

Running Speed and Food Intake of the Matrotrophic Viviparous Cockroach *Diploptera punctata* (Blattodea: Blaberidae) during Gestation

Laufgeschwindigkeit und Nahrungsaufnahme der matrotroph viviparen Schabe *Diploptera punctata* (Blattodea: Blaberidae) während der Trächtigkeit

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Summary: *Diploptera punctata* is the only cockroach, which has been clearly characterized as matrotrophic viviparous. Our observations on courtship and mating generally confirm the data from the literature. Courtship and mating correspond to type I (male offers himself under wing fluttering, female mounts the male, nibbles on his tergal glands, dismounts, turns to achieve the final mating position, i.e. abdomen to abdomen, heads in the opposite direction). We document photographically mating and courtship of fully sklerotized, sexually experienced males with teneral females immediately after the last moult, and with fully sclerotized females several hours after the final moult. Effects of sexual dimorphism (females are larger than males) and pregnancy (females gain weight) became apparent from the running speed cockroaches reached, when disturbed. Males and females ran significantly faster during daytime than at night, but males ran always faster than females. As pregnancy progresses, females obviously become slower, which disables them more during the day than at night. When individual non gravid and gravid females were tested every week, both became slower in the course of time probably due to habituation. However, also in this case decrease of running speed of gravid females was stronger. Initial studies on food intake suggest that the females eat more or less continuously during the gestation period. The amount of food ingested by gravid females varied, but seemed to be somewhat larger than the amount consumed by the non gravid control female. Food intake appears relatively high at the beginning of the gestation period, but probably decreases later, which may indicate hidden costs of viviparity.

Key words: Cockroach, matrotrophic viviparity, locomotion; pregnancy, costs of reproduction, habituation

Zusammenfassung: *Diploptera punctata* ist die bisher einzige Schabe, die eindeutig als matrotroph vivipar charakterisiert worden ist. Unsere Beobachtungen zur Balz und Paarung dieser Art bestätigen im Wesentlichen die Daten aus der Literatur. Balz und Paarung entsprechen dem Paarungstyp I (das Männchen bietet sich mit Flügelflattern an, das Weibchen klettert auf das Abdomen des Männchens, beknabbert seine Tergaldrüsen, steigt ab und dreht sich dabei so, dass die Kopulationsendstellung erreicht wird, d.h. Abdomen an Abdomen, Köpfe in entgegengesetzter Richtung). Wir dokumentieren Paarung und Balz von vollständig sklerotisierten, sexuell erfahrenen Männchen mit noch nicht sklerotisierten Weibchen unmittelbar nach sowie mit vollständig sklerotisierten Weibchen mehrere Stunden nach der Imaginalhäutung. Der Geschlechtsdimorphismus (die Weibchen sind größer als die Männchen) und die Trächtigkeit (die Weibchen werden schwerer) spiegeln sich auch in der Laufgeschwindigkeit wider, welche die Tiere erreichen, wenn sie gestört werden. Männchen und Weibchen liefen am Tage zwar signifikant schneller als in der Nacht, Männchen waren jedoch stets schneller als die Weibchen. Mit fortschreitender Trächtigkeit wurden die Weibchen langsamer. Dies

ist tagsüber sehr viel deutlicher als nachts. Einzelne nicht trüchtige und trüchtige Weibchen, die über einen längeren Zeitraum einmal pro Woche getestet wurden, rannten im Laufe der Zeit langsamer, ein Phänomen, das sehr wahrscheinlich auf Habituation zurückzuführen ist. Dennoch war die prozentuale Abnahme der Laufgeschwindigkeit bei trüchtigen Weibchen höher. Erste Untersuchungen zur Nahrungsaufnahme machen wahrscheinlich, dass die Weibchen während der Trüchtigkeit mehr oder weniger kontinuierlich fressen (müssen). Die Menge an Futter, die trüchtige Weibchen zu sich nahmen schwankte und war im Schnitt geringfügig größer als die Menge, die ein nichttrüchtiges Kontrollweibchen verzehrte. Zu Beginn der Trüchtigkeit scheint mehr Nahrung aufgenommen zu werden als später, was auf versteckte Kosten der Viviparie hinweist.

Schlüsselwörter: Schaben, matrotrophe Viviparie, Lokomotion, Trüchtigkeit, Kosten der Fortpflanzung, Habituation

1. Introduction

Reproduction is a costly matter and reproductive activities in their broadest sense increase the predation risk. Females for example have to invest in the production of eggs; in viviparous species they have to provide specific “brood pouches”, “brood sacs” or “uteri” that may serve either as an “incubator” only, if growth and development of the offspring until birth is exclusively yolk-dependent (= lecithotrophic viviparity), or as a “refectory”, if the offspring depends on the delivery of maternal nutrition (matrotrophic viviparity). In both cases females have to carry the developing offspring for a while, which may impair locomotion. Further, females of matrotrophic viviparous species need additional energy in certain phases of gestation to supply the young (for a general treatment of this topic see CALOW 1979; BRODIE 1989; MAGNHAGEN 1991; regarding cockroaches see notes in NALEPA & BELL 1997; BELL et al. 2007).

The Pacific beetle cockroach *Diploptera punctata*, a native species on Hawaii and other Pacific islands (FULLAWAY & KRAUSS 1945), is a nocturnal, cryptically coloured cockroach with a noticeable, well-studied reproductive biology. Sexes are slightly dimorphic in size; females measure ca. 2 cm, males, however, ca. 1.5 cm in length. Typically mating takes place immediately after the final moult of the female, i.e. at a time, when she is still teneral, whereas males court and mate suc-

cessfully later and when fully sklerotized (e.g. STAY & ROTH 1958; WOODHEAD 1986). After fertilization eggs are covered by a reduced egg case (= ootheca). First the female slightly extrudes the ootheca, rotates it 90 degrees and finally retracts it into the ectodermal brood sac, an infolding of the thin cuticle between sternite VII and VIII; in the brood sac embryogenesis takes place (e.g. ROTH & WILLIS 1955a; STAY & COOP 1973). After a gestation period of about 70 days (or longer as the gestation period strongly depends on the environment, especially temperature) females give birth to 9-14 relatively large and well-developed nymphs or larvae that grow usually through three (males) and four (females) stages until maturity (e.g. ROTH & WILLIS 1958; WILLIS et al. 1958; ROTH & STAY 1961, ROTH 1967). To date it is widely accepted that *D. punctata* is the only “truly viviparous” cockroach (e.g. HAGAN 1951; ROTH 1970; NALEPA & BELL 1997; WILLIFORD et al. 2004; BELL et al. 2007; MARCHAL et al. 2013). In this context, *D. punctata* is also used for decades as “model system” for studying the production of the juvenile hormone and its regulation (for review see MARCHAL et al. 2013).

The argument in favor of the uniqueness of the reproduction mode in *D. punctata* among cockroaches is based on the fact that pregnant females secrete a specific “uterine milk” into the brood sac, which is rich in carbohydrates and proteins and is actively drunk by the embryos after their reatively

early confluence of the fore- and midgut (e.g. STAY & COOP 1973, 1974; INGRAM et al. 1977; WILLIFORD et al. 2004).

According to the literature all other blaberid cockroaches practice various forms of “ovoviviparity” and are supposed to have in common that the embryos solely depend on their yolk reserves for nutrition as do embryos from oviparous species. Yolk dependency is here considered the crucial character of ovoviviparity by many authors (for review see BELL et al. 2007, especially table 7.1.).

To standardize and simplify terminology, it was previously suggested to rely initially on what one immediately sees and to call both, “ovoviviparous” cockroaches and the “viviparous” *D. punctata*, viviparous, and to distinguish between lecithotrophic and matrotrophic viviparity when the trophic relationships between mother and offspring have been clarified (e.g. GREVEN 1995). This appears relevant since there is some evidence that several so called “ovoviviparous” cockroach species appear to be (matrotrophic) viviparous similar to *D. punctata* (unpublished findings; see also the discussion in SNART et al. 1984a, b; BELL et al. 2007). However, in *D. punctata* supply of nutrients to the developing offspring is particularly intense. Protein content and dry weight of the young as well as their size increase enormously before they are born (e.g. ROTH & WILLIS 1955a; STAY & COOP 1973).

To meet their own energy needs and those of the developing young, gravid females should therefore feed during the gestation period, and, consequently, should be active during this period to search for food. BELL et al. (2007) noticed that gravid females forage, but did not give any further details. However, at the same time locomotion should be affected, as the weight and volume of females increase during gestation. Gravid females of the probably lecithotrophic viviparous *Nauphoeta cinerea* (“ovoviviparous” according to the current terminology, cf. BELL et al. 2007) run slower than virgin fe-

males of the same age (MELLER & GREVEN 1996b), but stop locomotor activity and food intake a short time after mating and become active again about a week before parturition (MELLER & GREVEN 1996a). Simultaneously, females of this species obviously reduce their basal metabolism not directly associated with reproduction (SCHULZE-MOTHEL & GREVEN 1998). Also females of the oviparous *Blattella germanica* that carry their ootheca externally until hatching of the nymphs, reduce their activity during this period. This behavioural change is supposed to protect the females against predators and prevent dehydration rather as being a strategy to save energy (LEE 1994, LEE & WU 1994).

From the above survey, some questions arise, from which we try to answer the following:

- 1) Do males and females of *D. punctata* run at different rates?
- 2) Do pregnant females run more slowly?
- 3) Do females take up food during the gestation period?

In addition, we photographically document courtship and mating of fully sclerotized males with teneral females immediately after the final moult and with females already sclerotized.

2. Material and Methods

2.1. Origin, keeping and breeding of *Diploptera punctata*

Breeding stocks of *Diploptera punctata* came from commercial dealers. The cockroaches were kept in ventilated plastic boxes of different sizes. The bottom of the boxes were covered with a layer of coconut humus and litter for small animals; egg cartons and cardboard tubes served as hiding place, a glass bowl containing moist cotton as drinking through. Animals were fed with Tetrapond® Pond Sticks, apples, cucumbers, carrots, dog food and oatmeal. The temperature ranged from 22 to 26 °C.

2.2. Mating

Female nymphs were individually housed in transparent plastic boxes (5.5 x 3.5 x 5.5 cm). After final moult, 16 pair combinations were observed using nine virgin females 1-27 h after final moult and 15 males from the stock culture (see Tab. 1), which were gently introduced in a plastic box (9.5 x 6.0 x 9.5 cm) on a white background. The box was lit with a halogen desk lamp (20 W); photographs were taken with a digital camera (Panasonic LUMIX DMC-TZ7, Lens: Leica DC Vario-Elmar 4.1-49.2 mm).

2.3. Running speed

2.3.1. Experiment I

Trials were made with animals marked with nail polish (16 males and 35 females in different stages of gestation; see below) taken directly from the stock culture. Immediately after the trials (see 2.3.2.) females were killed at -18 °C and individually packed in small plastic bags. Later they were weighed (1/1000 g accuracy), dissected and roughly classified into four stages (F1-F4) based on the size of the brood sac and the developmental state of the embryos (Fig. 1A-C; cf. STAY & COOP 1973). We obtained data from nine F1 (brood sac inconspicuous and small, i.e. non gravid), eight F2 (ootheca with small embryos; Fig. 1A); seven F3 (embryos with head, eye pigments; anlagen of extremities; Fig. 1B); eleven F4 (embryos > 4 mm long; large eyes, limbs and developed mouthparts; Fig. 1C).

2.3.2. Experiment II

Contrary to experiment I we tested the individual animals every week over a long period (see below). We used three females already gravid at the beginning of the experiment, two females impregnated immediately after their final moult, and seven non pregnant

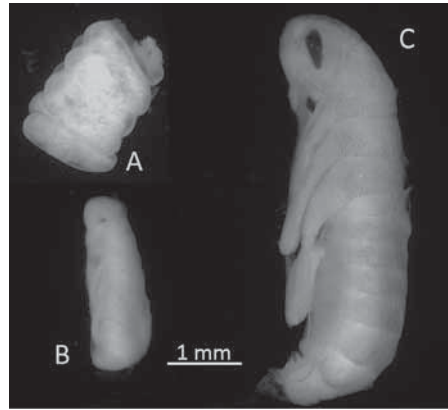


Fig. 1: Developmental stages of *Diploptera punctata*, classified as F2-F4 (see experiment I). Note the enormous increase in size. **A** Ootheca with embryos (F2). **B** Head and legs begin to develop. Note pigmentation of eyes (F3). **C** Advanced development; note the mouth parts and the relatively large eye (F4).

Abb. 1: Embryonalstadien von *Diploptera punctata*, klassifiziert als F2-F4 (s. Experiment I). Man beachte die Größenzunahme. **A** Oothek mit Embryonen (F2). **B** Beginn der Kopf- und Extremitätenentwicklung. Man beachte die Pigmentierung der Augen (F3). **C** Fortgeschrittene Entwicklung. Man beachte die Mundwerkzeuge sowie die größeren Augen (F4).

females. Specimens were individually tagged with nail polish on the tegmina and kept separately according to their sex.

2.3.3. Experimental setup

For the experiments, a circular arena (diameter 1 m) bordered by a 30 cm high, transparent PVC-wall was used. The bottom of the arena was covered with graph paper. Recording device was a DB Power Wireless IP Camera with Night vision function equipped with infrared LEDs (experiment I) and a Webcam Logitech Quickcam Express supported by a LED lamp (5 W) coated with a red film (experiment II). The camera was mounted at a height of 70 cm above the arena and aligned horizontally. In experiment I the view of the camera was rectan-

gular (68 x 56 cm) in daytime and circular (diameter 56 cm) at night. Thus, the cockroaches occasionally ran a somewhat longer distance during the day to leave the view of the camera, which, however, is negligible when calculating the velocity (m s^{-1}). In experiment II, we restricted the area to be analyzed to a circle of 31 cm in diameter. The camera sent the recordings via a wireless connection to a netbook. For the operation of the camera and recording the runs the IPCMonitor program, version 11.0.11.14 (attached to the camera) and Logitech Webcam Software Ver. 12.10.1113.0 were used.

2.3.4. Test procedure

The cockroach was placed under an inverted petri dish (3.5 cm diameter) in the center of the arena. A cord on the dish allowed to lift it quickly. After starting the camera with the IPCMonitor program via netbook, the petri dish half was lifted. Immediately after they had been released, almost all individuals of *D. punctata* ran on a relatively short, but slightly curved path to the wall of the arena. However, in the course of experiment II specimens often needed a slight nudge to start to run. The recording was stopped as soon as the cockroach had left the view of the camera. Each cockroach run one to four times per day (between 1 and 5 p.m) and at night (between 9 and 12 p.m.). Data from these runs were averaged. For the experiments at night a dim light was used briefly to take the cockroaches out of their containers and to place them in the arena.

2.3.5. Analysis

Experiment I included a total of 255 videographed runs (117 in the daytime, 138 at night) of 51 individuals (16 males, 35 females in different stages of gestation; see above), experiment II included a total of 1087 videographed runs (542 in the daytime; 545 at night) of 18 individuals

(five gravid females: 177 in the daytime, 187 at night; seven non-gravid females: 347 in the daytime, 340 at night. Video sequences were saved with the open source video editing software (VirtualDub version 1.9.11) in an AVI format usable for Viana, which reduced the frame rate to 4 fps. Calibration was performed using graph paper on the floor of the arena. Evaluation was done manually frame-by-frame, because of the weak illumination and the relatively dark colouration of the animals. The running speed was calculated with the open source video editing program Viana, versions 3.64 and 4 (BÖCKMANN et al. 2012).

2.4. Food intake

Seven female nymphs shortly before the final moult were individually kept in plastic boxes (114 x 114 x 58 mm); each nymph was kept together with two males. As males preferably mate with females immediately after the final moult ("0-day virgins", WOODHEAD 1986) and oviposition (into the brood sac) follows approx. eight days later (STAY & COOP 1973), we took the second week as the beginning of gestation.

The boxes were checked weekly and all fully sclerotized female were maintained in separate plastic boxes (230 x 155 x 170 mm). From these females four females became pregnant. Their gestation period lasted 13-14 weeks. Number of newborns varied from 10 to 12. A non pregnant female was used as control.

Once a week females were given a portion of food (about 300 mg) weighed with an accuracy of 0.0001 g (Sartorius BP 210S). After one week the remaining food was replaced by a new sample and stored in tightly sealed plastic containers until final weighing. The experiment was terminated after the female has given birth. Data from the week of birth were not considered because the newborns could have eaten from the portions.

2.5. Statistics

For further processing of the data we used the standard Windows program Excel version 2010 or 2013 and for the statistical analysis the program GraphPad Prism 6, i.e. normality tests (Wilcoxon Signed Rank, Shapiro-Wilk-Test), Student's t-test ($p =$ two-tailed, unpaired, $p^* =$ two tailed, paired), and the Pearson correlation coefficient (expressed as coefficient of determination R^2).

3. Results

3.1. Courtship and mating

Table 1 summarizes the behavioural elements of the males (1-6) and the female (A-G). The male (1) palpates the female with his antennae, and (2) with his labial palps; (3) pursues the female, (4) pushes the female ahead; (5) flaps his wings, while

lifting them occasionally up to 90°; (6) grasps her genitals. The female (A) flees, (B) vibrates with her wings, (C) allows pushing, (D) mounts the male, while palpating his abdomen, (E) dismounts the male on one side and allows hooking together; then, the couple assumes an opposed position with their heads facing in opposite directions; (F) does not respond, or reacts especially to elements 1 and 2 (of the male), while pressing the body against the substrate (see Figs 1, 2; Table 1).

Thirteen of the 16 males courted, but only eight males mated. The latter showed all elements listed in table 1 with exception of the elements 3 (pursuing) and 4 (pushing) that are not typical display elements. All but one courting males reached the wing-flapping stage. Courtship started 2 s to 14:46 min after the couple was introduced into the box. The time until the onset of copulation, i.e. when the couple has reached the final position, varied between 24 s and 12:32 min

Tab. 1: Combinations of pairs and the several parameters recorded during the trials. White teneral females in bold. For further explanations see text.

Tab. 1: Paarkombinationen und die während der Versuche bestimmten Parameter. Noch nicht sklerotisierte Weibchen fett gedruckt. Weitere Erklärungen im Text.

No.	Combination	Age of ♀ (h after final moult)	Time to onset of courtship (♂) (min)	Courtship elements of ♂	Reactions of ♀	Time to onset of copulations (min)	Duration of copulations (min)
1	♀1 + ♂1	1:00	4:12	1, 2, 5	B, F	-	-
2	♀1 + ♂2	2:00	0:04	1, 2, 4, 5, 6	C, D, E	1:51	29:46
3	♀2 + ♂3	8:00	3:14	1, 2, 3, 5	A	-	-
4	♀2 + ♂4	8:30	4:21	1, 2, 4, 5, 6	C, D, E	9:33	64:34
5	♀3 + ♂5	10:00	14:46	1, 2, 5	B, F	-	-
6	♀3 + ♂6	10:30	-	-	-	-	-
7	♀3 + ♂7	11:00	11:24	1, 2	F	-	-
8	♀4 + ♂8	8:00	0:19	1, 2, 5, 6	D, E	0:24	43:23
9	♀5 + ♂9	14:00	0:02	1, 2, 5, 6	D, E	1:40	69:42
10	♀6 + ♂10	10:00	0:51	1, 2, 5, 6, 3	D, E, A	2:33	0:07
11	♀6 + ♂11	10:30	-	-	-	-	-
12	♀6 + ♂12	14:30	0:04	1, 2, 5, 6	D, E	0:57	34:28
13	♀7 + ♂13	27:00	1:09	1, 2, 5, 6	F, D, E	12:32	70:02
14	♀8 + ♂14	10:00	-	-	-	-	-
15	♀8 + ♂15	10:30	9:05	1, 2, 5, 6	F, D, E	11:17	74:31
16	♀9 + ♂16	1:00	0:07	1, 2, 5, 6	D, E	0:30	55:11

Abb. 2: Elemente der Balz und Kopula eines *Diptera punctata*-Männchens mit einem noch weißen Weibchen etwa 1 h nach der Imaginalhäutung. Das Männchen berührt das Weibchen mit seinen Antennen (A) und Palpen (B), dreht sein Abdomen in Richtung Weibchen (C) und beginnt mit den Flügeln zu flattern (D). Endgültige Kopulationsstellung (E). Weitere Erklärungen im Text.

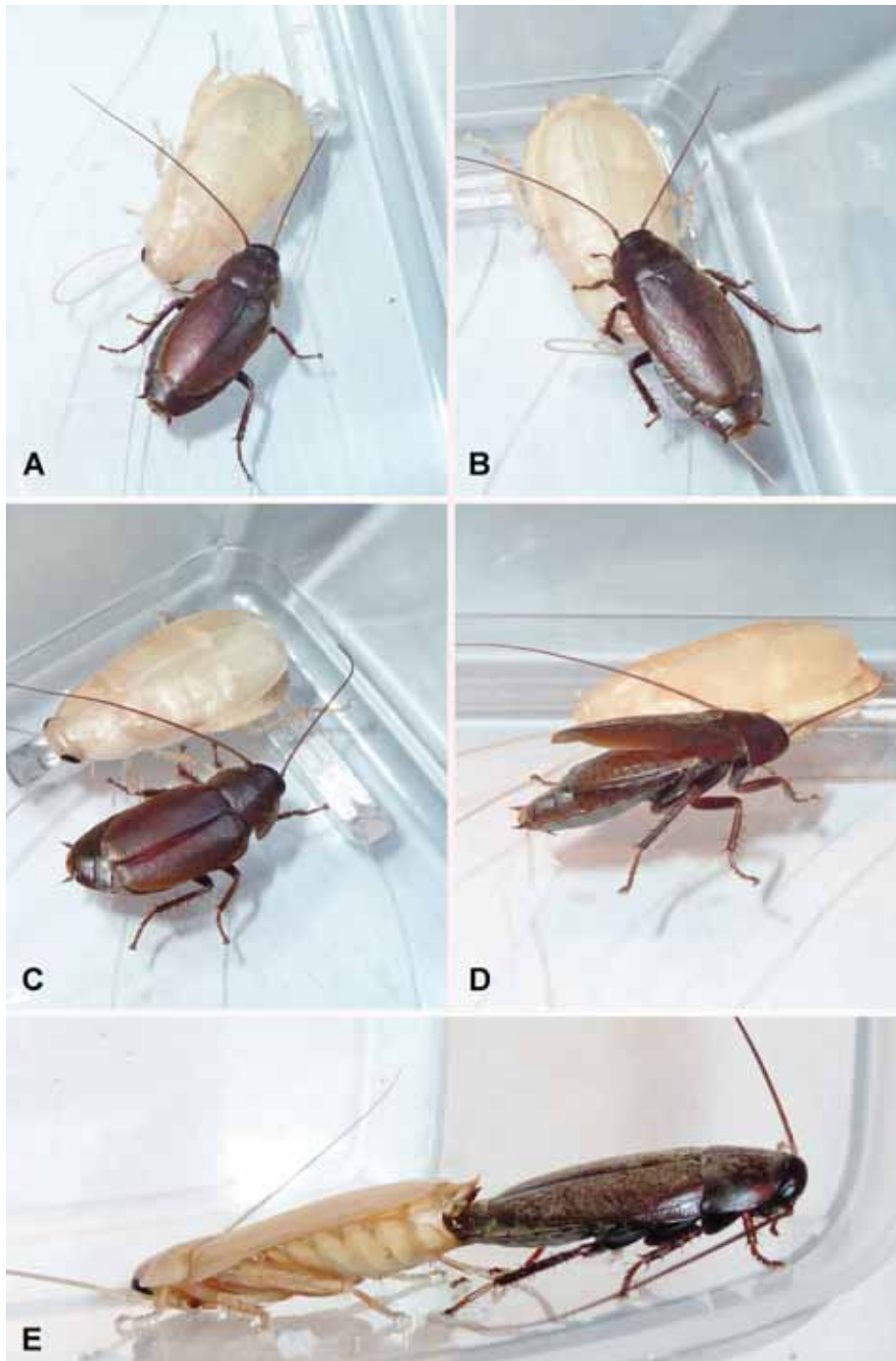
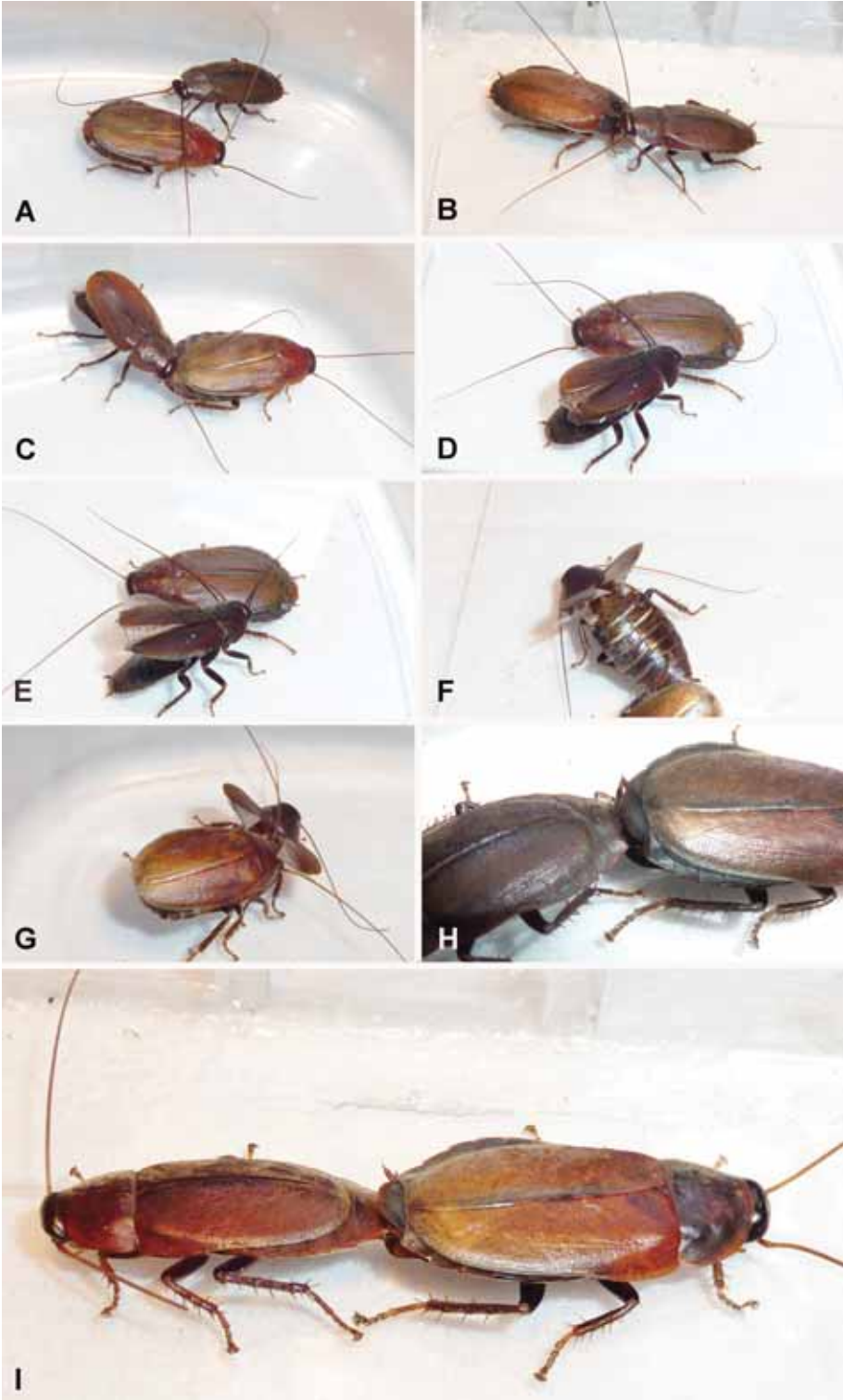


Fig. 2: Elements of courtship and mating of *Diptera punctata* male with a teneral female ca. 1 h after the final moult. The male touches the female with his antennae (A) and palps (B), turns his abdomen towards the female (C), and starts flapping his wings (D). Final opposed position for copulation (E). For further explanations see text.



and the duration of copulations between 29:46 and 74:31 min (the short copulation of 7 s excluded). Further data can be seen in table 1.

Females answered variously to the male's courtship. Both, the white (1-2 h after final moult), and the brown females (8-27 h after the final moult) showed similar responses. Where encounters resulted in a copulation, the typical sequence was C (pushing by the male), D (mounting), E (dismounting) or mostly D, E; in two cases females first reacted defensively (F). Interestingly, in two trials females vibrated with the wings before the male started courtship.

The time to onset of copulation was largely determined by the behaviour of the female. During copulation, the pair kept motionless, but occasionally cleaned their antennae. After copulation sexual partners were usually sitting side by side for a while.

3.2. Running speed

3.2.1. Experiment I

Differences between day and night: In daytime the cockroaches (females of unknown reproductive stage and males from the breeding tanks) reached a mean running speed of $0.108 \pm 0.065 \text{ m s}^{-1}$ (range of variation 0.025 to 0.245) and at night of $0.066 \pm 0.028 \text{ m s}^{-1}$ (range of variation 0.019 to 0.144). The difference between the running speed during the day and at night is highly significant (Fig. 4).

Sex differences and effect of gestation: In daytime the day females (gravid and non gravid) reached $0.0912 \pm 0.033 \text{ m s}^{-1}$ (range of variation 0.025 to 0.149) and at night $0.057 \pm 0.021 \text{ m s}^{-1}$ (range of variation 0.019 to 0.104). Males reached $0.144 \pm 0.042 \text{ m s}^{-1}$ (range of variation 0.086 to 0.250) in daytime and at night 0.084

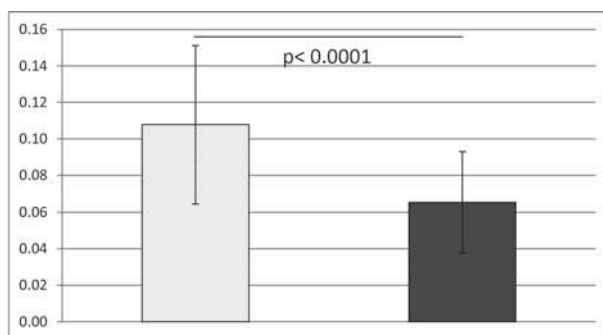


Fig. 4: Mean running speed (m s^{-1}) and standard deviation of all animals used (females and males) (day: grey column; $n = 51$; night: black column; $n = 50$).

Abb. 4: Durchschnittliche Laufgeschwindigkeit (m s^{-1}) und Standardabweichung von allen getesteten Tieren am Tag ($n = 51$, graue Säule) und in der Nacht ($n = 50$, schwarze Säule).

Fig. 3: Courtship and mating elements of an older *Diploptera punctata* male (the smaller specimen) with a fully sklerotized female. The male touches the female with his antennae (A, B) before flapping (C, D, E) and raising his wings (F). Shortly before copulation the female mounts the male (G). Final opposed position for copulation (H, I). For further explanations see text.

Abb. 3: Elemente der Balz und Kopulation eines älteren *Diploptera punctata*-Männchens (die kleinere Schabe) mit einem vollständig sklerotisierten Weibchen. Das Männchen berührt zunächst das Weibchen mit den Antennen und Palpen (A, B), bevor es beginnt, mit den Flügeln zu flattern (C, D, E) und diese anzuheben (F). Kurz vor der Kopulation besteigt das Weibchen das Männchen (G). Endgültige Kopulationsstellung (H, I). Weitere Erklärungen im Text.

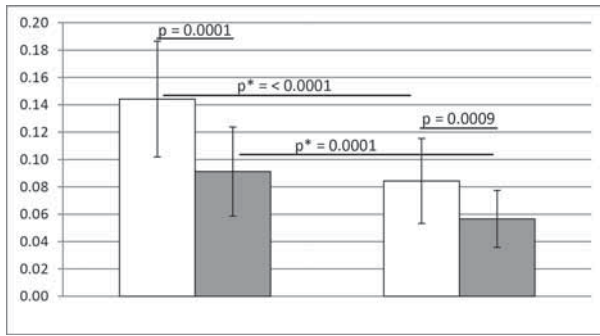


Fig. 5: Mean running speed (m s^{-1}) and standard deviation of males (white columns; $n = 16$) and females (grey columns, $n = 35/\text{day}$ and $34/\text{night}$) in daytime (left) and at night (right).

Abb. 5: Durchschnittliche Laufgeschwindigkeit (in m s^{-1}) plus Standardabweichung von Männchen (weiße Säulen, $n = 16$) und Weibchen (graue Säulen, $n = 35$ Tag und $n = 34$ Nacht) bei Tag (links) und bei Nacht (rechts).

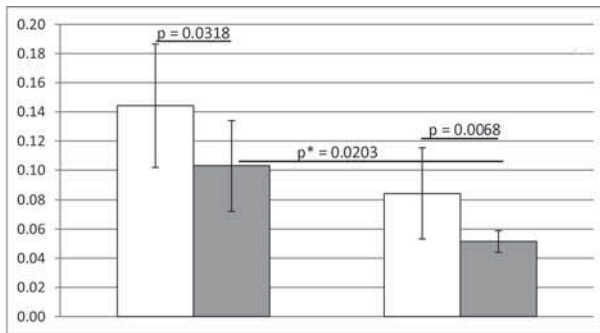


Fig. 6: Mean running speed (m s^{-1}) and standard deviation of males ($n = 16$; white columns) and non gravid females F1 ($n = 9$; grey columns) in daytime (left) and at night (right).

Abb. 6: Durchschnittliche Laufgeschwindigkeit (in m s^{-1}) und Standardabweichung von Männchen (weiße Säulen, $n = 16$) und nicht trächtigen Weibchen F1 (graue Säulen, $n = 9$) bei Tag (links) und bei Nacht (rechts).

$\pm 0.031 \text{ m s}^{-1}$ (range of variation 0.034 to 0.144). Males and females reached significantly higher speeds in daytime than at night, but generally speeds of females were significantly lower at both times of the day (Fig. 5).

These significant differences remained when comparing males only with non gravid F1 females. Non gravid females ran $0.103 \pm 0.031 \text{ m s}^{-1}$ (range of variation 0.061 to 0.148) in daytime and $0.051 \pm 0.007 \text{ m s}^{-1}$ (range of variation 0.038 to 0.063) at night (Fig. 6).

Figure 7 shows the speed of males and the F1-F4 females. Differences between night and day within each group are as follows (data for males and F1 females are given above; Figs 5, 6): F2 females reached $0.117 \pm 0.023 \text{ m s}^{-1}$ (range of variation 0.075 to 0.148) in daytime and $0.073 \pm 0.031 \text{ m s}^{-1}$ (range of variation 0.028 to 0.104) at night ($p^* = 0.0024$), F3 females $0.078 \pm 0.023 \text{ m s}^{-1}$ (range of variation 0.061 to 0.107) in daytime and $0.049 \pm 0.012 \text{ m s}^{-1}$ (range of variation 0.039 to 0.065) at night ($p^* = 0.0186$), and F4 females 0.071

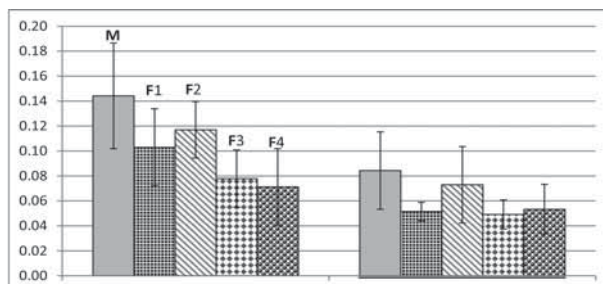


Fig. 7: Mean running speed (m s^{-1}) and standard deviation of all groups (M, F1-F4) during the day (left side) and at night (right side). Males (M, $n = 16$); females (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, $n = 11$ (day), $n = 10$ (night)).

Abb. 7: Durchschnittliche Laufgeschwindigkeit (in m s^{-1}) und Standardabweichung von allen Gruppen bei Tag (links) und Nacht (rechts). Männchen (M, $n = 16$); Weibchen (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, Tag, $n = 11$ (tagsüber), $n = 10$ (nachts)).

$\pm 0.053 \text{ m s}^{-1}$ (range of variation 0.025 to 0.127) in daytime and $0.053 \pm 0.019 \text{ m s}^{-1}$ (range of variation 0.032 to 0.081) at night ($p^* = 0.001$). Differences between F1 and F4 are distinct in daytime ($p = 0.036$), but not at night ($p = 0.7902$). Figure 8 based on these data shows that the running speed decreases as gestation progresses (Fig. 8A), but at night this relation is not clear (Fig. 8B).

Gestation and weight: Males weighed $0.136 \pm 0.005 \text{ g}$ (range of variation 0.131 to 0.143), the females I $0.254 \pm 0.052 \text{ g}$ (range 0.184 to 0.346), females II $0.291 \pm 0.05 \text{ g}$ (range of variation 0.218 to 0.362), females III $0.323 \pm 0.0244 \text{ g}$, and the females IV $0.34 \pm 0.029 \text{ g}$ (range of variation 0.308 to 0.418). The weight of the females increases when gestation proceeds (Fig. 9). Females of stage I weighed on average 33 % less than females of stage IV. The further gestation progresses, the heavier are the females.

3.3.2. Experiment II

Figure 10 shows the mean running speed (2-5 runs per trial) attained over time by seven non-gravid females and figure 11 shows the same for five gravid females. Despite individual differences, for all specimens the running speed decreases with

time. When comparing the first day and the last day of the experiments, the running speed of the seven non gravid females was reduced by $60.54 \pm 12.47 \%$ in daytime (range of variation 44.35 - 81.92 %) and $69.14 \pm 13.55 \%$ at night (range of variation 46.59 - 85.39 %; at night) on average. R^2 varies between 0.0312 and 0.6809 (in daytime) and 0.1037 and 0.7256 (at night). The relevant data of the five pregnant females are $81.73 \pm 5.42 \%$ (range of variation 74.76 - 90.21 %; in daytime) and $87.75 \pm 6.64 \%$ (range of variation 74.06 - 91.89 % at night) on average. R^2 varies between 0.4963 and 0.7729 (in daytime), and 0.5831 and 0.9188 (at night) showing a relative low variance compared with the data of non gravid females.

3.4. Food intake

Compared to the non gravid control animal, gravid females seem to change their feeding behaviour (Figs 12, 13). The gravid individuals obviously have eaten every week, whereas food intake of the non pregnant control female was more variable. For example, in the seventh week the female ate 0.055 g food (approximately a quarter of the total ingested food); before and after this week the ingestion was considerably lower. Over the time this

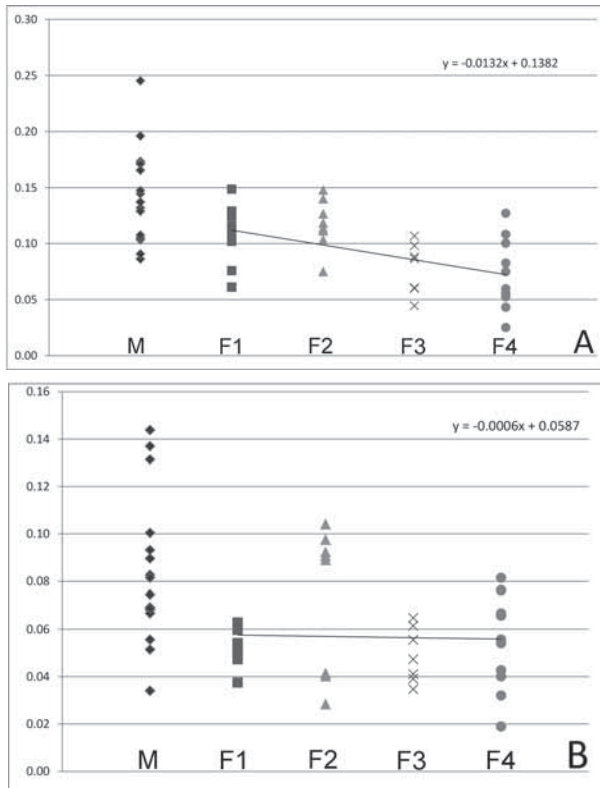


Fig. 8: Mean running speed (in m s^{-1}) of all groups (M, F1-F4) in daytime (A) and at night (B). Males (M, $n = 16$), and females (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, $n = 11$), and trend line for the females. $R^2 = 0.2338$ (A) and 0.001 (B).

Abb. 8: Mittlere Laufgeschwindigkeiten (in m s^{-1}) aller Gruppen (M, F1-F4) am Tag (A) und in der Nacht (B). Männchen (M, $n = 16$), Weibchen (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, $n = 11$) sowie die Trendlinie für die Werte der Weibchen. $R^2 = 0,2338$ (A) und $0,001$ (B).

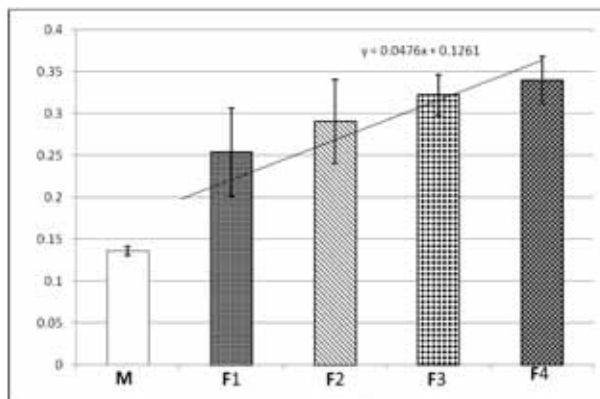


Fig. 9: Mean weight in g (ordinate) of males (M, $n = 6$), and females (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, $n = 11$), and trend line for the females. $R^2 = 0.8625$.

Abb. 9: Gewicht in g (Ordinate) von Männchen (M, $n = 6$) und Weibchen (F1, $n = 9$; F2, $n = 8$; F3, $n = 7$; F4, $n = 11$) sowie Trendlinie für die Weibchen. $R^2 = 0.8625$.

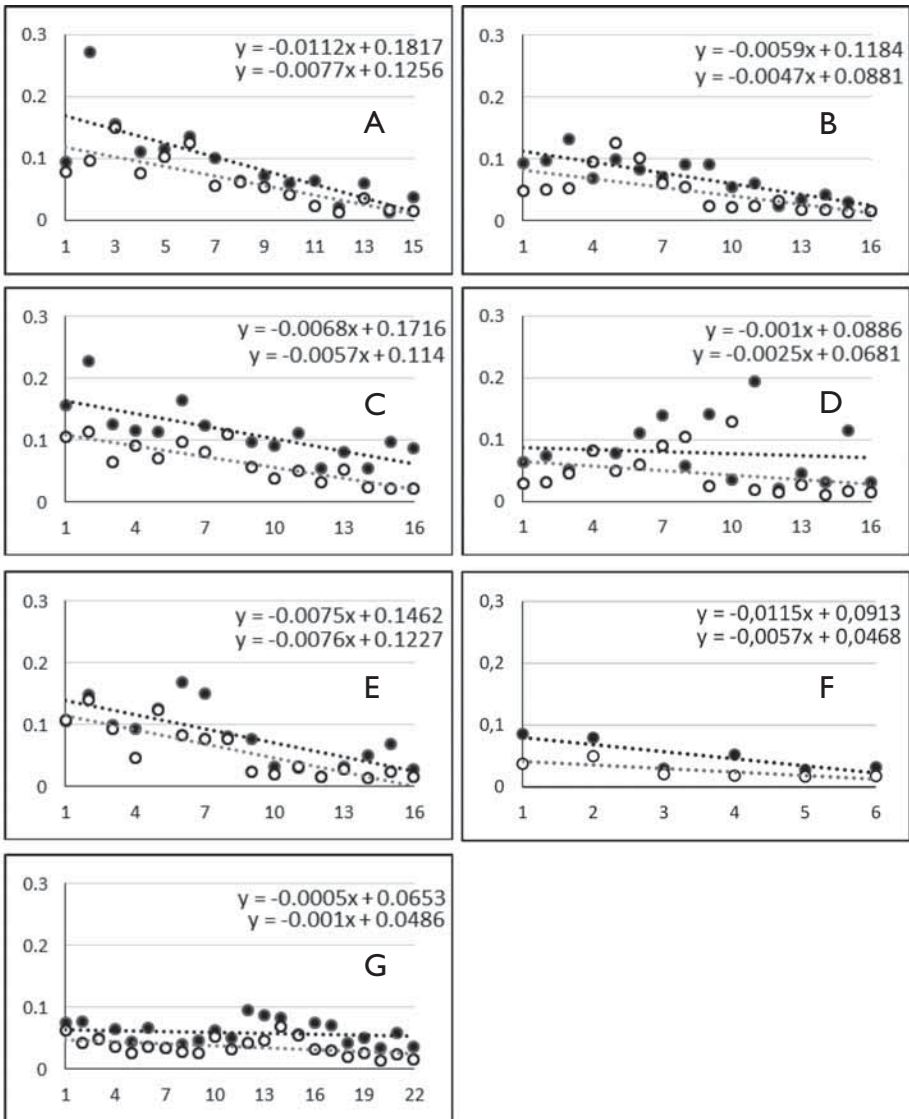


Fig. 10: Running speed (ordinate: m s^{-1}) of seven non pregnant females (A-G) measured weekly over various periods (abscissa: weeks) in daytime (black dots) and at night (grey dots). **A** $R^2 = 0.6037$ (day) and 0.6816 (night). **B** $R^2 = 0.4646$ (day) and 0.4377 (night). **C** $R^2 = 0.5712$ (day) and 0.7235 (night). **D** $R^2 = 0.0198$ (day) and 0.1037 (night). **E** $R^2 = 0.5380$ (day) and 0.7256 (night). **F** $R^2 = 0.6809$ (day) and 0.6141 (night). **G** $R^2 = 0.0312$ (day) and 0.2108 (night). **Abb. 10:** Laufgeschwindigkeiten (Ordinate: m s^{-1}) von sieben nichtträchtigen, wöchentlich über unterschiedlich lange Zeiträume (Abszisse: Wochen) am Tage (schwarze Punkte) und in der Nacht (graue Punkte) getesteten Weibchen.

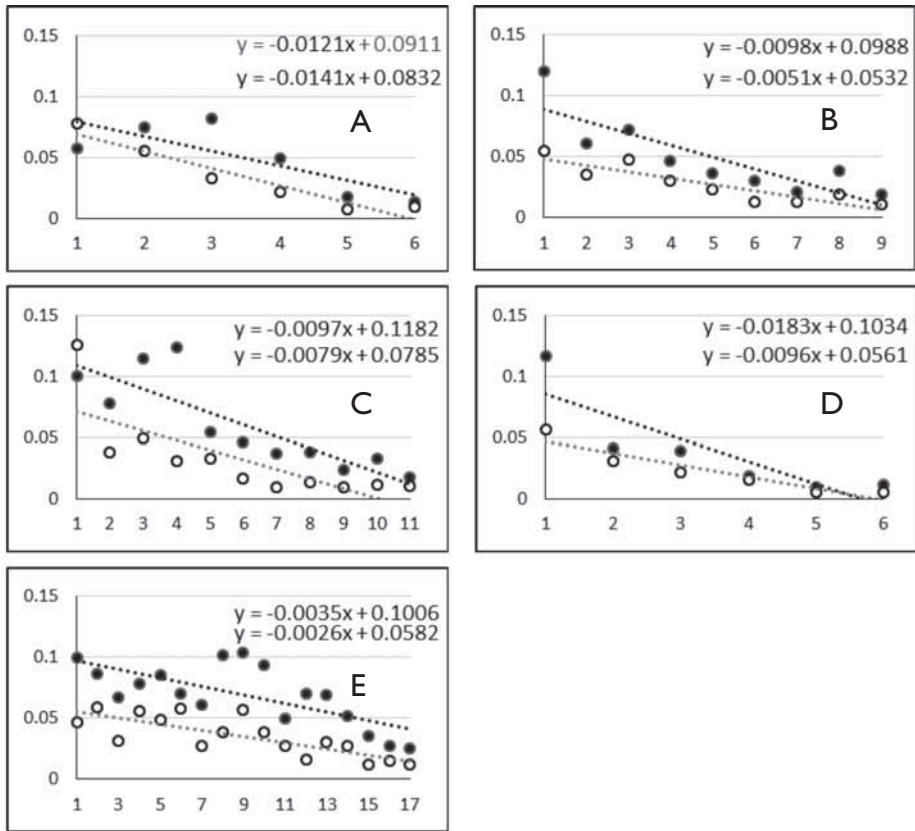


Fig. 11: Running speed (ordinate: m s^{-1}) of five gravid females (A-E) measured weekly over various periods (abscissa: weeks) in daytime (black dots) and at night (grey dots). **A** $R^2 = 0.6242$ (day) and 0.9188 (night). **B** $R^2 = 0.7229$ (day) and 0.8795 (night). **C** $R^2 = 0.7228$ (day) and 0.5831 (night). **D** $R^2 = 0.7229$ (day) and 0.8105 (night). **E** $R^2 = 0.4963$ (day) and 0.6132 (night).

Abb. 11: Laufgeschwindigkeiten (Ordinate: m s^{-1}) von fünf trächtigen, wöchentlich über unterschiedlich lange Zeiträume (Abszisse: Wochen) am Tage (schwarze Punkte) und in der Nacht (graue Punkte) getesteten Weibchen.

female consumed 0.2220 g food and gravid females $0.2743 \pm 0.056 \text{ g}$ ($0.2224 - 0.3606 \text{ g}$). These few data should not be taken to suggest that gravid females necessarily must eat more, but obviously they must eat more regularly. In addition, figure 13 indicates that without one exception intake of food was relatively high at the beginning of the gestation period, but then declined more or less continuously. This does not hold for female IV (Fig. 13E) that consumed relatively much food throughout the entire gestation period and the non pregnant control female (Fig. 13F).

4. Diskussion

4.1. Courtship and mating

Our observations on courtship and mating of *Diploptera punctata* agree with those previously reported (cf. STAY & ROTH 1958; WOODHEAD 1986). Females do not emit a sex pheromone for long distance attraction, but males produce an “aphrodisiac” sex pheromone that serves to elicit female mounting and tergal contact. Courtship and mating corresponds to “type 1”, a widespread

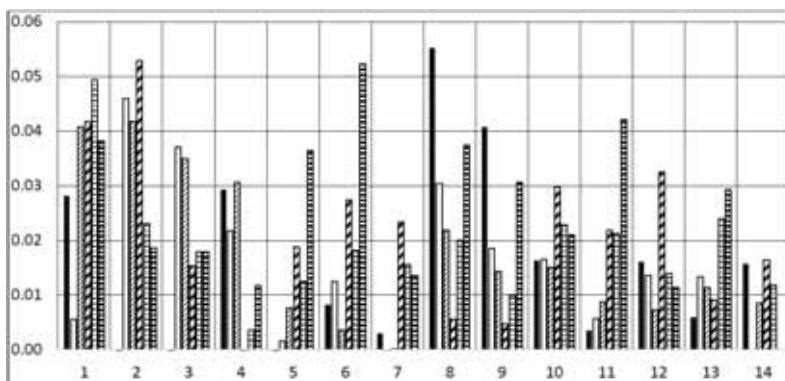


Fig. 12: Food intake (ordinate, g) of five females (patterned columns) during the course of gestation (abscissa: weeks) and a non pregnant female (black column).

Abb. 12: Futteraufnahme (Ordinate, g) von fünf Weibchen (gemusterte Säulen) im Verlauf der Trächtigkeit (Abszisse: Wochen) und eines nichtträchtigen Weibchen (schwarze Säulen).

pattern among cockroaches (e.g. BELL et al. 2007). Although usually observed during courtship, flapping with the wings has no influence on the choice of the female (STAY & ROTH 1958). Males that did not court in our trials might be too young (STAY & ROTH 1958). The same may be true for the trials, in which the females did not respond to the courtship of the males that probably did not have a sufficient amount of tergal gland secretions (WOODHEAD 1986). There are many factors, which determine the duration of a copulation, such as the age of the male, whether a male copulated immediately after mating with another female, etc. (STAY & ROTH 1958; for details see WOODHEAD 1986). This has not been considered in the present study.

4.2. Running speed

Most cockroach species are nocturnal (for review see BELL et al. 2007.). According to obviously unpublished data, *Diploptera punctata* forages in the field (Hawaii) from 6:00 p.m to 10:00 a.m. (see BELL et al. 2007, p. 62). This predominantly nocturnal activity can be seen also in the laboratory (unpublished). However, activity and circadian activity rhythms of female cockroaches are

significantly influenced by the reproductive cycle (see BELL & ADIYODI 1981). For example, females of *Nauphoeta cinerea* stop their activity almost completely a short time after mating and became active again a few days before giving birth (MELLER & GREVEN 1996), while gravid females of *D. punctata* are active throughout the gestation period (unpublished).

Cockroaches usually escape when disturbed, but running speeds depend on various parameters such as body design, mass, temperature, substrate, age, sex, the use of specific running patterns (e.g. quadro- and bipedalism of *Periplaneta americana* at a very high speed of approx. 1.5 m s^{-1} ; FULL & TU 1991), and experimental design using of wind puffs as aversive stimuli or tread mill respirometers with specified speed to study escape behaviour and energetics of locomotion (e.g. WILLE 1920 cit. after BELL et al. 2007; CAMHI & TOM 1978, HERREID et al. 1981; FULL & TULLIS 1990; see also BELL et al. 2007) Therefore direct comparisons with data from literature make little sense, although running speeds obtained herein for *D. punctata* correspond roughly to those measured for males and females of *Nauphoeta cinerea* (e.g. MELLER & GREVEN 1996b).

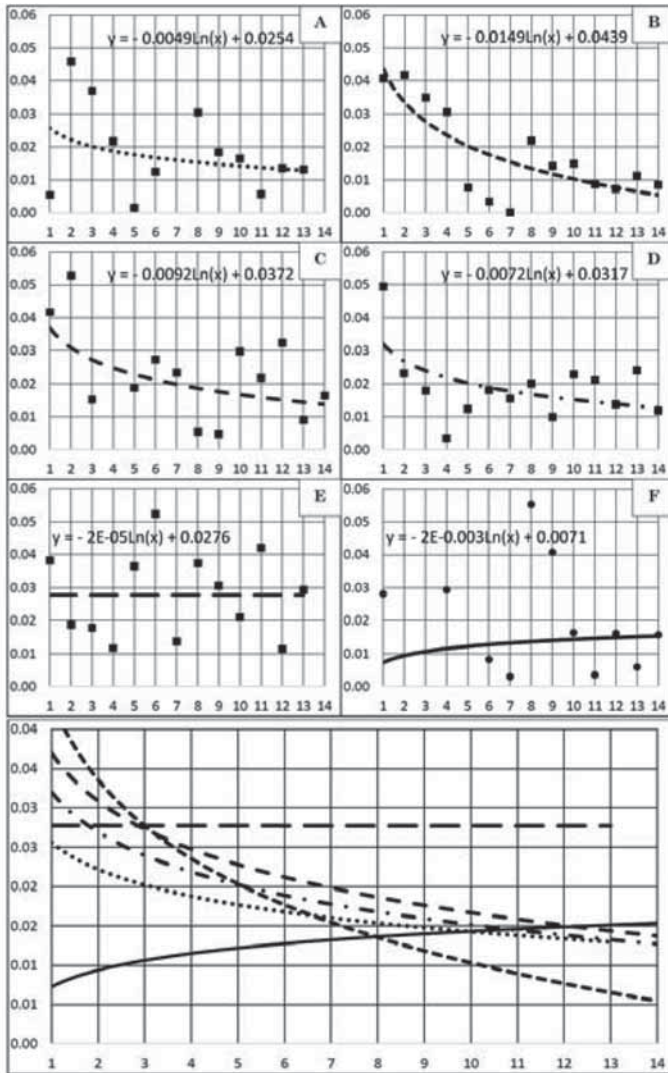


Fig. 13: Logarithmic trend lines of the data (summarized below) adopted from figure 12 showing the food intake of five females (A-E) during the course of gestation and of a non-gravid female (F). Ordinate: ration in g; abscissa: time in weeks. **A** $R^2 = 0.0744$; **B** $R^2 = 0.6338$; **C** $R^2 = 0.1988$; **D** $R^2 = 0.263$; **E** $R^2 = 2E-06$; **F** $R^2 = 0.0105$.

Abb. 13: Logarithmische Trendlinien (unten zusammengefasst) nach den Daten aus Abbildung 12 der Futteraufnahme von fünf Weibchen im Verlauf der Trächtigkeit (A-E) und eines nichtträchtigen Weibchens (F). Ordinate: Futtermenge in g; Abszisse: Zeit in Wochen.

When comparing the data obtained in experiment I and experiment II, some similarities, but also some differences can be seen.

(1) In both experiments *D. punctata* specimens ran significantly slower at night than

during the day regardless of sex. To our knowledge comparable data from literature do not exist. This difference is undoubtedly linked to the negative phototaxis typical for many cockroaches with a nocturnal lifestyle

(BELL et al. 2007). We think *D. punctata* can “afford” to run slower at night to some extent due to its specific defense mechanisms (see below) and its concealing colouration giving some protection. The colour protects at least against nocturnal predators, which orient themselves visually. When comparing the running speeds during the day and at night, the standard deviation at night was noticeably lower than during the day (0.36 day/0.28 night). One reason for this could be that the individual differences of the cockroaches (such as the stage of pregnancy and sex) may influence speed more during fast runs (during the day) than during relatively slow runs (at night).

(2) In both experiments it was also evident that the running speed of the larger and heavier females was generally lower than that of males. This holds for the females, which have been randomly taken from the breeding tank (of which the largest part was perhaps in different stages of gestation), and for gravid and non gravid females studied individually over a long time (the unusual long gestation period of these females was caused by the relatively low keeping temperature, but does not significantly impair the interpretation). That means that on average the large females run slower than the small males, and the running speed of females decrease in course of gestation mainly due to their increasing weight. However, weights of the females in the four stages distinguished in experiment I overlapped to some extent. This is probably due to the fact that the number of embryos from female to female may vary according to temperature, food and age. Running speed is also affected in gravid females of the lecithotrophic viviparous *Nauphoeta cinerea* (MELLER & GREVEN 1996a), and even in species that carry their ootheca externally until hatching of the young like *Blattella germanica* (LEE 1994).

(3) In all individually studied non gravid and gravid specimens (experiment II) the running speed decreased over time and the mean

percentage of this decrease appeared to be higher at night than during the day. We think that the experimental animals have adapted to the experimental situation, which is supported by the following observation: At the beginning of the experiment the majority of the cockroaches immediately started running after release and left the recording area as quick as possible. Later, however, many did not appear to be excessively disturbed when released. They started with delay or after a slight nudge. We believe this is an indication of habituation, because cockroaches appear to exhibit noticeable learning capacities and memory (e.g. MIDORI & MAKOTO 2001; DECKER et al. 2007; BROWN & STRAUSFELD 2009) depending among others on the time, on which something is learned. For example, cockroaches appear to retain (olfactory) learning contexts acquired in the early night better than those acquired in the morning (DECKER et al. 2007).

4.3. Food intake and foraging

Diploptera punctata is matrotrophic viviparous (see above). Upon exhaustion of the relatively little yolk the growing embryos are dependent on food supply from the mother, (see introduction). Thus, *D. punctata* females do not tolerate periods of starvation during gestation (STAY & COOP 1973).

Generally, cockroaches eat at the beginning of the reproductive cycle and/or immediately after the final moult. As far as known, females of most oviparous and lecithotrophic viviparous species eat large quantities of food shortly after the last moult, but stop feeding (and activity) after copulation until the release of their young (e.g. *Blattella germanica* COCHRAN 1983, LEE & WU 1994; *Nauphoeta cinerea* MELLER & GREVEN 1996 a, 1997). Further, it has been shown that *N. cinerea* reduces its basal metabolism probably to compensate for its negligible food intake during gestation (SCHULTZE-MOTHEL & GREVEN 1998)

Our results suggest that pregnant females of *D. punctata* feed more frequently and regularly and may take up more food than non pregnant specimens do. Our preliminary data show that in contrast to *N. cinerea* gravid females of *D. punctata* remain active to some extent at night (unpublished observations). This activity is obviously related to foraging suggesting an increased energy intake during gestation, which may be largely invested in the production of the uterine milk (see STAY & COOP 1973, 1974). Interestingly, the amount in food intake seems to decrease towards the end of gestation. This might be due the fact that the brood sac enormously expands during the course of gestation and that this expansion simply limits the uptake of larger portions of food for mechanical reasons. Such indirect costs of viviparity by volumetric constraints have been discussed for example for viviparous teleostes (e.g. WEEKS 1996) and this issue deserves further attention concerning “pregnant” insects. ENGELMANN & RAU (1965) discuss that in the “ovviviparous” *Leucophaea maderae* the information about the distension of the brood sac that goes together with a restriction of feeding in this species might be transmitted via ventral nerves to higher centres. So far, mechanoreceptors in the brood sac of *D. punctata* (and “ovoviviparous” cockroaches) were associated with the inhibition of the corpora allata-activity during embryogenesis and secretion of the “uterine milk” (GREENBERG & STAY 1974).

Both nymphs and adults of *D. punctata* produce p-benzoquinones in tracheal glands associated with the second abdominal spiracles. Discharge of these substances has (under laboratory conditions) repellent effects especially against ants and carabid beetles (ROTH & STAY 1958; EISNER 1958; BALDWIN et al. 1990). Apart from the fact that some predators may accept *D. punctata* as food, this mechanism (as well as the concealing colour and the hard tegmina) may decrease predation risk of the foraging female during

the long gestation period, in which she is handicapped to a certain extent (see above). However, survival rates of gravid females in the field and under laboratory conditions are unknown.

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