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Role of feeding in the reproductive 'group effect' in females of the German cockroach *Blattella germanica* (L.)

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Abstract

We have found that whether a female German cockroach, *Blattella germanica* (L.), is kept alone or in the presence of another female has a major impact on how fast it reproduces and how much it eats. By the sixth day of adulthood, females paired since adult eclosion had substantially larger oöcytes than did females isolated during the same time, and females paired with intact females, or with ones rendered incapable of feeding, consumed more rat chow in the first six days of adulthood than did isolated females. The stimulatory effect of pairing on reproduction was, however, partially independent of feeding because the oöcytes of solitary and paired females differed in size on day 6 even when they were given, and had consumed, the same amount of food. This result was confirmed with analysis of covariance using the total food intake of a female as the covariate in the analysis. A female's social condition probably influenced the development of its oöcytes by affecting the quantity of juvenile hormone synthesized by its corpora allata. The corpora allata of paired females produced more hormone than did those of isolated ones, even when all females had consumed an equivalent amount of food. Moreover, females treated with a juvenile hormone analog, fenoxycarb, reproduced more quickly than identically reared and fed control females, showing that juvenile hormone could influence reproduction independently of feeding. We conclude that both group rearing and food intake accelerate oöcyte development by diminishing the brain's inhibition on the synthesis of juvenile hormone.

Keywords: Cockroach; Reproduction; Feeding; Group effect; Social facilitation

1. Introduction

In cockroaches, the synthesis of yolk proteins and the deposition of them into the oöcytes are prominent features of the female reproductive cycle (Engelmann, 1979). In some species, such as the American cockroach *Periplaneta americana*, the investment of yolk into a single brood is slight—especially in relation to a female's mass—and females can produce several batches of eggs without feeding (Kunkel, 1966; Weaver and Pratt, 1981). By contrast, feeding is essential for the induction of vitellogenesis in the German cockroach *Blattella germanica* (L.), and starved females do not reproduce (Roth and Stay, 1962; Kunkel, 1966; Durbin and Cochran, 1985; Piulachs, 1988; Schal et al., 1993; Osorio et al., 1998).

Other extrinsic factors, apart from food, influence German cockroach reproduction (reviewed in Schal et al., 1997). For instance, Gadot et al. (1989a) found that the oöctyes of females maintained in groups matured more quickly than did those of females kept alone. Differences like this in the traits of grouped and isolated animals are known as 'group effects' (Grassé, 1946; Gervet, 1968), and the best characterized of these pertain to larval growth (Chauvin, 1946; Long, 1953; Wharton et al., 1968; Izutsu et al., 1970; Holbrook and Schal, 1998) and adult morphology (Iwanaga and Tojo, 1986; Zera and Tiebel, 1988). Reproductive group effects have been noted, however, primarily in the Orthoptera (Norris 1950, 1952; Highnam and Haskell, 1964; Bradley, 1985) and in only two dictyopterans, *B. germanica* (Gadot et al., 1989a) and *P. americana* (Weaver, 1982).

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Reproduction in *B. germanica*, as in other cockroaches, is regulated by the gonadotropin juvenile hormone, which is a product of the corpora allata (Roth and Stay, 1962; Bellés et al., 1987). It is therefore unsurprising that both nutritional and social factors impinge upon female reproduction by affecting the synthesis of juvenile hormone. The corpora allata of females fed a continuous supply of high quality food become highly active and produce adequate hormone to initiate a reproductive cycle (Schal et al., 1993; Schal and Chiang, 1995). Starved females, on the other hand, do not reproduce because their corpora allata produce almost no hormone. Social interaction has a less dramatic impact on the activity of the corpora allata, for the glands synthesize abundant hormone in both solitary and grouped females. But in the latter, they produce greater hormone earlier in the gonadotrophic cycle (Gadot et al., 1989a).

While it is now clear that both social interaction and food intake affect the synthesis of juvenile hormone, it is not known whether they do so independently. It is possible that the quantity of hormone produced by the corpora allata is entirely dependent on the amount—and of course, quality—of food consumed and that social interaction influences juvenile hormone synthesis, and thus reproduction, by affecting feeding. We have addressed this hypothesis in the experiments described herein and, in so doing, have clarified the interaction between nutritional and social factors in modulating rates of reproduction in the German cockroach.

2. Materials and methods

2.1. Insects

The *B. germanica* colony was kept at 27±0.5°C under a 12 h light:12 h dark photoperiodic regime and provided a continuous supply of water and rat chow (# 5012; Purina Mills, St Louis, Missouri). Females, which were to be used in experiments, were separated from the colony within 8 h of becoming adults.

2.2. Experimental set-up

Newly eclosed adult females were placed either alone or in pairs in 100×20 mm Petri dishes, each provisioned with water in a cotton-plugged, 12×75 mm culture tube and finely ground rat chow in a flat-bottomed, 7×12 mm plastic cup (Immulon® 1, Dynatech Laboratories, Chantilly, Virginia). To prevent females from toppling the diet cups, we inserted each cup into a steel nut, the inner diameter of which was slightly larger than the outer diameter of the cup.

Food intake in each of the first six days of adulthood was measured by weighing a diet cup, with its food, at the beginning of an experiment and re-weighing it on each day thereafter. When both females of a pair were able to feed, the daily food intake of a female was calculated as half the amount of food eaten by the pair. For statistical purposes, only a single food consumption value was obtained on each day from a Petri dish containing two insects capable of feeding.

In some experiments, it was essential to know, and control, the exact amount of food consumed by one female of a pair. In these cases, the mouthparts of one of the females were damaged, rendering her incapable of feeding. Females were briefly anesthetized with carbon dioxide and then positioned supine on a paraffin wax block. The mandibles and first and second maxillae of the females were transversely bisected with fine scissors, and the severed distal portions were removed.

In some cases, females were provided ample food at the beginning of an experiment to last until its end, but in others they were given small daily allotments of food. These females, when isolated or paired with mouthpart-ablated females, received on each day the mean amount of food that isolated females were found to have consumed on that day. When both females of a pair were capable of eating, the Petri dish containing the two was provisioned daily twice the amount of food given to isolated females. Females that failed to consume their daily allotment within 24 h were eliminated from an experiment.

In a final type of experiment, newly eclosed females were paired with mouthpart-ablated females and fed ad libitum. The amount of food that the females ate in the first three days of adulthood was measured; and the females were subsequently partitioned almost equally into two treatments, one in which they were continued paired and another in which they were isolated. All females in the two treatments were kept in Petri dishes devoid of food, but containing water.

2.3. Oöcyte measurements

Ovaries were obtained from ice-anesthetized females through a longitudinal incision made with scissors in either the left or right abdominal pleurites. Basal oöcytes were dissected from the ovaries beneath cockroach saline (Kurtti and Brooks, 1976), and three were selected at random from each female and measured for length using an ocular micrometer in the eyepiece of a dissecting microscope. The measurements were averaged, and the resulting value was the oöcyte length determination of a female.

2.4. Juvenile hormone release

A radiochemical assay (Pratt and Tobe, 1974; Feyereisen and Tobe, 1981; Gadot et al., 1989b) was used to quantify the juvenile hormone released in vitro by the corpora allata. The basis of this assay is the stoichio-

metric incorporation of a radiolabelled methyl group from methionine into juvenile hormone III under equilibrium conditions. Corpora allata were obtained from females by first decapitating them and then immersing their severed heads in cockroach saline. The glands were carefully excised from the heads and transferred into 6×50 mm culture tubes, where they were incubated for 60 min at 27°C in 100 μl TC199 medium (Specialty Medium, Lavalette, New Jersey) containing 25 mM HEPES, 5 mM $CaCl_2$, 20 mg/ml Ficoll type 400, and 100 μM L-[methyl-^{3}H]methionine (198 mCi/mmol; New England Nuclear, Wilmington, Delaware). The corpora allata were then shifted to fresh medium in different culture tubes, where they were incubated for an additional 3 h at 27°C. Afterward, the glands were removed from the medium, and the medium was extracted with 250 μl isooctane, 100 μl of which was suspended in liquid scintillation cocktail for radiospectrometry. Medium in which no corpora allata had been incubated was also extracted to quantify radioactivity in the isooctane phase not attributable to juvenile hormone. All glands were floated at the medium surface (Holbrook et al., 1997) and rotated at 90 rpm on a variable plane mixer.

2.5. Treatment of insects with juvenile hormone analog

Females were briefly chilled on ice and then immobilized with plasticine to a paraffin wax block. The four wings of a female were lifted with blunt forceps, and 1 μl acetone, with or without 1 μg fenoxycarb, was administered with a Hamilton syringe to the surface of the anterior-most abdominal tergites. After the acetone had evaporated, the wings were released to their natural position.

2.6. Statistics

One-way analysis of variance (ANOVA) was carried out with the computer program StatView 4.5 (Abacus Concepts, Berkeley, California). Repeated measures ANOVA, two-way ANOVA, and analysis of covariance (ANCOVA) were performed with a generalized linear model procedure (PROC GLM) in SAS® 6.12 (SAS Institute, Cary, North Carolina). The decision criterion for rejecting null hypotheses was α=0.05. Standard error of the mean (S.E.M.) is reported with all means.

3. Results

3.1. Social effects on food intake

Repeated measures ANOVA showed that whether a female was kept alone or with another female had a significant effect ($F_{1,22}$=16.25, $P<0.0001$; Fig. 1) on how much it ate in the first six days of adulthood. This finding was, however, rendered somewhat ambiguous by a significant interaction ($F_{5,110}$=8.26, $P<0.0001$) between a female's age and the treatment it received. We therefore used the Bonferroni–Dunn procedure to detect differences in the amount of food eaten by similarly aged solitary and paired females. Paired females ate no more rat chow than did isolated ones on days 0 and 5 but significantly more ($P<0.05$) on days 1 through 4 (Fig. 1). And overall, during the entire six-day period, paired females ate about 54% more rat chow (54.8±2.0 mg per female) than did their isolated counterparts (35.5±2.8 mg).

3.2. Role of food consumption in oöcyte development

On day 6, the oöcytes of females paired since adult eclosion were 1.40±0.05 mm in length (Fig. 2A), much larger (*t*-test, t=4.83, df=30, $P<0.0001$) than those of females kept alone during the same time (1.00±0.06 mm; Fig. 2A). The faster reproduction of paired females might have been attributable to their greater food intake (Fig. 1). To test this hypothesis, we provided isolated and paired females an equal amount of food on a per-individual basis: Petri dishes with one female were supplied 35.5 mg rat chow on day 0, whereas those with two received twice this amount (Fig. 2B). On day 6, the oöctyes of the paired females (1.26±0.05 mm) were still larger (t=3.04, df=33, P=0.0046) than those of the isolated ones (1.07±0.04 mm). This suggested that social condition could affect oöcyte development independently of feeding, but the faster rate of feeding of paired

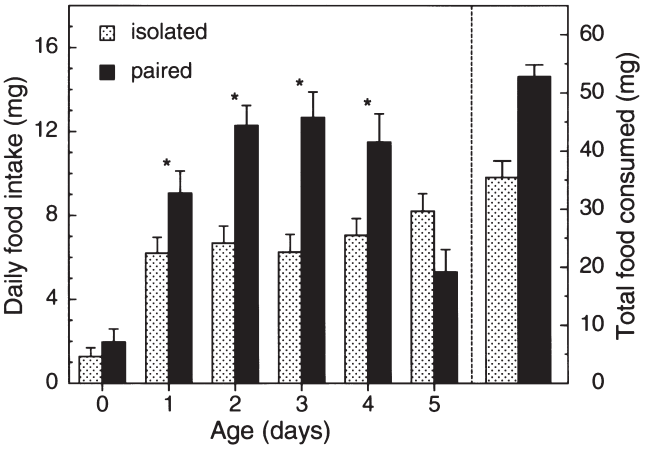

Fig. 1. Food intake of isolated and paired females in the first six days of adulthood. Females were kept either alone or in pairs in Petri dishes containing ground rat chow and water. The food intake of a paired female was calculated as half the amount eaten by the two members of a pair. Bars represent mean food intake on a given day or in the entire six-day period. An asterisk denotes that isolated and paired females consumed a different amount of food on the indicated day (Bonferroni–Dunn procedure, $P<0.05$). The error bars show +S.E.M., and n=16 and 8 for isolated and paired females, respectively.

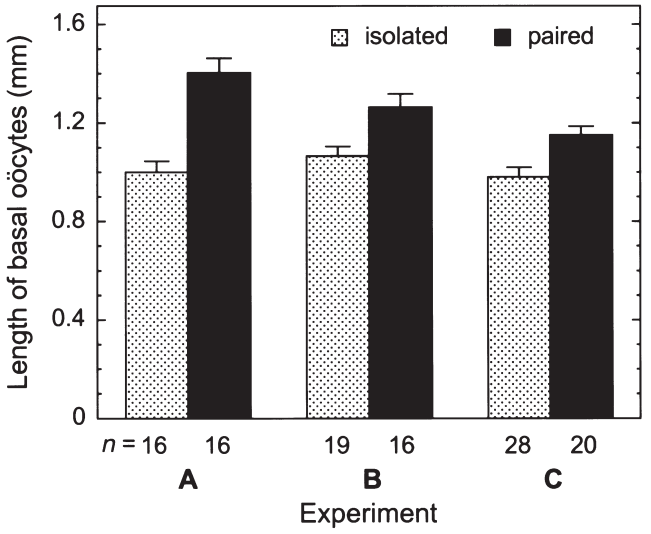

Fig. 2. Size of the oöcytes of isolated and paired females. Females were maintained as in Fig. 1, but separate groups of them were fed differently. (A) Females were provided ample rat chow on day 0 to last until they were six-days-old. (B) Isolated females were given 35.5 mg rat chow on day 0, whereas pairs of females were given twice this amount. (C) On each day, isolated females were given the mean amount of rat chow shown previously to have been eaten by isolated females on that day (see Fig. 1), while pairs of females were supplied twice this amount. The oöcytes of all females were measured on day 6. The number of insects is shown beneath each bar, and error bars show +S.E.M.

females (Fig. 1) might have accounted for their larger oöctyes. To assure that isolated and paired females were consuming food at a similar rate, we gave females on each of the first six days of adulthood the mean amount of food that isolated females were found to have consumed on those days (Fig. 1). Petri dishes with one female were provisioned 1.3, 6.2, 6.7, 6.3, 7.1, and 8.2 mg ground rat chow on days 0 through 5, respectively, whereas those with two females received twice these amounts. Under this dietary regime (Fig. 2C), the oöctyes of six-day-old, paired females (1.15±0.04 mm) were yet again larger (t=3.07, df=46, P=0.0036) than those of identically aged, isolated ones (0.98±0.04 mm).

3.3. Role of partner feeding in stimulating food intake

In the previous experiments, both females of a pair were able to feed. This design fostered behavioral reciprocity but did not allow us to know, or control, the amount of food eaten by a single female of a pair. This could be achieved only by preventing one female from feeding, which we accomplished by surgically excising females' mouthparts. The surgery was successful in eliminating feeding because pairs of mouthpart-ablated females consumed no rat chow in the first six days of adulthood, and their oöctyes, like those of starved females (Roth and Stay, 1962; Schal et al., 1993), were no larger (t=0.34, df=18, P=0.74) on day 6 (0.45±0.03 mm, n=10) than on day 0 (0.44±0.01 mm, n=10). Though unable to consume food, and in all likelihood water, females with damaged mouthparts lived 9–13 days (11.3±0.3 days, n=12).

Mouthpart-ablated females might have disrupted the feeding behavior of their intact partners, but a repeated measures ANOVA showed that a female's food intake in the initial six days of adulthood was not affected by the ability of its partner to feed ($F_{1,21}$=0.03, P=0.87; compare the paired females in Fig. 1 and Fig. 3). Indeed, females paired with either intact or operated females showed nearly identical patterns of food consumption (Fig. 1 and Fig. 3). Moreover, females whose partners were mouthpart-ablated ate, in six days, nearly the same amount of food (52.3 mg) as females whose partners were intact, but substantially more (one-way ANOVA, $F_{2,36}$=16.96, $P<0.0001$; Tukey–Kramer test, $P<0.05$) than isolated females (Fig. 1). These results justified the pairing of females that could feed with those that could not in subsequent experiments.

We next examined the reproduction of paired and isolated females that we now knew had fed identically. Females were either isolated or paired with mouthpart-ablated females from day 0 to 5 and provided on each day the mean amount of food eaten by isolated females (Fig. 1). On day 6, the oöctyes of paired females capable of eating (1.19±0.02 mm, n=16) were larger (t=3.32, df=30, P=0.0024) than those of isolated females (1.03±0.04 mm, n=16).

That paired females reproduced more quickly than identically fed isolated ones was verified with ANCOVA. Newly eclosed females were paired with mouthpart-ablated females in the initial three days of adulthood, and the food they consumed in this time was measured. The females were then assigned to one of two treatments: they were either continued paired or isolated, and in both cases provided water but no food. Analysis

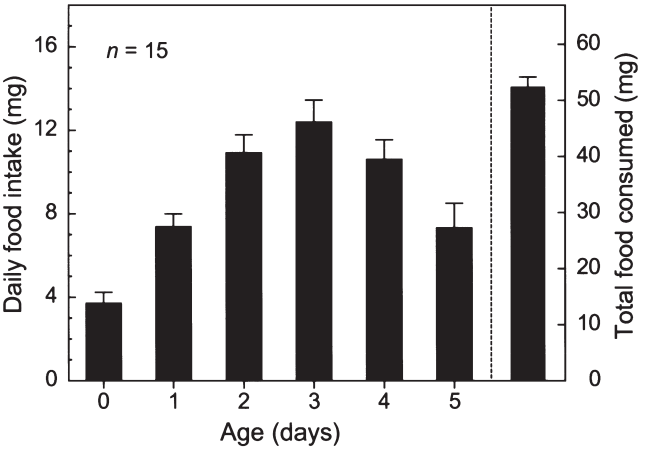

Fig. 3. Daily and total food intake of females paired with females whose mouthparts had been surgically excised. Error bars show +S.E.M.

Table 1
Results of an ANCOVA on the effect of social condition and food intake on the size of the oöcytes of 6-day-old females[a]

Source of variation	*df*	MS	*F*	*P*
Social condition after day 3	1	0.0682	4.47	0.041
Food intake through day 3	1	0.7711	50.55	<0.0001
Error	38	0.0153		

[a] Females were paired with mouthpart-ablated females from adult eclosion till day 3, during which they were provided ground rat chow ad libitum. On day 3, they were transferred to new Petri dishes and either isolated or paired without food until day 6, at which time their oöcytes were measured.

of covariance—with the covariate being the amount of food eaten by a female in the first three days of adulthood—showed that food intake accounted for much of the variation in oöcyte size in six-day-old females (Table 1). Oöcyte size was, in addition, affected by social condition after day 3 (Table 1), with paired females reproducing more quickly than isolated ones (Fig. 4). An interaction term, when incorporated into the analysis, was not significant ($F_{1,37}$=1.51, P=0.23), justifying its exclusion from the model and indicating that the oöcytes of paired females were expected to be larger than those of isolated ones at all levels of food intake. The expected difference was, in fact, about 0.08 mm, as the adjusted means for the oöcyte lengths of solitary and paired females were 0.77±0.03 mm and 0.85±0.03 mm, respectively.

3.4. Role of juvenile hormone in the group effect

Because oöcyte development in the German cockroach is regulated by juvenile hormone, we examined the impact of social interaction on the activity of the corpora allata. The corpora allata of females paired with mouthpart-ablated females and provided an unlimited supply of rat chow produced significantly more (t=2.39, df=26, P=0.024; Fig. 5) juvenile hormone, 7.13±0.37 pmol h^{-1}, on day 6 than did those of isolated females (5.36±0.65 pmol h^{-1}). A disparity in the activity of the corpora allata existed even when females were given, on each day, the mean amount of food eaten by isolated females (Fig. 1). On day 6, the corpora allata of paired females produced more (t=2.78, df=37, P=0.0085; Fig. 5) juvenile hormone (6.54±0.44 pmol h^{-1}) than did those of identically fed isolated ones (5.01±0.35 pmol h^{-1}).

For juvenile hormone to be responsible for paired females reproducing more quickly than identically fed isolated ones, the hormone would have to be capable of having an effect on reproduction independent of feeding. We tested this by examining whether females treated with a juvenile hormone analog, fenoxycarb, reproduced more quickly than identically reared and fed females not

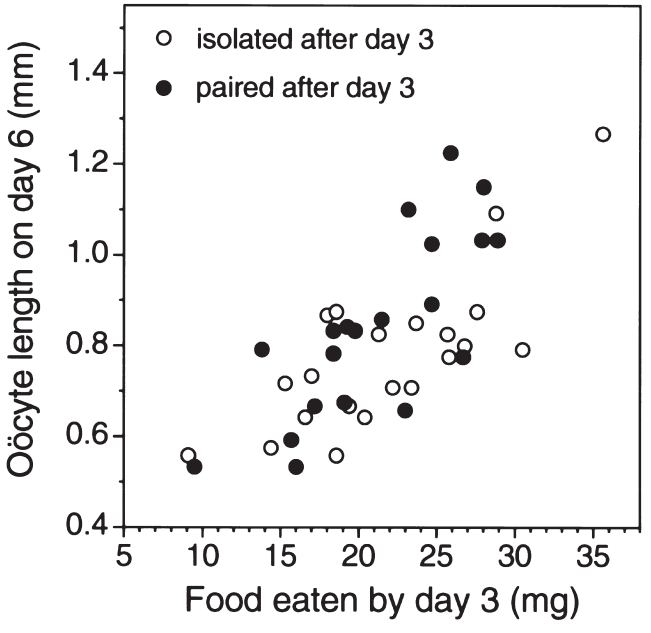

Fig. 4. Relationship between oöcyte length and food intake. The average length of the oöcytes of six-day-old females is plotted against their total food intake in the first three days of adulthood. Females were paired with mouthpart-ablated females until day 3 and fed ad libitum. Afterward, they were isolated or continued paired and provided no food. A total of 41 females were fed until day 3; 21 of these were isolated thereafter and the rest were paired.

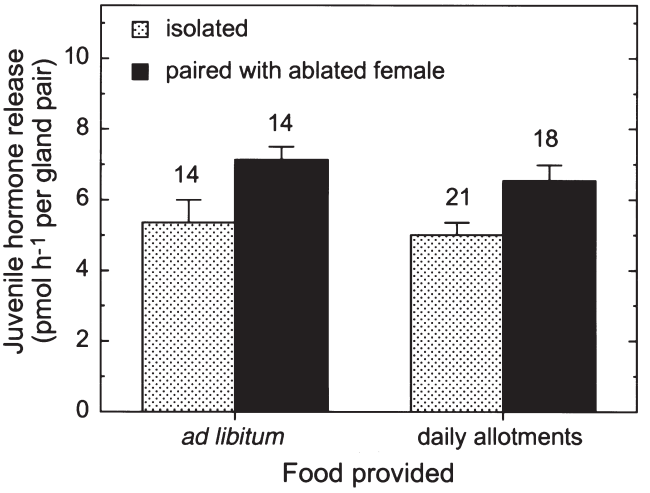

Fig. 5. Production of juvenile hormone by the corpora allata of six-day-old isolated and paired females. Females were either supplied sufficient rat chow on day 0 to last through day 6 or provided on each day an amount of rat chow equivalent to what isolated females were found to have consumed on that day (Fig. 1). Pairs of females consisted of one female capable of feeding and another surgically rendered incapable of doing so. A radiochemical assay was used to quantify the juvenile hormone released by the corpora allata; gland pairs were incubated for 3 h in TC199 medium containing 100 μM L-[methyl-^{3}H]methionine. The number of gland pairs is shown above each bar. Error bars represent +S.E.M.

treated with analog (Fig. 6). A two-way ANOVA—the two factors being the age at which a female finished eating a 25 mg allotment of rat chow and the treatment it received (acetone or fenoxycarb in acetone)—was highly significant ($F_{5,55}$=5.48, P=0.0004). Neither the interaction between age and treatment ($F_{2,55}$=0.34, P=0.71) nor the main effect of age ($F_{2,55}$=1.69 P=0.19) was significant, as opposed to the main effect of hormone analog treatment, which was significant ($F_{1,55}$=14.43, P=0.0004). Fenoxycarb, therefore, stimulated oöcyte development across all age levels.

4. Discussion

4.1. Social effects on reproduction—the role of juvenile hormone

Among insects, the effect of social interaction on reproduction has been perhaps best studied in the Orthoptera, and interaction between or among individuals accelerates the onset and completion of the reproductive cycle in females of many orthopteran species. For example, female desert locusts (*Schistocerca gregaria* Forsk.) of the gregarious phase maintained in groups of 20—composed of a like number of males and females—sexually mature earlier and oviposit sooner than do females kept with a single male (Norris, 1952). Moreover, the vitellogenic ovaries of the European house cricket *Acheta domesticus*, increase in weight much faster in paired females than they do in isolated ones (Bradley, 1985). It is worth noting, however, that not all orthopterans reproduce more quickly in larger groups. Indeed, adult females of the gregarious phase of the African migratory locust, *Locusta migratoria migratorioides*, maintained in large, mixed-sex groups sexually mature much later than do females kept with a single male (Norris, 1950).

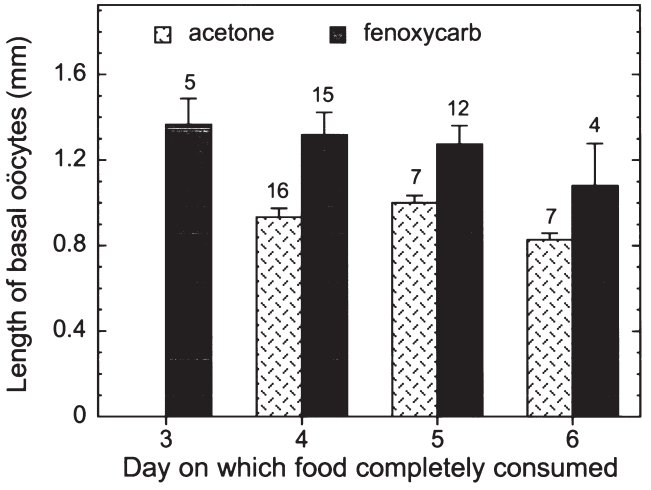

Fig. 6. Effect of a juvenile hormone analog on the development of the oöcytes. Newly eclosed adult females were dosed with 1 μg fenoxycarb in acetone or acetone alone, isolated, and given 25 mg ground rat chow. Each female was monitored daily to identify when it had eaten all its food, and females that had not finished their food by day 6 were removed from the experiment. Adjacent bars show the mean lengths of the oöcytes on day 6 of acetone- and fenoxycarb-treated females that had finished their food on the indicated day. None of the acetone-treated females consumed their food in entirety by day 3. The number of insects is shown above each bar, and error bars represent +S.E.M.

Social interaction, no matter whether it stimulates or inhibits reproduction, appears to exert its effect by influencing how much juvenile hormone the corpora allata produce. In the vast majority of studied insects, juvenile hormone regulates, and more specifically, stimulates vitellogenesis and oöcyte maturation. In accordance with this, Dale and Tobe (1986) found that the corpora allata of isolated females of *L. migratoria* produced greater hormone than did those of crowded ones, and correspondingly, the oöcytes of isolated females developed more quickly. And, as would be expected, the titer of juvenile hormone in the hemolymph was higher in solitary females (Joly and Joly, 1974; Joly et al., 1977; Dale and Tobe, 1986). In the desert locust, the activity of the corpora allata was also found to correlate well with the rate of reproduction; the glands of rapidly reproducing, crowded females synthesized, in general, more hormone than did those of slowly reproducing, solitary females (Injeyan and Tobe, 1981).

As in the orthopterans, social interaction has a disparate effect on reproduction across dictyopteran species. The oöcytes of adult female German and American cockroaches, but not of brown-banded cockroaches (*Supella longipalpa*), develop more quickly when females are maintained in groups (Fig. 2; Weaver, 1982; Gadot et al., 1989a; Chon et al., 1990). It is, however, possible that a reproductive group effect exists in *S. longipalpa* but is difficult to detect owing to the rapid rate of reproduction, and therefore contracted gonadotrophic cycle, of this species. Nevertheless, in another cockroach with prolonged reproductive cycles, *Blabera fusca*, there is apparently little or no social effect on oöctye development (Brousse-Gaury and Cassier, 1975). Social stimulation of reproduction is therefore not ubiquitous in cockroaches, although in the species in which it occurs—*B. germanica* for example—juvenile hormone appears responsible for the faster reproduction of grouped females (Fig. 4; Gadot et al., 1989a).

4.2. The role of feeding in reproduction

A female German cockroach feeds prodigiously during the reproductive cycle but only intermittently and sparingly after it oviposits and while it is carrying its egg case (Cochran, 1983; Hamilton and Schal, 1988). After dropping its egg case, however, a female once again feeds intensively while its next batch of oöcytes

develops. Oviposition and diminished feeding follow, and the process recurs several times throughout a female's life. Long before these feeding cycles were first characterized in the German cockroach, it was known that food consumption was more than correlated with reproduction but was, in fact, a prerequisite for it. Roth and Stay (1962) ascertained that starved females did not reproduce, a finding that has since been confirmed by others (Durbin and Cochran, 1985; Piulachs, 1988; Schal et al., 1993).

Food is but one of many factors impinging upon German cockroach reproduction. For instance, mating stimulates juvenile hormone synthesis and thus oöcyte development, as does maintaining females in groups (Gadot et al., 1989a; Holbrook et al., 2000). Nevertheless, unlike food, the social environment of a female and its mated status do not determine outright whether it will reproduce, only how fast it does. An unmated female kept alone will still oviposit (an inviable egg case), albeit much later than a female mated and grouped (Gadot et al., 1989a). But a starved female will never reproduce, regardless of whether it has been grouped or given the opportunity to mate (Schal and Chiang, 1995; Schal et al., 1997). It was this absolute dependence of reproduction on feeding that led us to hypothesize that social interaction affected oöcyte development by changing food intake, which in turn, we speculated, affected juvenile hormone synthesis by the corpora allata.

Females maintained in pairs showed a distinct cycle of feeding in the first six days of adulthood (Fig. 1), and by day 6, they had consumed about 50% more rat chow and had 40% larger oöcytes (Fig. 2) than did females maintained alone. It was therefore plausible that a disparity in food intake was responsible for the difference in reproduction of isolated and paired females. Nevertheless, when all females were limited to eating the same amount of food, provided in small daily rations, the oöctyes of paired females were still about 17% longer on day 6 than those of isolated females. So almost half the difference in oöctye development between paired and isolated females was not attributable to their dissimilar food intake, which was undoubtedly responsible for some of the difference. In any case, it is almost certain that both feeding and social interaction affect reproduction through the corpora allata. Feeding is known to stimulate juvenile hormone synthesis (Schal et al., 1993; Osorio et al., 1998), and as we have now elaborated, the corpora allata of paired females produce more hormone than do those of identically fed isolated ones (Fig. 5).

The results of the ANCOVA (Table 1) were of interest because they confirmed a direct effect of social interaction on reproduction that did not act through feeding. And more significantly, the ANCOVA addressed a potential bias in experiments in which females were fed small daily allotments of food. During the course of these experiments, females were removed if they did not consume, in entirety, any one of their daily allotments. Because isolated females tended to consume less food than paired ones, they were disproportionately eliminated from such experiments. The ANCOVA design overcame this bias by allowing all females to feed at will, and even in this case, paired females reproduced more rapidly than identically fed isolated ones.

Of greatest interest, perhaps, the ANCOVA also showed that isolation in only the second three days of adulthood was sufficient to depress female reproduction. This suggests that a change in social condition has an immediate impact on the activity of the corpora allata. It is indeed conceivable that sudden isolation causes a rapid release of neuropeptides (allatostatins), which instantly inhibit the synthesis of juvenile hormone (Bellés et al., 1994; Stay et al., 1994). Nevertheless, in a preliminary experiment we found the oöcytes to be similar in size in six-day-old females whose social condition differed in only the two days before their oöcytes were measured (unpublished results by the authors). It may therefore take at least three days for a change in social condition to affect reproduction. If so, social interaction or its absence—like the ovary and egg case (Chiang et al., 1991)—probably influence juvenile hormone synthesis by bringing about slow, synchronous changes in the structure of corpus allatum cells rather than fast changes in the activity of enzymes in the juvenile hormone biosynthetic pathway.

Some of our results have precedence. Norris (1960) found that paired and crowded males of *S. gregaria* ate more and sexually matured earlier than did solitary males. The greater food intake of grouped males was, nonetheless, probably not entirely responsible for their earlier sexual maturation because males that ate least under a given social condition matured earliest (Norris 1960, 1962). Norris did not examine corpora allata function in her studies, which unfortunately limits the comparisons that can be made between her work and ours.

4.3. What prompts the heightened feeding of paired females?

In many vertebrate species, the feeding of one individual prompts, or socially facilitates, that of another (Clayton, 1978). For instance, a Norway rat emits volatiles of food it has eaten, which in turn stimulate other rats to seek out and consume the food (Galef and Wigmore, 1983). Our current results show that feeding is also socially stimulated in adult female *B. germanica*. When both members of a pair were able to eat, they consumed more rat chow than expected based on the food intake of a single female kept alone. The implication of this finding was that the feeding of one female directly induced that of another—as in rats—yet females paired with females unable to feed also consumed more than solitary females. Therefore, the simple presence of

another female, rather than its feeding, is very likely the stimulus prompting feeding. Further investigation is nonetheless required, for it is possible that mouthpart-ablated females attempted to eat and, in this manner, stimulated their partners to feed.

Social interaction accelerates reproduction in the German cockroach, and it probably does so by reducing brain inhibition on juvenile hormone synthesis. The best evidence for this was provided by Gadot et al. (1989a), who found that severing the nerves between the brain and corpora allata resulted in isolated females reproducing as quickly as grouped ones. Their investigation did not, however, control for differences in animal feeding, which we have now done. In so doing, we have learned that social interaction has an effect on reproduction that is partially independent of food intake. A fruitful line of research would be to examine how social information is relayed to and processed by brain centers involved in regulating juvenile hormone synthesis. It would be equally worthwhile to investigate how paired females achieve more rapid reproduction than identically fed isolated ones, especially since reproduction so greatly depends on feeding.

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