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Social influences on nymphal development in the cockroach, *Diploptera punctata*

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Abstract. Solitary male nymphs of the cockroach *Diploptera punctata* (Eschscholtz) (Blattaria: Blaberidae) took significantly longer to reach adulthood than males paired with either a male or female nymph or grouped with four other male nymphs since birth. When isolated throughout nymphal development, 15.8% of males passed through 3 stadia before adult eclosion, and the remainder went through 4 stadia. In contrast, 61.3% of paired males became adults in 3 stadia. Males need not, however, be isolated or paired for the entire nymphal period to express isolated or paired patterns of development. About 60% of males paired in just the first stadium or its initial 9 days became adults in 3 stadia, and only 20.4% of males isolated in the first stadium and the first 3 days of the second reached adulthood within 3 stadia. Although the first stadium was a critical period in which social condition determined the course of future development, analyses of covariance showed that isolated males gained less weight than paired ones, not only in the first stadium, but in the second as well. Moreover, the degree of growth of a male in the second stadium, measured as either weight gain or relative growth rate, did not depend on the male's social condition in the first stadium, because isolated second-instar males grew less than paired ones, even when both sets of insects had been paired in the first stadium. Female nymphal development, unlike that of males, was not greatly affected by social factors.

Key words. Cockroach, group effect, isolation, nymphal development, growth rate, life history, beetle cockroach, *Diploptera punctata*.

Introduction

The juveniles of many insect species, when reared in groups of two or more, grow faster and reach adulthood sooner than those reared in isolation (Long, 1953; Chauvin, 1958; Wharton, 1968). Such alterations in development and/or physiology attributable to social interactions between or among individuals have been termed 'group effects', and these have been distinguished from 'mass effects', which are changes in animal physiology in response to alterations in the environment induced by the animal population (Grassé, 1946; Gervet, 1968). Although accelerated growth under grouped conditions is a commonly measured group effect, other such effects have been well documented. For example, the tendency of aggregated female nymphs of *Psyllipsocus ramburi* (Psocoptera) and *Nilaparvata lugens* (Homoptera) to become macropterous adults is considered a group effect, because the majority of solitary nymphs become micropterous or brachypterous adults (Badonnel, 1948; Iwanaga & Tojo, 1986).

In addition to influencing the time it takes to become an adult, social factors can govern the number of stadia that an insect goes through before adult eclosion and, in so doing, can determine the size of an insect at adulthood. For example, Woodhead & Paulson (1983) found that isolated males of the beetle cockroach, *Diploptera punctata* (Eschscholtz) (Blattaria: Blaberidae), were far more likely than grouped ones to take more than 3 stadia to reach adulthood, and because of this, isolated males were, on average, significantly larger as adults than grouped males. Moreover, Long (1953) found that the isolated larvae of at least one lepidopteran species, *Plusia gamma*, passed through additional stadia and became larger adults.

Adult size is an important life history trait that is often positively correlated with female fecundity (Gilbert, 1984) and male reproductive success (Partridge *et al*., 1987; Simmons, 1988; Clark & Moore, 1995). It is therefore reasonable to posit that social factors might influence the reproductive potential of many insects by modulating the number of stadia through

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which they develop. Given this possibility, it is surprising that little recent research has concerned the means by which social interaction accelerates nymphal development. Instead, most recent efforts have addressed the restraining effects of crowding on growth and metamorphosis (Weaver & McFarlane, 1990; Hirashima *et al*., 1995) or have described the impact of social interactions among nymphs on imaginal morphology (Iwanaga & Tojo, 1986; Zera & Tiebel, 1988).

Diploptera punctata is an ideal species in which to study social influences on development. Grouped males of *D. punctata* take less time to complete nymphal development and become smaller adults than those that are isolated (Woodhead & Paulson, 1983). In this report, the effect of social interaction on developmental parameters in both male and female nymphs of *D. punctata* is described.

Materials and Methods

Insect rearing and experimental set-up

Nymphs of *D. punctata* were reared at moderate density in large plastic boxes (27.5 × 40 × 16 cm), from which newly eclosed adults were collected daily. Adult males were maintained in small plastic boxes (13.5 × 18.5 × 9.5 cm), whereas adult females were mated and kept thereafter in groups of ten to twenty in 150 × 25 mm Petri dishes. All cockroaches were reared at 27 ± 0.3°C and were supplied Purina rat chow (#5012; Purina Mills, St. Louis, MO) and water *ad libitum*.

Adult females oviposit 8 days after mating and retain their brood internally until parturition, which occurs about 65 days after oviposition (Holbrook *et al*., 1998). Neonates were collected from maternal cages within 8 h of birth, and female nymphs were identified by the presence of a median notch in the posterior margin of the ninth abdominal sternite (Woodhead & Paulson, 1983).

Nymphs used in experiments were placed in 100 × 20 mm Petri dishes, each containing a rat chow biscuit and a 10 × 75 mm cotton-stoppered water tube. When nymphs were paired (two per Petri dish) or grouped (five per Petri dish) just after birth, all nymphs within a Petri dish were born on the same day and, except where noted, were of the same sex. When nymphs were switched from an isolated to a paired condition in the first or second stadium, they were paired with insects of the same chronological age from birth or from the first moult. In some experiments, nymphal weight was recorded over time. In such cases, it was essential to know the identity of an insect throughout an experiment. Therefore, when a nymph was paired, its partner was an identically aged nymph of the opposite sex. A nymph's sex was determined before it was weighed.

Insect growth

The rate at which nymphs gained weight in the first and second stadia was quantified with the index, relative growth rate. This index was calculated by dividing the weight gain of an insect during a stadium by the product of the stadium's length and the average weight of the insect during the stadium (Waldbauer, 1968). The length of a stadium was the time in days from birth to first ecdysis or from first to second ecdysis. The weight gain of an insect during a stadium was the insect's weight on the first day of the stadium subtracted from its weight on the first day of the next. To determine a nymph's average weight during a stadium, its weight on the first day of the stadium and on the first day of the next were added, and the resulting value was divided by two. All insects were weighed to the nearest 0.1 mg within 8 h of birth or ecdysis, before they had consumed food or water.

Statistical analyses

Differences in the proportions of males and females becoming adults in 3 stadia and less than 5 stadia, respectively, were detected with a normal approximation procedure (Zar, 1996). When a significant difference was found among proportions, the proportions were arcsin transformed, and a Tukey-type multiple comparison test was used to compare all proportions, or a Dunnett-type procedure was used to compare treatment proportions to a control proportion (Zar, 1996). Differences in the weight gain of nymphs under different social conditions were detected with analysis of covariance (ANCOVA), carried out with a generalized linear model procedure (PROC GLM) in SAS (SAS Institute Inc, 1990). The covariate in all analyses was weight at birth or just after the first moult, the dependent variable was weight after the next moult, and the independent variable was the social environment in which insects were reared. All other statistical analyses were carried out with the computer programme STATVIEW- II (Abacus Concepts, Berkeley, California). Standard error of the mean (SEM) was used as the measure of dispersion in the data.

Results

Effect of social condition on nymphal development

Solitary males of *D. punctata* took significantly more time to become adults (64.5 ± 0.9 days, $n = 125$; Mann–Whitney test, $U' = 10867.5$, $Z = 8.58$, $P < 0.001$, $n = 125$) than paired males (55.9 ± 0.7 days, $n = 105$). This difference was reflected in significant variation ($\chi^2 = 47.025$, d.f. = 3, $P < 0.001$) in the number of stadia that males passed through under different rearing regimes (Table 1). When males were paired with males for the entire nymphal period, 61.3% became adults in 3 stadia, and the remainder went through 4 stadia (Table 1). In contrast, when males were isolated, only 15.8% reached adulthood in 3 stadia. Males paired with females or grouped with four other males showed a pattern of development similar to that of males paired with males, and in all cases, a higher proportion of paired or grouped males completed nymphal development in 3 stadia than solitary males ($P < 0.05$, Tukey-type test). The number of stadia through which females passed before the imaginal moult did not vary significantly ($\chi^2 = 2.927$,

Table 1. Social effects on male and female development.

Social condition*	*n*	Number of stadia†		
		Three	Four	Five +
Males				
Isolated	76	12 (15.8[a])	64 (84.2)	0 (0.0)
Paired with male	62	38 (61.3[b])	24 (38.7)	0 (0.0)
Paired with female	55	33 (60.0[b])	21 (38.2)	1 (1.8)
Grouped (5 males)	45	31 (68.9[b])	14 (31.1)	0 (0.0)
Females				
Isolated	41	0 (0.0)	33 (80.5)	8 (19.5)
Paired with female	50	1 (2.0)	45 (90.0)	4 (8.0)
Paired with male	55	0 (0.0)	49 (89.1)	6 (10.9)

*Males were isolated, paired with a male or female nymph, or grouped with four other male nymphs from birth. Females were isolated or paired but not grouped.
†The total number of stadia before adulthood was recorded for each insect. Values represent the number and percentage (in parentheses) of insects in a treatment which underwent either 3, 4, or 5 or more stadia. Percentages followed by different letters differ from each other ($P < 0.05$, Tukey-type multiple comparison of proportions).

d.f. = 2, $P = 0.23$) under different social conditions (Table 1). Between 80 and 90% of both isolated females and females paired either with males or females went through 4 stadia, and the remainder went through either 3 stadia or more than 4 stadia. Because the development of males in pairs was nearly identical to that of males in groups of five, males were either isolated or paired, but not grouped, in all remaining experiments. Moreover, because nymphs of both sexes developed similarly when paired with either males or females, males and females were housed with nymphs of the opposite sex in experiments in which the weight of paired nymphs was tracked over time.

Critical time periods in nymphal development

To determine whether there was a critical time period during nymphal development in which the social condition of a male fixed its course of future development, males were paired and isolated for differing lengths of time and the number of stadia through which they passed before the imaginal moult was measured. The proportion of males reaching adulthood in 3 stadia increased ($\chi^2 = 57.616$, d.f. = 8, $P < 0.001$) as males were isolated for decreasing lengths of time (Fig. 1). Isolation in only the first two stadia (b) or in the first stadium and the initial 6 (c) or 3 (d) days of the second was sufficient for males to develop as if isolated throughout nymphal development (a) ($P > 0.05$, Dunnet-type procedure). In all these cases, the percentage of males becoming adults in 3 stadia never exceeded 20.4%. When males were isolated for the entire first stadium (e) or for its initial 9 (f) or 6 (g) days, the percentage completing post-embryonic development in 3 stadia increased to between 30 and 33%, but these values were no higher than in the control (a) ($P > 0.05$). The proportion of males becoming adults in 3 stadia did, however, increase significantly ($P < 0.05$) when males were isolated for just the first 3 days after hatch (h) or in only the second stadium (i) (50.0 or 61.1%, respectively).

In a converse series of experiments, the proportion of males reaching adulthood in 3 stadia decreased ($\chi^2 = 23.551$, d.f. = 5, $P < 0.001$) as males were paired for shorter lengths of time (Fig. 2). However, the percentage of males becoming adults in 3 stadia decreased significantly ($P < 0.05$, Dunnet-type procedure) compared to the control (a, 61.3%) only when males were paired for just the first day after hatch (f, 29.4%). When they were paired for the entire first stadium (b) or for its initial 9 (c) days, 59.6 and 66.2%, respectively, became adults in 3 stadia. Pairing in just the first 6 (d) or 3 (e) days after hatch caused a decline in the percentage of males reaching adulthood in 3 stadia to 45.5 and 48.9%, respectively, but these values did not differ from the control (a).

Social influences on growth in the first stadium

We hypothesized that the growth (increase in mass) of males in the first stadium would be affected by social factors, because the social environment of first-instar males greatly influenced their pattern of development (Figs 1, 2). To test this conjecture, ANCOVA was used to compare the gain in weight of isolated and paired males in the first stadium. There was a significant ($P < 0.001$) linear correlation between birth weight and weight after the first moult in both solitary ($r = 0.84$, $t = 11.53$, d.f. = 57) and paired ($r = 0.87$, $t = 13.73$, d.f. = 61) males (Fig. 3, top graph). The lack of a birth weight by social condition interaction ($P = 0.71$, Table 2) revealed that the slopes of the regression lines did not differ and therefore justified the use of ANCOVA. The main effect of social condition was highly significant ($P < 0.001$, Table 2), indicating that paired males gained more weight than isolated ones across all birth weights (Fig. 3). The difference in weight gain was about 2.3 mg, as

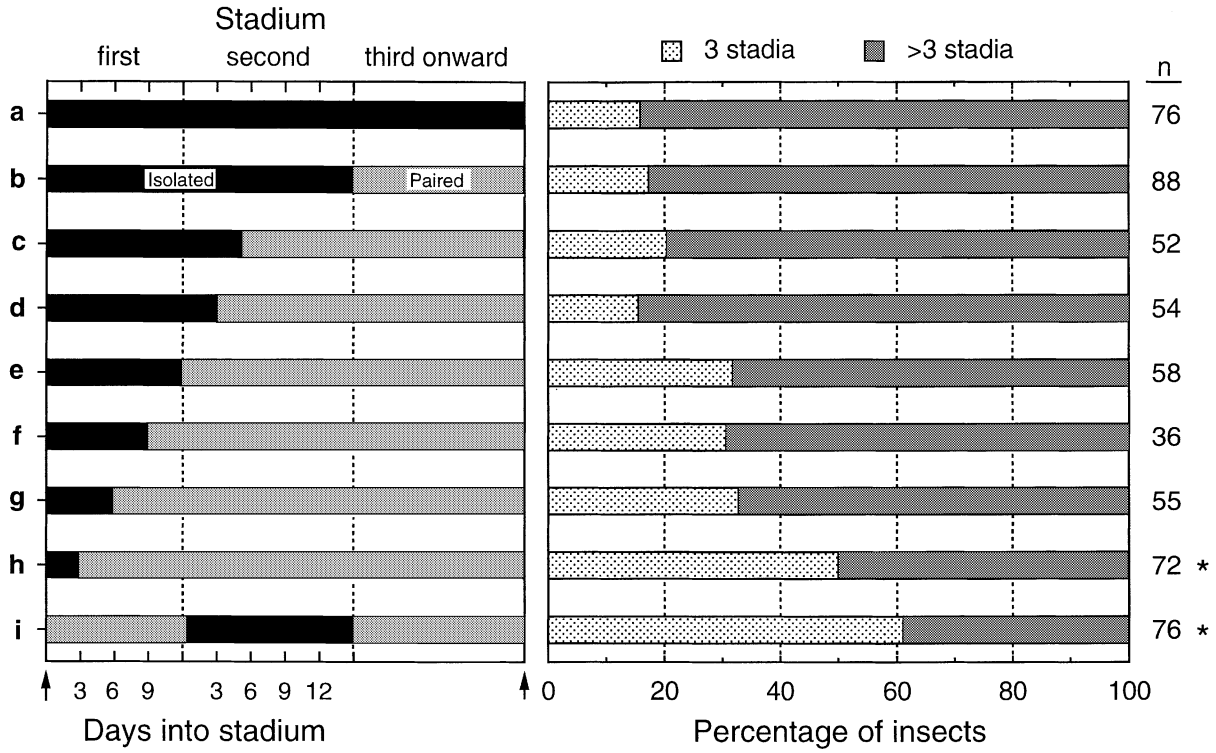

Fig. 1. Critical periods for isolation during nymphal development of *D. punctata*. The left panel shows the time periods during which males in different groups, labelled 'a' to 'i', were isolated (black bars) or paired (shaded bars). Time periods corresponding to the first, second, and third stadium onward are separated with vertical dashed lines. The first and second stadia which lasted about 13 and 15 days, respectively, are subdivided into 3 day intervals. The left and right arrows indicate the times of hatch and adult eclosion. The right panel shows the percentage of males becoming adults in 3 (stippled) or more than 3 (shaded) stadia in the different treatments. The number of nymphs is shown at the right of the panel, and an asterisk indicates that a significantly higher proportion ($P < 0.05$, Dunnet type test) of males in a treatment became adults in 3 stadia than in the control (a).

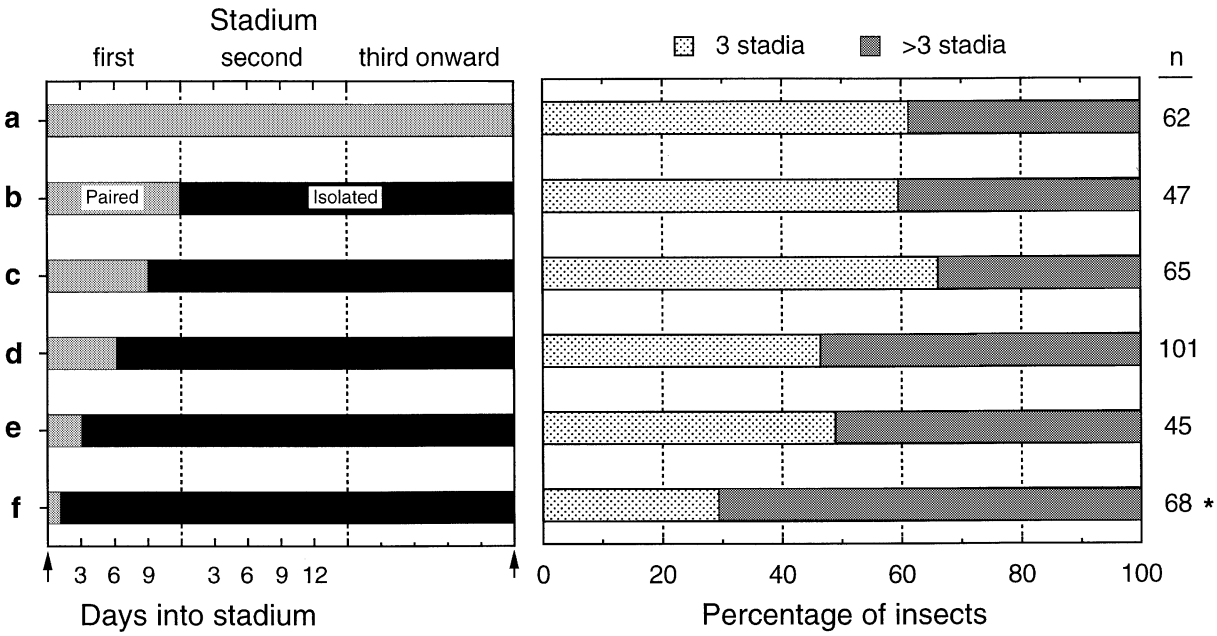

Fig. 2. Critical periods for pairing during nymphal development of *D. punctata*. The left and right panels are as described in Fig. 1. An asterisk indicates that a significantly lower proportion ($P < 0.05$, Dunnet type test) of males in a treatment became adults in 3 stadia than in the control (a).

the adjusted mean weights of paired and isolated males were 29.6 ± 0.3 and 27.3 ± 0.3 mg, respectively.

Although females did not pass through different numbers of stadia under isolated and paired conditions (Table 1), this did not preclude a social influence on female growth. We therefore examined changes in the weight of females in the first stadium. In females, birth weight and weight after the first moult were linearly correlated ($P < 0.001$) under isolated ($r = 0.81$, $t = 9.28$, d.f. = 44) and paired ($r = 0.73$, $t = 8.28$, d.f. = 59) conditions (Fig. 3, bottom graph), and the social condition by birth weight interaction was not significant ($P = 0.92$, Table 2). The main effect of social condition was also not significant ($P = 0.85$, Table 2), indicating that females at all birth weights gained similar weight whether isolated or paired (Fig. 3). The adjusted mean weights of isolated (30.6 ± 0.5 mg) and paired (30.4 ± 0.4) females were accordingly nearly identical.

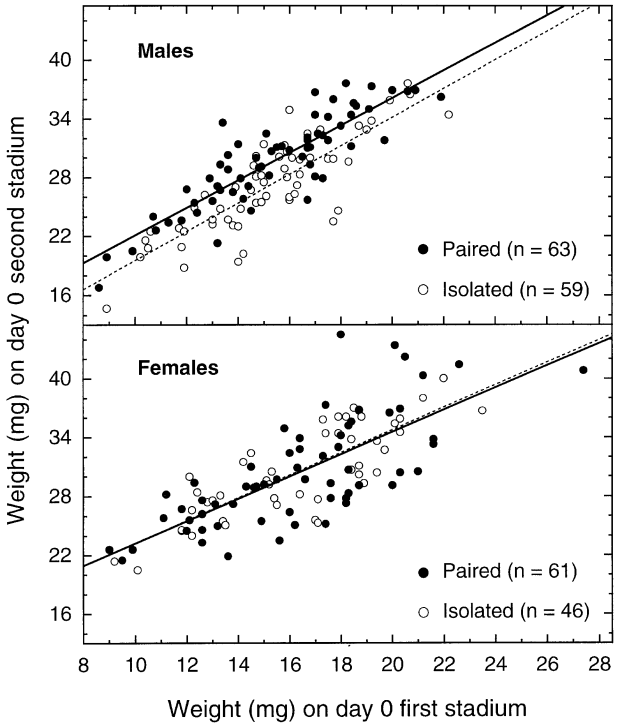

Fig. 3. Growth of isolated and paired nymphs in the first stadium. Weight just after the first moult is plotted against birth weight for males (top) and females (bottom) that were paired or isolated for the entire first stadium. The solid lines are the regression lines for paired nymphs (males, $y = 1.41x + 8.07$; females, $y = 1.13x + 11.91$), and the dashed lines are the regression lines for isolated nymphs (males, $y = 1.47x + 4.87$; females, $y = 1.15x + 11.72$).

Social influences on growth in the second stadium

To test whether social factors influenced the growth of males only in the first stadium, the weight gain of paired and isolated second instars which had been reared under the same conditions since birth were examined. In the second stadium, initial and final weight were positively correlated ($P < 0.001$, Fig. 4) in males (paired, $r = 0.82$, $t = 10.39$, d.f. = 51; isolated, $r = 0.85$, $t = 15.15$, d.f. = 86) and females (paired, $r = 0.80$, $t = 9.67$, d.f. = 53; isolated, $r = 0.85$, $t = 10.12$, d.f. = 40), and the regression lines were parallel for each sex, as the initial weight by social condition interaction was not significant in either males ($P = 0.95$) or females ($P = 0.69$; Table 2). As in the first stadium, the main effect of social condition was significant for males ($P < 0.001$) but not for females ($P = 0.63$). The adjusted mean weight of paired males (64.3 ± 0.8 mg) was 5.4 mg greater than that of isolated males (58.9 ± 0.6).

These results suggested that the growth of males in the second stadium was influenced by their immediate social environment. However, the social condition of a male in the first stadium may have affected its later growth. The weight gain of second-instar males was therefore examined under two additional rearing regimes; males were paired in the first stadium and isolated in the second, or isolated in the first

Table 2. Results from analyses of covariance on the effect of social condition on the weight gain of nymphs in the first and second stadia.

	Males				Females			
Source*	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
First stadium								
Social condition	1	156.7	24.77	0.001	1	0.4	0.04	0.85
Birth weight	1	2014.2	318.28	0.001	1	1657.4	144.33	0.001
Error	119	6.3			104	11.5		
Second stadium†								
Social condition	1	960.6	27.26	0.001	1	6.9	0.24	0.63
Day 0 weight	1	12037.0	341.55	0.001	1	5439.0	187.12	0.001
Error	138	35.2			94	29.1		

*The results of the social condition × weight interactions for the four groups were as follows: first-instar males, d.f.= 1,118, $F = 0.14$, $P = 0.71$; second-instar males, d.f. = 1,137, $F < 0.01$, $P = 0.95$; first-instar females, d.f. = 1,103, $F = 0.01$, $P = 0.92$; second-instar females, d.f. = 1,93, $F = 0.16$, $P = 0.69$.
†Males and females, analyzed in the second stadium, had been isolated or paired since birth.

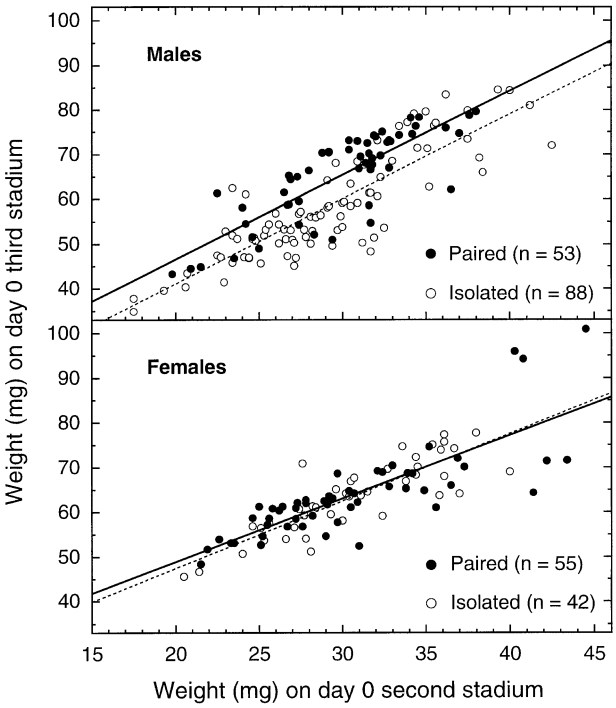

Fig. 4. Growth of isolated and paired nymphs in the second stadium. All insects were reared under the same social condition since birth. Weight just after the second moult is plotted against weight on day 0 of the second stadium for both isolated and paired males (top) and females (bottom). The solid regression lines are for paired nymphs (males, $y = 1.88x + 8.96$; females, $y = 1.42x + 20.54$), and the dashed regression lines are for isolated nymphs (males, $y = 1.90x + 3.13$; females, $y = 1.51x + 17.25$).

stadium and paired in the second. ANCOVA (Table 3) showed that males paired in the second stadium, after having been isolated in the first, gained more weight ($P = 0.021$) in the latter stadium than males isolated since birth. Also, males that were isolated in the second stadium, after having been paired in the first, gained less weight ($P = 0.033$) in the second stadium than those paired since birth. These results showed that the growth of second-instar males was influenced by the environment in which they were reared.

Growth rate in the first and second stadia

Analysis of weight gain alone provided incomplete information on the dynamics of nymphal growth. By measuring stadium duration, in addition to weight gain, we found that paired males grew more quickly than their isolated counterparts (Table 4). Because the length, in days, of the first stadium was shorter ($U' = 11865.5$, $Z = 5.745$, $P < 0.001$) in paired [12.7 ± 0.10 days, data combined from (a) and (b) in Table 4, $n = 116$] than isolated [13.4 ± 0.10, data combined from (c) and (d), $n = 147$] males, both shorter duration of the stadium and greater weight gain (Fig. 3) contributed to the 16% higher growth rate ($U' = 11850$, $Z = 5.427$, $P < 0.001$) of paired (0.050 ± 0.0008, $n = 116$) over isolated (0.043 ± 0.0008, $n = 147$) males. There was no difference in growth rate between isolated and paired females ($U' = 1207.5$, $Z = 0.382$, $P = 0.70$), even though the duration of the first stadium was slightly greater in females reared alone (e and f).

Changes in the rate of growth of nymphs were also examined across the first two stadia (Table 4). Nymphs of either sex that were paired or isolated in both the first and second stadia did not differ in their rates of growth in the two stadia (Wilcoxon paired-sample test, $P > 0.05$). In contrast, males that were isolated in the first stadium and then paired in the second showed a significant increase (Wilcoxon test, $Z = 3.491$, $P < 0.001$) in their growth rate in the latter stadium. Moreover, the growth rate of males decreased significantly ($Z = 3.478$, $P < 0.001$) when males were isolated in the second stadium after having been paired in the first. Thus, a shift in social condition affected not only the amount of weight that nymphs gained, but also the rate at which they gained weight.

Discussion

Social effects on nymphal development

Social factors have been shown to influence rates of nymphal development in all cockroach species examined to date (Landowski, 1938; Pettit, 1940; Chauvin, 1946; Willis *et al*., 1958; Wharton *et al*., 1967, 1968; Izutsu *et al*., 1970; Deleporte, 1978). For instance, isolated nymphs of the German cockroach, *Blattella germanica*, take at least 10% longer than paired ones to become adults at 25°C (Izutsu *et al*., 1970), and grouped males of the American cockroach, *Periplaneta americana*, at 27°C reach adulthood 45 days sooner than those in isolation (Deleporte, 1978). We have now found, as did Woodhead & Paulson (1983), that rearing conditions affect nymphal development in *D. punctata*. Isolation increased the duration of the nymphal stage in males by about 15% and also caused 45% of males to pass through at least one more stadium before the imaginal moult. The development of female nymphs was not as affected by social factors, as both solitary and paired females usually became adults in 4 stadia. Nevertheless, the time it takes for females to reach adulthood is still influenced by rearing conditions. Woodhead & Paulson (1983) found that solitary females took a few days longer than paired ones to complete nymphal development. A slightly greater amount of time spent by isolated females in each stadium (Table 4) probably accounts for this difference.

Isolation, in addition to prolonging nymphal development, can decrease the rate at which insects gain weight. For instance, solitary nymphs of *Acheta domesticus* (Chauvin, 1958; McFarlane, 1962) and *P. americana* (Wharton *et al*., 1968) weighed substantially less than identically aged grouped nymphs throughout much of post-embryogenesis. However, the studies on these two species did not fully characterize the differences in growth between nymphs reared alone and in groups. Most notably, it was not reported whether the disparity in weight between isolated and grouped nymphs was attributable to solitary nymphs gaining less weight per

Table 3. Results of analyses of covariance on the weight gain of males in the second stadium.†

Source*	d.f.	MS	*F*	*P*
Isolated in the first stadium				
Social condition	1	164.1	5.40	0.021
Day 0 weight	1	14325.1	468.92	0.001
Error	144	30.4		
Paired in the first stadium				
Social condition	1	133.0	4.67	0.033
Day 0 weight	1	10452.3	366.84	0.001
Error	113	28.5		

†Two experimental groups were examined; males were isolated in the first stadium and then paired or isolated in the second or paired in the first stadium and then paired or isolated in the second.
*Results of the social condition × weight interactions for the two groups were as follows: males isolated in the first stadium, d.f. = 1,143, $F = 0.94$, $P = 0.33$; males paired in the first stadium, d.f. = 1,112, $F = 2.67$, $P = 0.11$.

Table 4. Social effects on stadium duration and relative growth rate.†

		First stadium			Second stadium		
Group	*n*	Social condition	Duration (days)	Relative growth rate	Social condition	Duration (days)	Relative growth rate
Males							
a	53	P	12.7 ± 0.10	0.050 ± 0.0013	P	14.9 ± 0.20	0.050 ± 0.0008
b	63	P	12.7 ± 0.17	0.051 ± 0.0010	I	15.5 ± 0.27	0.046 ± 0.0008*
c	88	I	13.3 ± 0.08	0.044 ± 0.0011	I	14.9 ± 0.16	0.045 ± 0.0007
d	59	I	13.6 ± 0.21	0.042 ± 0.0010	P	14.7 ± 0.24	0.048 ± 0.0008*
Females							
e	55	P	12.4 ± 0.12	0.049 ± 0.0015	P	13.6 ± 0.15	0.052 ± 0.0011
f	42	I	12.8 ± 0.09	0.048 ± 0.0014	I	14.4 ± 0.16	0.049 ± 0.0009

†Males were weighed at birth and placed in one of four treatments. They were either paired (P) with a female nymph or isolated (I) in both the first and second stadia (**a**, **c**) or were paired in the first stadium and isolated in the second (**b**) or *vice versa* (**d**). Nymphs were weighed immediately after the first and second moults, and these data along with stadium duration were used to calculate relative growth rate. Females were placed in two treatments; they were paired with male nymphs (**e**) or isolated (**f**) for the entire nymphal period.
*Growth rates in the first and second stadia within each treatment were compared with the Wilcoxon paired-sample test. * = $P < 0.05$.

stadium than grouped nymphs, or spending more time in a stadium while gaining the same amount of weight. We have now found that the slower growth of isolated males of *D. punctata* is due to both decreased weight gain per stadium and increased stadium length. Our results differ from those of Woodhead & Paulson (1983) who found that solitary and paired males of *D. punctata* grew at the same rate throughout post-embryonic development. The discrepancy in results is perhaps due to the small sample size used by Woodhead & Paulson and to our use of ANCOVA, which corrected for the effect of size at birth or after the first moult upon the gain in weight of nymphs.

Investigators have seldom used ANCOVA to examine social effects on insect growth and have instead often compared the average weight (Chauvin, 1946; Wharton *et al*., 1967, 1968; Woodhead & Paulson, 1983) or relative growth rate (Watler, 1982) of insects reared under different conditions. However, the heuristic value of these descriptors is limited, because they impart information only on the responses of groups and not of individuals to social factors. In our present study, ANCOVA showed that paired males at all initial weights gained more weight than isolated ones in both the first and second stadia. This provides strong evidence that the growth of every male is affected by its social environment. Nevertheless, substantial variation in the amount of weight gained by identically reared insects of similar initial weight (Figs 3, 4) suggests that unknown factors, perhaps of genetic origin, may influence nymphal growth. Indeed, genetic

control of cockroach development was found by Kunkel (1981) who selected for two lines of *B. germanica*, *or66* and *pld77*, the nymphs of which became adults in almost exclusively 6 and 7 stadia, respectively.

Growth of male and female nymphs

The growth rates of male and female cockroaches can differ greatly, even under identical rearing regimes (Woodruff, 1938; Woodhead & Paulson, 1983). Nevertheless, previous studies on several blattarian species have shown that the growth rates of both sexes are affected similarly by social factors; isolation retards growth and grouping promotes it (Willis *et al*., 1958; Wharton *et al*., 1967; Izutsu *et al*., 1970). Our present results with *D. punctata* are, therefore, unprecedented. Isolated males gained much less weight than paired ones in both the first and second stadia, but females gained the same weight no matter what their social condition. Sex-based differences in the development of males and females under different social conditions have, however, been noted previously in taxa outside Blattaria. For instance, females of the brown planthopper, *N. lugens*, become brachypterous at adulthood when isolated as nymphs, but macropterous when reared in groups of ten, whereas males become macropterous under both rearing regimes (Iwanaga & Tojo, 1986). It is difficult to interpret our results from a physiological perspective, but developmental differences between male and female *D. punctata* may prove useful in efforts to identify mechanisms involved in the group effect.

Critical periods in post-embryonic development

The social environment of an insect during a limited period of post-embryonic development may irreversibly fix its subsequent course of development. For example, nymphs of *A. domesticus*, which are paired in only the first half of post-embryogenesis and isolated thereafter, become adults in the same time as those paired from hatch to adult eclosion (Watler, 1982). Previous studies on cockroaches have failed to identify critical time periods during which social condition influences future development, and have instead shown that developmental rates are always dependent on immediate, and never on prior, social condition (Wharton *et al*., 1967; Izutsu *et al*., 1970). This was best illustrated in a study on nymphs of *P. americana*, which took decreasing amounts of time to reach the tenth moult as they were isolated progressively later after hatch (Wharton *et al*., 1967). Males of *D. punctata* are therefore unique among cockroaches, in that their development, particularly the number of stadia which they go through, is greatly influenced by their social environment during a brief period just after hatch.

Although a male's social environment in the first stadium fixed its pattern of development, the growth rate of males after the first stadium continued to vary with social condition. Paired second-instar males gained more weight and grew more quickly than isolated ones, even when both groups had been paired in the first stadium. Thus, male growth in *D. punctata*, as in other cockroaches, is probably always affected by social factors, regardless of whether a male has committed to passing through a particular number of stadia before adulthood.

The rate of nymphal growth in *D. punctata* appears to respond to changes in social condition not only between, but within, stadia as well, because males isolated or paired for varying amounts of time in the first stadium showed different patterns of development. For instance, when the time spent by males in isolation just after birth was reduced from 6 to 3 days, the percentage of males becoming adults in 3 stadia increased from about 30 to 50%. This suggests that males isolated only until day 3 grew more rapidly between days 3 and 6 than those isolated until day 6. However, further investigation will be necessary to determine how quickly the growth rate of a male changes in response to a shift in social environment. The change may be sudden, however, as locust nymphs lose solitarious and gain gregarious behaviours within an hour of being transferred from isolated to crowded conditions (Roessingh & Simpson, 1994).

In addition to influencing juvenile development, social factors during a brief period of post-embryogenesis can affect adult traits. In many aphids, for example, larvae that are crowded for only a short time, often soon after hatch, become alate adults, whereas those that are isolated during the same time become apterous adults (Lees, 1966; Bonnemaison, 1968). Likewise, in males of *D. punctata*, social condition during a critical period, the first stadium, influenced adult characteristics. Males grouped only in the first stadium were far more likely to go through 3 stadia, and as a result became smaller adults (Woodhead, 1984), than those isolated during the same period. The differences in adult size brought about by social factors may be of reproductive significance. Larger, four-instar males produce more sizable spermatophores than three-instar males, and females mated with larger males can, under some circumstances, be more fecund (Woodhead, 1984).

Physiological correlates of the group effect in nymphs

The physiological mechanisms underlying group effects in nymphs are poorly understood. Watler (1982) found that grouped nymphs of *A. domesticus* consumed about 40% more food than isolated counterparts, providing strong evidence that greater food consumption accounts for faster growth under grouped conditions. Nevertheless, it remains to be determined whether social factors stimulate feeding directly, possibly through neural pathways, or indirectly, perhaps through the action of an intermediary factor such as juvenile hormone (JH), which has been shown to modulate feeding in cockroaches. In adult females of *B. germanica*, removal of the corpora allata, the source of JH, suppresses food consumption (Schal *et al*., 1994), but feeding is restored to near-normal levels when females are treated with a JH analogue (authors' unpublished data). There is, as yet, no evidence showing that JH is responsible for the differences

in food consumption of nymphs reared under different conditions. Nevertheless, evidence supporting a role for JH in the nymphal group effect was provided by Injeyan & Tobe (1981), who found that patterns of JH synthesis differed greatly between isolated and crowded nymphs of *Schistocerca gregaria* in both the fourth and fifth stadia.

Although social factors may influence nymphal development through JH, it is unlikely that they act directly on the corpora allata, because corpora allata activity is regulated by the brain (Stay *et al*., 1994). It is more likely, at least in cockroaches, that sensory perception of a conspecific sends neural signals to the brain, which in turn releases inhibition of the corpora allata. This hypothesis has been tested in adults of *B. germanica* (Gadot *et al*., 1989; Schal *et al*., 1997) and will be tested in nymphs of *D. punctata*.

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