °C) over 7 days (25 °C) to 6 days (30 °C) after the imaginal moult. A similar temporary shift can be observed for the maximum fecundity (i.e. the daily maximum of produced eggs), because this peak is displaced from day 12 at 20 °C towards day 10 at 30 °C (Fig. 2). This phenomenon is accompanied by a remarkable increase of the maximum egg number, being enhanced from 38 ± 13 eggs at 20 °C to 105 ± 16 eggs at 30 °C. After passing the fecundity peak at a rather early stage of adult's life, egg production continuously decreases in a fluctuating fashion, until the end of fertility is reached. The termination of egg production occurs between the 35th and 45th day after the imaginal moult. The experimentally generated curves were used for a validation of the fecundity data derived from the program CRICKTHERM (grey lines in the graphs of Fig. 2). Based on the present state of the art, differences between experiments and model are on an average order of 10 to 20 %, whereby goodness-of-fit increases with rising environmental temperature.

Life-time Egg Production

As a consequence of the results described above, also the total number of eggs produced during the adult life span strongly depends upon the environmental temperature. Evidence for this important fact is given by the graph of Fig. 3. At 20°C, the total egg number, which can be obtained by integrating the curves in Fig. 2, amounts to 453 ± 82. This value is increased to 631 ± 115 at 23°C, 856 ± 188 at 25°C, and, finally, to 1108 ± 204 at 30°C. However, significant differences ($p < 0.01$) within this statistical data set occur between 23 and 25°C as well as between 25 and 30°C.

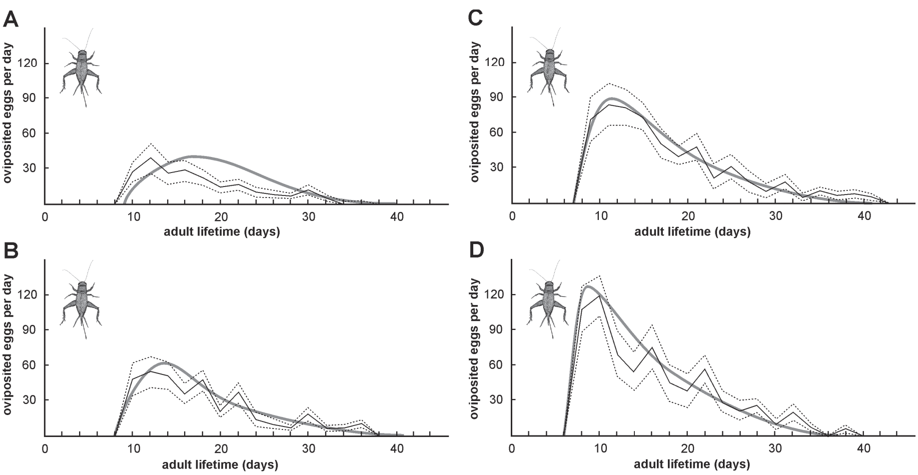

Fig. 2: Dependence of daily cricket fecundity on environmental temperature. (**A**) 20 °C, (**B**) 23 °C, (**C**) 25 °C, (**D**) 30 °C. Black lines represent mean values, whereas dashed lines mark the standard deviations. The thick grey lines show the respective out put produced by CRICKTHERM and should give an impression about the validity of the used model.

Relationship between Ovary Weight and Environmental Temperature

Following the experiments of BARKER & HERMAN (1976), the weight of ovaries isolated from 5-day old and 10-day old females was also measured as a function of the environmental temperature. Results of this evaluation are summarized in the graph of Fig. 4. Concerning adult females with an age of 5 days, ovary weight is not significantly affected by temperature. Small discrepancies of this parameter are only recognizable between 23 and 25 °C (Fig. 4). A completely different behaviour of the ovary weight can be observed for 10-day old adults of female *Teleogryllus*, increasing from 0.038 ± 0.012 g at 20 °C to 0.131 ± 0.027 g at 30 °C. This corresponds to a respective growth of nearly 300% within the studied temperature range. Similar to the number of oviposited eggs, significant differences ($p < 0.01$) between the measuring data are recognizable between 23 and 25 °C as well as between 25 and 30 °C (asterisks in Fig. 4).

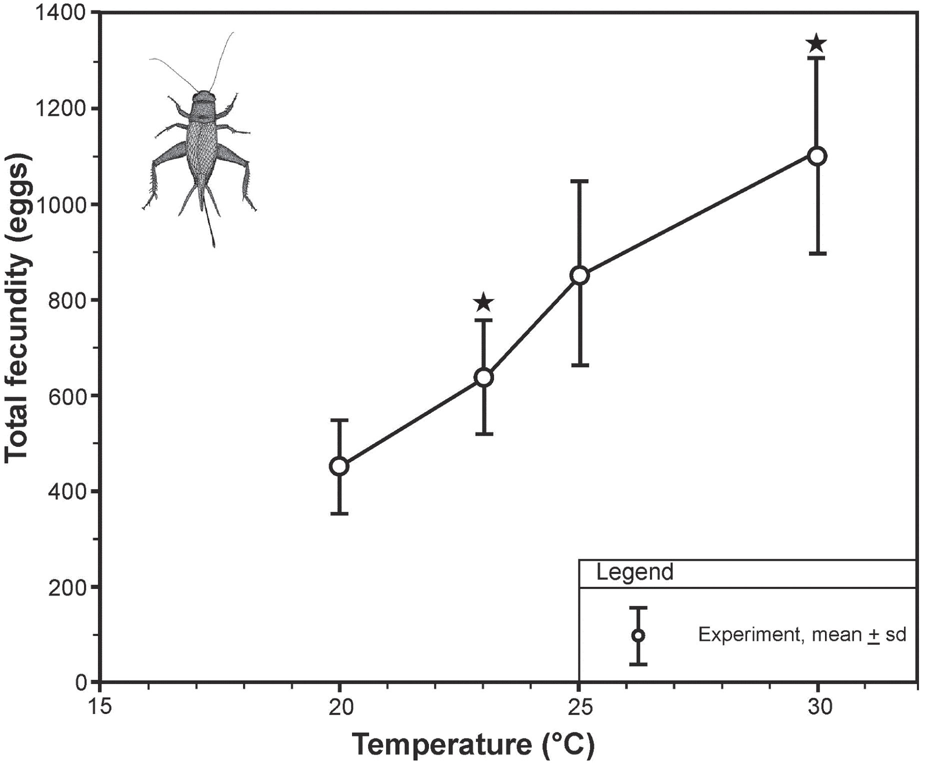

Fig. 3: Total fecundity of female *Teleogryllus commodus* WALKER for different environmental temperatures (20 °C, 23 °C, 25 °C, and 30 °C). Asterisks indicate significant differences between neighbouring points ($p < 0.01$).

Theoretical Predictions with the Computer Model

Computer simulations of fecundity-time functions were carried out by theoretically varying environmental temperature, photoperiod, protein content of the food, and population density (Fig. 5). Concerning the temperature predictions, simulations with both constant and alternating temperatures were done, whereby for the latter case switch of temperatures happened every 12 hours. As shown by the curves of Fig. 5A, maximum fecundity is increased by about 10 %, when changing thermal conditions from constant 27 °C to 27°C/18 °C. Another increase by about 10 % may be observed due to a reduction of the lower frame temperature from 18 °C to 12 °C. Regarding changes of the photoperiod, only insignificant changes of daily fecundity are predicted by the program. Generally, prolongation of the light period from 12 to 16 hours causes an enhancement of both maximum daily fecundity and total fecundity by about 15 % (Fig. 5B). More dramatic changes are predicted for varying protein contents in the food, with maximum fecundity being subject to a reduction of about 50 %, if protein content decreases from 30 % to 10 %. An increase of the protein content from 30 % to 50 %, on the other hand,

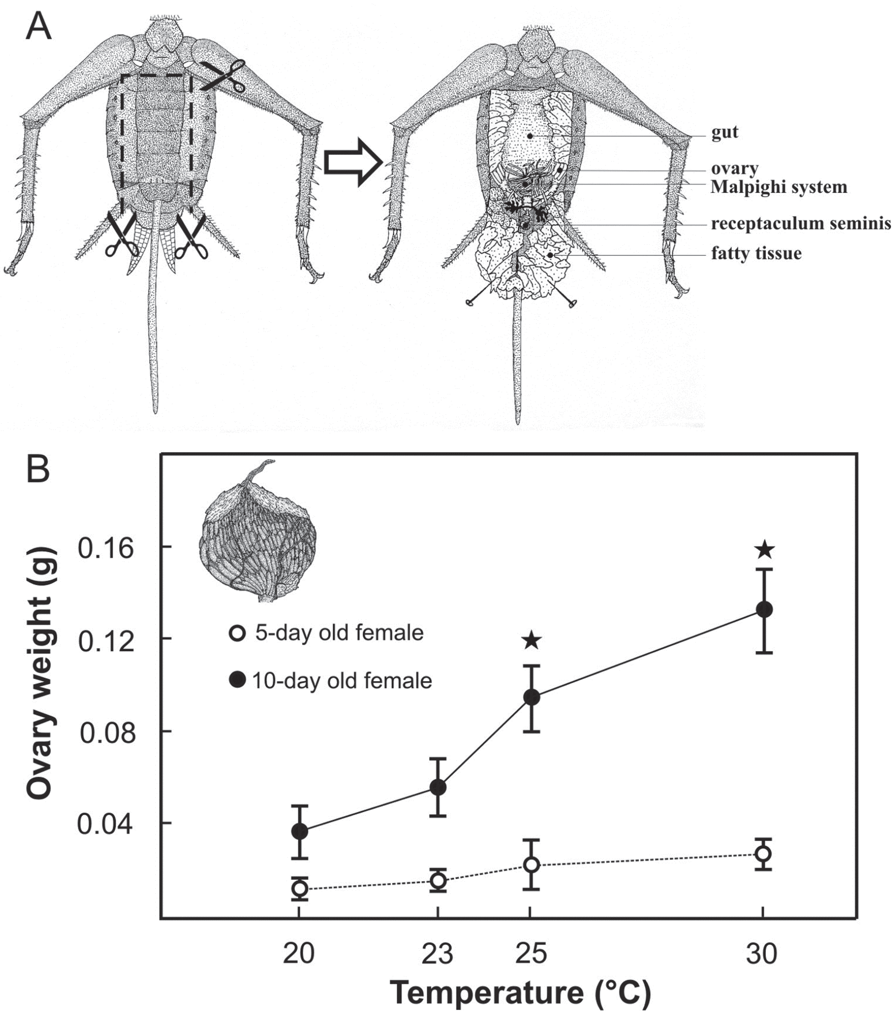

Fig. 4: Results concerning the investigation of ovary weights and their dependence on environmental temperature. A) Scheme showing the preparation procedure necessary for the dissection of the ovaries. B) Graph illustrating the dependence of ovary weight in grams on environmental temperature. Ovary weights from 5-day old females (pre-oviposition period) and 10-day old females (oviposition period) have been compared. Points and error bars denote mean values and standard deviations (asterisks mark significant differences between neighbouring points, $p < 0.01$).

causes a significant rise of the maximum fecundity, amounting to about 25 % (Fig. 5C). The effect of population density on cricket fecundity is exhibited in Fig. 5D, with maximum fecundity decreasing continuously with rising number of individuals per m^2. Doubled number of individuals causes a reduction of the respective value by about 40 %, while quadruplicating of the individual number leads to a reduction by about 50 %.

Discussion

Detailed knowledge on the reproduction of insects may be of higher importance for 1) the development of countermeasures, where these organisms occur as remarkable pasture pests, and 2) the enhancement of rearing efficiencies, where these animals are needed for e.g. experimental concerns. Crickets are regarded as favourite model organisms on the one side and food animals for reptiles and amphibians on the other side, because their population may be increased exponentially without a great technical effort. Regarding this group of insects, numerous ecophysiological data were published in the past decades, describing mainly the influence of environmental temperature and food on the animals' development and reproduction (e.g. HOFFMANN 1985, 1995; STURM 1999).

Concerning daily fecundity of female *Teleogryllus commodus*, a positive correlation between oviposition activity and environmental temperature could be demonstrated experimentally, whereby several significant changes of the fecundity graph of Fig. 2 were observed. These included 1) a shift of the start of oviposition towards the time point of imaginal moult, 2) an earlier occurrence of maximum fecundity, 3) a remarkable increase of the maximum, and 4) a decrease of the half width of fecundity. The results obtained from this study are similar to those derived from the investigations of *Gryllus bimaculatus* in the 1970s and 1980s (HOFFMANN 1974; BEHRENS et al. 1983; HOFFMANN 1985; RATTE 1985). As exhibited by BEHRENS et al. (1983), the Mediterranean field cricket increases its fecundity dramatically within the temperature interval ranging from 23 °C to 34 °C, whereas at 20 °C and 38 °C oviposition comes to a stand still (i.e. the lower and upper threshold temperature are exceeded). Besides a decrease of fecundity half width, the authors could additionally proof a significant decline of the duration of fecundity and longevity itself with rising temperature. From an ecological point of view, shift of the fecundity maximum to an earlier adult lifetime with increasing environmental temperature might have several reasons, including e.g. a premature ensuring of the descendants due to intra- and interspecific competition, being also increased with growing temperatures. As a logical consequence of the results derived from the daily fecundity experiments, also total fecundity of *Teleogryllus commodus* (i.e., the total number of eggs oviposited during adult's lifetime) depended upon environmental temperature. As illustrated in Fig. 3, females kept at 30 °C oviposited about three times as many eggs as females kept at 20 °C. Again, some parallelisms with the Mediterranean field cricket examined by BEHRENS et al. (1983) can be found, because also this orthopteran multiplies its number of oviposited eggs, if environmental temperature is subject to a significant increase. In the concrete case, total fecundity may be further increased by applying alternating temperatures (e.g. 28 °C for 12 hours and 14 °C for 12 hours). As clearly demonstrated by the results of this study and the results from literature, total fecundity is characterized by high uncertainties, expressing a remarkable intrasubject variability concerning egg-laying activity. Generally, oviposition activity reflects the physiological condition of the female, i.e. animals, which were disturbed in their development due to increased food competition or a decreased number of rest phases, produce a lower number of descendants and vice versa. Regarding total fecundity of *Teleogryllus commodus*, not only laboratory data but also respective data of animals living in their natural habitat are available from the literature (BLANK et al. 1988). According to BLANK et al. (1988), total fecundity of such crickets ranges from 60 to 1000 eggs with a mean of 360 eggs. Assuming a mean daily temperature of 20 °C, the results obtained from field studies are about 50 % lower than respective experimental values (Fig. 3). However, reproduction of free-living black field crickets is more strongly influenced by external factors than reproduction of crickets reared in the laboratory, where phases of e.g. increased humidity or aridity can not be simulated. Hence, cricket fecundity explored under laboratory conditions may be evaluated as an optimum fecundity, indicating a maximum possible egg production.

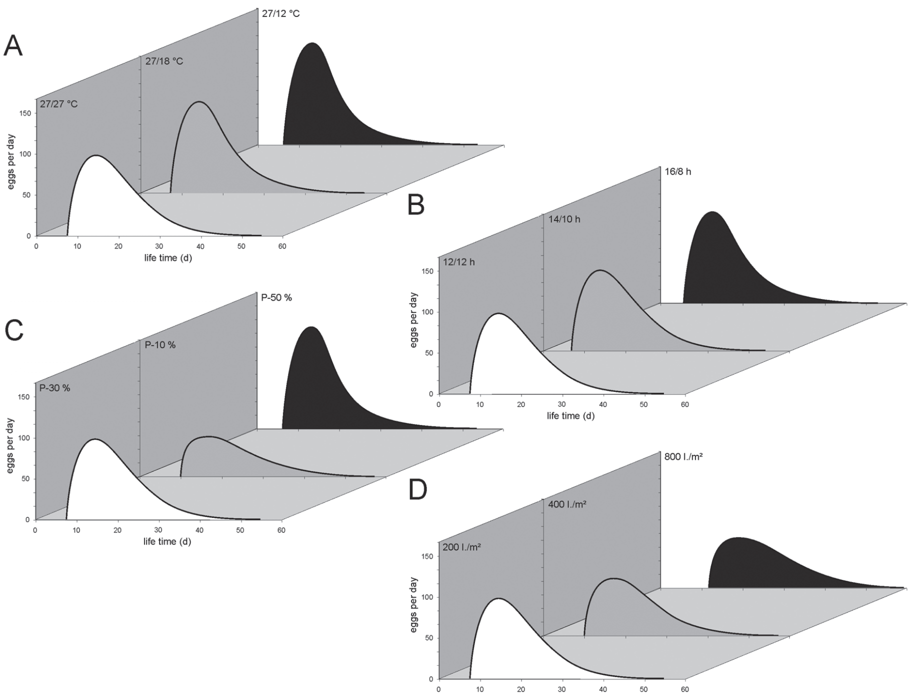

Fig. 5: Preliminary results obtained from the computer program CRICKTHERM. Dependence of fecundity on (**A**) temperature, (**B**) photoperiod, (**C**) protein content in food, (**D**) population density (individuals per square metre).

Measurement of ovary weight should give an impression on the total potential of reproduction in *Teleogryllus commodus*, since not all eggs produced in the ovaries are oviposited into the substrate. Concerning 10-day old females, also this parameter exhibits a positive correlation with environmental temperature, while for 5-day old females ovary weight does not significantly depend upon temperature (Fig. 4). The results suggest that main production and maturation of the eggs starts immediately prior to the fecundity period. Comparable data of other insects are very rare, but BARKER & HERMAN (1976) made similar investigations with *Danaus plexippus*, finding a significant increase of the weight of the reproduction organs between 20 °C and 28 °C. At higher temperatures gonadal weight is again subject to a decrease. The authors discuss a possible effect of temperature and photoperiod on the neuro-endocrine system of *Danaus*, which itself controls the maturation of the gonads. Detailed molecular mechanisms standing behind this phenomenon are not fully decoded hitherto.

Theoretical simulations of fecundity using the computer program CRICKTHERM were carried out for different environmental conditions, whereby data obtained at different temperatures were partly validated with experimental results (Fig. 2). Based on a good correspondence between hypothetical and experimental results, further simulations showed that photoperiod and protein content of the food have a positive effect on fecundity, while population density has a negative influence on oviposition behaviour. Predictions of CRICKTHERM correspond with respective results published in the literature (e.g. MERKEL 1977; HOFFMANN 1985, 1995), making the program useful for various applications. Deficits of program mainly include the limited number of available experimental data for crickets, reducing the reliability of CRICKTHERM in several aspects. However, the overcome of this drawback should be mastered in future studies.

Zusammenfassung

Adulte Eiproduktion in Weibchen der Grille *Telegryllus commodus* WALKER 1869 (Insecta: Orpthoptera): Experimentelle Ergebnisse und theoretische Vorhersagen – Die Eiablageaktivität bei Weibchen der australischen Feldgrille Teleogryllus commodus wurde für vier verschiedene Umgebungstemperaturen (20 °C, 23 °C, 25 °C und 30 °C) untersucht, wobei neben der Anzahl der täglich abgelegten Eier auch die totale Fekundität zur Bestimmung gelangte. Zur Ermittlung jener Eimenge, welche bei unterschiedlichen Temperaturen in den Ovarien gelagert ist, wurden die Ovargewichte von fünf und zehn Tage alten Weibchen gemessen und miteinander verglichen. Als hauptsächliches Ergebnis der vorliegenden Studie ist eine deutliche Erhöhung der Anzahl abgelegter Eier mit steigender Umgebungstemperatur zu nennen. Konkret legten Weibchen bei 30 °C etwa fünfmal so viele Eier in das Substrat ab wie Weibchen, deren Haltung bei lediglich 20 °C erfolgte. Die Dauer der Ovipositionsperiode erhöht sich ebenfalls mit der Temperatur, weil die Weibchen früher mit der Eiblage starten und diese bis in höheres Alter fortzusetzen in der Lage sind. Neben der Anzahl abgelegter Eier lässt auch die Menge der in den Ovarien gelagerten Eier eine positive Korrelation mit der Umgebungstemperatur erkennen: Das Ovargewicht eines zehn Tage alten Tieres steigt bei einem Sprung von 20 °C auf 30 °C etwa auf den drei- bis vierfachen Wert an. Zusätzlich zu den experimentellen Daten gelangt ein Computermodell mit der Bezeichnung CRICKTHERM zur Präsentation, welches die Erstellung von Kurven zur totalen Fekundität erlaubt und sich zudem für Vorhersagen von Ovipositionseffizienzen und ihrer Abhängigkeit von verschiedenen Umweltvariablen (Temperatur, Luftfeuchtigkeit, Photoperiode, Populationsdichte) eignet.

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