Tactile stimuli trigger group effects in cockroach aggregations

MATHIEU LIHOREAU & COLETTE RIVAULT

CNRS-UMR 6552, Ethologie-Evolution-Ecologie, Université de Rennes 1

In many gregarious species, social interactions among group members have such a potent influence on the physiology and/or the behaviour of individuals that isolation has dramatic consequences for their development and survival. Although 'group effects' have been described in many insect species, the mechanisms involved in these processes remain poorly documented. Our aim was to shed light on group effects in cockroaches by investigating the nature of the social stimuli triggering differences in developmental rates between grouped and isolated individuals. Group effects were absent in nonaggregating species (*Blattella lituricollis*, *Blattella biligata*), but present in species that form social aggregations (*Blattella germanica*, *Symploce pallens*). The presence of conspecifics increased rates of both nymphal development and oothecae production in *B. germanica*. Tactile stimuli were sufficient to trigger developmental group effects in this gregarious cockroach. *Blattella germanica* nymphs reared with tactile stimuli, either from a rotating feather or from insects of other species, grew faster than isolated nymphs. Although the role of tactile stimuli has been understudied, they could be involved in group effects in many insect species.

Living in groups is widespread and provides different kinds of benefits such as decreased predation risks, decreased energetic costs of movement, increased foraging efficiency or increased encounters with potential mates (Krause & Ruxton 2002). Although a large variety of animals aggregate, the mechanisms responsible for group formation and complexity of communication differ between species (Parrish & Hamner 1997). Depending on these characteristics, conspecifics can have such a potent influence on the physiology and/or behaviour of individuals that social isolation has dramatic consequences for their development and survival (e.g. Harlow 1965; Wilson 1971; House 2001; Zeigler & Marler 2004; Perellóa et al. 2006). Two main categories of aggregations emerge from the many definitions that have been given (Parrish et al. 1997).

(1) In nonsocial aggregations, individuals are attracted by a given source but do not interact socially and they disperse when the source is consumed or vanishes. In this case, large increases in density at a source can induce microenvironmental modifications that happen to favour development. For example, under crowded conditions some dipteran and lepidopteran nymphs benefit from better regulation of body temperature and of water evaporation than singletons and thus their developmental rates increase (Clark & Faeth 1997; Slone & Gruner 2007). These differences between grouped and isolated individuals have been termed 'mass effects' and are generally observed in large groups of animals (Grassé 1946).

(2) In contrast, social aggregations are formed and maintained by mutual attraction among their socially interacting members. In this case, differences in physiological, morphological or behavioural traits between grouped and isolated individuals are mainly attributable to social interactions and have been called 'group effects' (Grassé 1946). They differ from mass effects in that they are caused by the perception of social stimuli emanating from conspecifics and can be observed as soon as only two individuals are grouped (Grassé 1946). Group effects have been described in many insects including orthopterans, aphids, coleopterans and blattodeans; their best-documented consequences pertain to modifications of developmental rates or group-induced phenotypic plasticity. Grouping often accelerates nymphal development (Chauvin 1946; Long 1953), although it can delay imaginal moulting in a few

Correspondence: M. Lihoreau, CNRS-UMR 6552, Ethologie-Evolution-Ecologie, Université de Rennes 1, Campus Beaulieu, Bât. 25, 35042 Rennes, France (email: mathieu.lihoreau@univ-rennes1.fr).

species (Tschinkel & Wilson 1971; Weaver & McFarlane 1990). The presence of conspecifics can also affect adult metabolic rates and accelerate female reproductive cycles and egg production (Highnam & Haskell 1964; Bradley 1985). Furthermore, in some species, frequency of interactions between individuals can orient nymphal development towards different phenotypes and influence adult morphology (Lees 1967; Iwanaga & Tojo 1986).

Group-reared cockroach nymphs, belonging to different families, develop faster and reach adulthood sooner than those reared in isolation (Roth & Willis 1960; Woodhead & Paulson 1983). Although these developmental delays were described some time ago, the underlying mechanisms and the sensory channels involved are still poorly understood. Most investigations have focused on two well-known species, *Blattella germanica* (L.) and *Periplaneta americana* (L.), which form social aggregates (Bell & Adiyodi 1982; Rust et al. 1995). These studies have investigated mainly the olfactory and visual channels, but failed to identify the nature of the social stimuli involved in developmental group effects (Wharton et al. 1968; Izutsu et al. 1970; Nakai & Tsubaki 1986). Although grouping facilitates food intake, Holbrook et al. (2000) found that metabolic rates of grouped *B. germanica* remained higher than those of isolated individuals even though all consumed the same controlled amount of food. Consequently, neither olfactory or visual stimuli nor facilitation of food intake can explain totally differences in developmental rates. Recent experimental evidence showed that physical contact between conspecific desert locusts, *Schistocerca gregaria* (F.), was sufficient to induce a behavioural phase change from the solitarious to the gregarious phenotype (i.e. gregarization; Roessingh et al. 1998; Hägele & Simpson 2000; Simpson et al. 2001; Rogers et al. 2003). These results suggest that the tactile channel, which is often underinvestigated, could be implicated in similar processes in other insect species. This opens an interesting line of research to analyse mechanisms involved in group effects. We hypothesized that tactile stimuli could trigger the observed developmental group effects in cockroaches.

Our aim in our study was to identify the stimuli responsible for group effects in cockroaches and to shed light on this old and still unsolved problem. First, we evaluated the consequences of grouping in different species in relation to their tendency to form social aggregations. Then we described, in detail, group effects in the gregarious species *B. germanica*, both at nymphal and adult stages. Finally, we investigated the nature of the stimuli involved in group effects, focusing particularly on tactile stimuli.

METHODS

Breeding Conditions

Experimental individuals came from four cockroach species: *Blattella germanica* (L.), *Blattella lituricollis* (W.), *Blattella biligata* (W.) and *Symploce pallens* (S.). All these insects were bred in large cages (120 × 80 cm and 30 cm high), at 25 ± 1 °C under a 12:12 h light:dark photocycle. They received water, turkey food pellets and shelters ad libitum. Experiments were carried out under the same controlled temperature, photocycle and food availability conditions as those used for breeding.

Aggregation Tendency

We used binary choice tests to evaluate the social aggregation tendency of each of the four cockroach species. In each test, a group of 20 first-instar nymphs received a choice between two filter papers (60 × 15 mm) to be used as resting sites in a test dish (140 mm in diameter and 20 mm high; Rivault et al. 1998). Tests were set up during the light phase of the photocycle and data were collected 24 h later, after the nymphs had spent an entire photocycle in the test dishes. At the end of a test, we counted the individuals on each resting site. When more than 80% of nymphs were on one of the papers, they were considered to be aggregated. We used the proportion of tests in which nymphs were aggregated to evaluate the aggregation levels of the different species (Leoncini & Rivault 2005).

Group Effects

Nymphal developmental rate

First-instar nymphs of each of the four cockroach species were reared either in groups or in isolation. Mature oothecae were placed individually in glass vials until hatching. Then, 11 nymphs were taken from each ootheca: 10 sibling nymphs were reared together (grouped) and one nymph was reared alone (isolated). Each replicate of these two experimental conditions was made with individuals originating from the same ootheca to avoid potential developmental rate differences caused by genetic variability (Kunkel 1981). Nymphs were reared in plastic boxes (80 mm in diameter and 50 mm high) until they became adult. We counted the nymphs of each instar in each box daily. These data provided the exact duration of nymphal development for each individual and the cumulative number of moulted individuals for each instar in relation to time. To compare developmental duration of the isolated individual to that of grouped individuals, we randomly chose one same-sex individual in each corresponding group.

Adult body size

We measured *B. germanica* adults at the end of the rearing experiments. Body size was estimated by maximal head width and length of the left mesothoracic femur, as these values are correlated with general body size in cockroaches (Lefeuvre 1966). Precise measures were obtained from photographs of heads and legs taken under a binocular microscope (×25), using homemade software (J.-P. Richard, CNRS-UMR 6552, Rennes, France). To compare the body size of isolated individuals to that of grouped individuals, we randomly chose one same-sex individual in each corresponding group.

Oothecae production

Virgin sibling *B. germanica* females were kept either in groups of two (grouped) or singly (isolated) in plastic boxes (80 mm in diameter and 50 mm high) from their imaginal moult until their death (range 21–226 days). Each replicate of these two experimental conditions was made with individuals originating from the same ootheca to avoid potential oothecae production differences caused by genetic variability. Under these conditions, all oothecae were sterile. Each day we counted the oothecae produced by each grouped or isolated female. The cumulative proportions of females that produced an ootheca for each ootheca rank were calculated from these data. To compare oothecae production of isolated females to that of grouped females, we randomly chose one female in each corresponding group.

Sensory Stimuli

Thermal stimuli

We measured temperature ($°C \pm 0.01$) with high-precision thermal sensors (LM335 National Semiconductor, Santa clara, CA, U.S.A.). One thermal sensor was placed inside a polystyrene box (8.2×2.8 cm and 2 cm high) containing cockroaches and another was placed inside an identical but empty box. The thermal difference recorded between the two boxes was therefore due to the presence of the cockroaches. Stabilized thermal gain was recorded 24 h after cockroach introduction. We carried out trials with either 0, 25, 50, 75, 100 or 125 final-instar *B. germanica* nymphs.

Olfactory stimuli

Isolated first-instar *B. germanica* nymphs were reared in plastic boxes (80 mm in diameter and 50 mm high) until their imaginal moult, under five experimental conditions (1–5).

(1) Nymphs were reared with nine first-instar *B. germanica* nymphs.

(2) Nymphs were reared with one filter paper.

(3) Nymphs were reared with one filter paper conditioned by *B. germanica* nymph odours. We obtained conditioned papers by placing them in a box with normally fed and watered nymphs with a ratio of 25 nymphs per paper for 4 days (Rivault & Cloarec 1998). Papers were conditioned with nymphs of the same age as the test nymphs and were renewed every 4 days. Similarly conditioned papers induce nymphs to aggregate (Rivault & Cloarec 1998).

(4) Nymphs were reared with one filter paper conditioned with *B. germanica* nymphal cuticular hydrocarbon (CHC) extracts. Papers were conditioned with CHC extracts of 25 nymphs in 1.5 ml dichloromethane for 2 min (Rivault et al. 1998). We made CHC extracts with nymphs of the same age as the test nymphs. Papers were renewed every 4 days. This CHC dose is enough to induce nymphs to aggregate in binary choice tests, which is not the case for lower doses (personal observation).

(5) Nymphs were reared with volatile odours from *B. germanica* nymphs. Isolated nymphs were placed in a flux of volatiles emitted by 25 aggregated nymphs of the same age as the test nymph. A pump pushed charcoal-purified humidified air at a constant flow rate (180 ml/min) from the aggregated nymph boxes through a Teflon tube (1.6 mm in diameter) to the boxes of the isolated nymph.

Tactile stimuli

Isolated first-instar *B. germanica* nymphs were reared in plastic boxes (80 mm in diameter and 50 mm high) until their imaginal moult, under four experimental conditions (6–9).

(6) Nymphs were reared with nine first-instar nymphs of the cockroach *S. pallens* which are the same size as *B. germanica* nymphs; their movements provided tactile stimuli.

(7) Nymphs were reared with nine first-instar nymphs of the locust *S. gregaria* which are much larger than the first-instar *B. germanica* nymphs; their movements provided tactile stimuli.

(8) Nymphs were reared with an immobile turkey feather fixed vertically in the cylindrical rearing box which provided no tactile stimuli when test cockroaches were motionless.

(9) Nymphs were reared with a mobile turkey feather oriented vertically in the cylindrical box. A motor rotated the feather continuously at the rate of 1 rev/min. The rotation of the feather swept the complete surface of the box (top, bottom and periphery). Therefore, when motionless, test cockroaches perceived tactile stimuli.

Each replicate of the nine experimental conditions was made with individuals from one ootheca to avoid differences in development caused by genetic variability. For all experimental conditions (1–9), the thermal difference between an empty control box and each experimental box was measured and taken into account as a covariable of nymphal development durations in the statistical analyses.

Statistical Analyses

We analysed the data with R 2.2.1. (Ihaka & Gentleman 1996). The usual statistical tests (binomial tests, Wilcoxon tests or Pearson correlation) were applied when adequate. For meta-analyses we used either analyses of variance (ANOVA) completed by Fisher least-significant difference (LSD) post hoc tests or analyses of deviance (generalized linear model, GLM, procedure) completed by Z tests (see McCullagh & Nelder 1989), in relation to the distribution of residuals. All statistical tests are two tailed.

RESULTS

Group Effects and Aggregation Tendency

Isolation significantly delayed nymphal development in *B. germanica* and *S. pallens*, but had no effect on the nymphal development of *B. biligata* or *B. lituricollis* (Table 1). When given the choice between two identical resting sites, both *B. germanica* and *S. pallens* nymphs aggregated on a single site in 60–85% of tests. In contrast, *B. biligata* and *B. lituricollis* nymphs did not aggregate significantly on a single resting site (Table 1).

Table 1. Group effects and aggregation tendency

Species	Social aggregation		Nymphal development			
	No. of choice tests	Aggregation level (%)	No. of rearing tests	Isolated (days)	Grouped (days)	$P*$
B. germanica	57	63.15	50	60.92±1.02	55.64±0.80	0.001
S. pallens	26	84.61	30	115.93±3.88	105.73±2.10	0.037
B. biligata	33	30.30	35	66.34±0.84	67.11±0.81	0.393
B. lituricolli	73	34.25	31	46.00±0.42	45.68±0.47	0.517

Aggregation levels (%) and nymphal development durations ($\overline{X} \pm$ SE, days) of isolated and grouped individuals are given for the four cockroach species tested.
*Wilcoxon test.

Group Effects in *B. germanica*

Isolated *B. germanica* nymphs (males and females) reached adulthood significantly later than grouped nymphs (Table 2). Moulting curves showed that differences in developmental rates between isolated and grouped nymphs became significant after the third nymphal instar (Fig. 1a). Growth delay accumulated progressively throughout development (Pearson correlation: delay for nymphal instar: $r_{48} = 0.47$, $P < 0.001$). Neither maximal head widths nor mesothoracic femur lengths differed significantly between isolated and grouped males or females (Table 2).

Both life span and social condition (grouped or isolated) significantly influenced total oothecae production of virgin females (ANOVA: life span: $F_{1,96} = 43.28$, $P < 0.001$; social condition: $F_{1,96} = 12.40$, $P = 0.001$). Although life span did not differ significantly between isolated and grouped *B. germanica* (life span*social condition: $F_{1,96} = 1.98$, $P = 0.163$), isolated females produced significantly fewer oothecae than grouped females (Table 3). Isolation delayed production of the first ootheca and this delay increased with each subsequent ootheca (Pearson correlation, delay for ootheca rank: $r_{48} = 0.51$, $P < 0.001$; Fig. 1b).

Sensory Stimuli

Thermal stimuli

Thermal gain increased linearly with cockroach density in the test boxes (Fig. 2). The thermal gain produced by one nymph was estimated at $0.0041 \pm 0.0003 \,^{\circ}$C/day under our experimental conditions.

Olfactory and tactile stimuli

Experimental rearing conditions (1−9) significantly modified developmental durations of nymphs (GLM with Poisson errors: experimental condition: $D_{8,290} = 269.87$, $P < 0.001$). However, differences in developmental durations were not related to thermal gain differences under each experimental condition (thermal gain: $D_{1,289} = 0.550$, $P = 0.860$). The interaction between experimental conditions and thermal gain was not significant (experimental condition*thermal gain: $D_{8,279} = 9.70$, $P = 0.290$). Therefore, neither groups of nymphs (1, 6, 7) nor experimental set-up (motor used to rotate feathers in 9) produced significant temperature increases likely to bias results.

The presence of conspecific odours (3−5) did not increase the developmental rate of isolated nymphs (Fig. 3). Perception of odours, by contact or from a distance, was not sufficient to stimulate nymphal development. However, the presence of live conspecifics (1), nymphs of another cockroach species (6), or nymphs of another insect order (7), significantly stimulated the developmental rate of *B. germanica* nymphs (Fig. 3). Developmental durations were similar when *B. germanica* nymphs were grouped with conspecifics (1) or with similar-sized cockroach nymphs (*S. pallens*; 6). However, they grew significantly faster when they were grouped with locust nymphs (*S. gregaria*; 7) than when they were grouped with cockroach nymphs (1, 6), suggesting that locusts provided more potent stimuli. Nymphs reared with a rotating feather (9) developed significantly slower than nymphs reared with groups of insects (1, 6, 7). Nevertheless, they grew significantly faster than isolated nymphs deprived of tactile stimuli (2, 5, 8; Fig. 3). Artificial tactile stimuli

Table 2. Group effects in *B. germanica* nymphs

	N	Nymphal development (days)	$P*$	Head (mm)	$P*$	Femur (mm)	$P*$
Males							
Isolated	25	60.56±1.46	0.005	1.92±0.02	0.555	2.84±0.04	0.920
Grouped	25	55.44±1.17		1.90±0.02		2.86±0.02	
Females							
Isolated	25	61.28±1.45	0.008	2.14±0.02	0.818	3.10±0.04	0.701
Grouped	25	55.84±1.31		2.15±0.02		3.13±0.04	

Nymphal developmental durations ($\overline{X} \pm$ SE, days) and adult body sizes (maximal head width, mesothoracic femur lengths; $\overline{X} \pm$ SE, mm) are given for isolated and grouped nymphs.
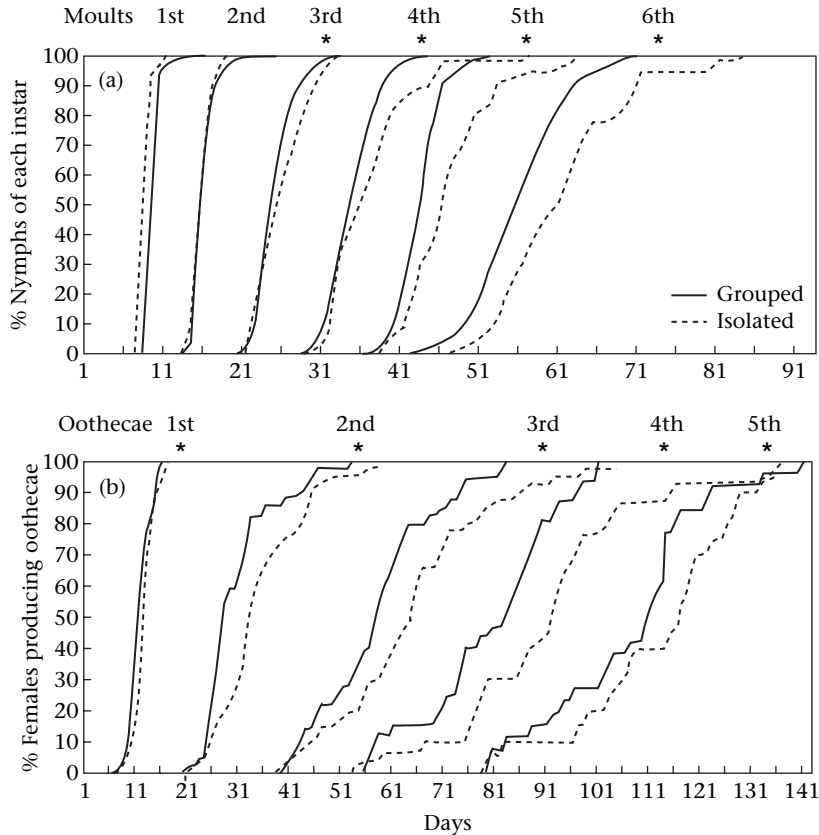*Wilcoxon test.

Figure 1. Group effects in *B. germanica*: (a) nymphal development and (b) ootheca production. (a) Cumulative moulting curves for each instar. Curves represent the proportion of nymphs at each instar in relation to time since hatching for grouped and isolated individuals. (b) Cumulative ootheca production curves. Curves represent the proportion of females that produced an ootheca for each ootheca rank in relation to time since their imaginal moult for grouped females and for isolated females. Each curve represents data for 50 individuals. Wilcoxon test: *$P < 0.05$.

were thus sufficient to enhance developmental rates, although under our experimental conditions, they did not compensate completely for the absence of conspecifics.

DISCUSSION

Our study shows that group effects are not common to all cockroach species. Delays in nymphal development under social isolation were observed in *B. germanica* and *S. pallens*, whereas they were absent in *B. biligata* and *B. lituricollis*. In aggregation tests, species not susceptible to group effects did not search actively for the presence of conspecifics when resting. In contrast, species presenting

strong group effects formed social aggregations independently of environmental conditions. The presence of conspecifics was a necessary condition for these species to develop at a normal rate. Group effects have been reported for at least nine other cockroach species belonging to different families including Blattidae, Blattellidae and Blaberidae (Roth & Willis 1960; Woodhead & Paulson 1983). Although the aggregation characteristics of these species are poorly documented, they are assumed to form social aggregations. Observed group effects in cockroaches may thus be considered as consequences of the evolution of gregariousness.

Our detailed investigation of group effects in *B. germanica* supports a previous study (Izutsu et al. 1970) and shows that the delay in nymphal development of isolated compared to grouped individuals accumulates gradually throughout the isolation period and affects nymphs of both sexes. Social isolation does not affects body size or weight of adults (Ishii & Kuwahara 1967), although it leads to an increase in adult body size and weight in species with nymphal development three or four times longer than that of *B. germanica*, for example *Periplaneta americana* (Wharton et al. 1967). In addition, isolation induced a gradual decrease of oothecae production rates in *B. germanica*. This finding is supported by previous reports showing that isolated virgin females produced

Table 3. Group effects in *B. germanica* females

	N	No. of oothecae	P*	Life span (days)	P†
Isolated	50	3.64±0.29 ⎱	0.018	143.77±6.64 ⎱	0.262
Grouped	50	4.46±0.30 ⎰		132.71±7.10 ⎰	

Ootheca production ($\overline{X} \pm$ SE) and adult life span ($\overline{X} \pm$ SE, days) are given for grouped and isolated females.
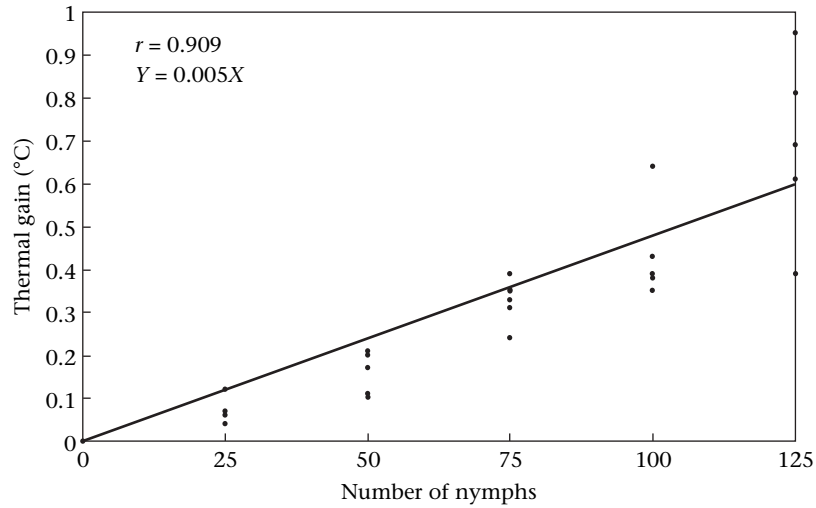*Fisher least-significant difference post hoc test.
†Wilcoxon test.

Figure 2. Thermal gain (°C) in relation to the density of *B. germanica* nymphs in the experimental box. r = Pearson correlation coefficient.

significantly smaller oocytes than grouped females at the same age (Gadot et al. 1989; Holbrook et al. 2000). The fact that living in groups enhances the developmental rates of individuals means that the presence of conspecifics has an impact on individual reproductive success. This is more important than expected at first sight in species that form social aggregations.

Although metabolic heat increased temperature in high-density groups, we found no significant temperature increases in test groups that could explain the growth rate increase. Therefore, mass effects related to modifications of microclimatic conditions can be discarded as the main cause of growth acceleration in this species under

our experimental conditions. In addition, previous reports showed that increases in developmental rates are not correlated with group size (Izutsu et al. 1970). These results suggest that differences in developmental rates have a social origin and raise the question of the social stimuli involved in group effects.

All our experiments involving conspecific odours failed to stimulate the developmental rate of isolated nymphs, confirming previous studies (Wharton et al. 1968; Izutsu et al. 1970; Nakai & Tsubaki 1986). Although relatively low levels of CHC extracts are able to induce cockroach aggregation (personal observation), these levels are not sufficient to induce the physiological responses
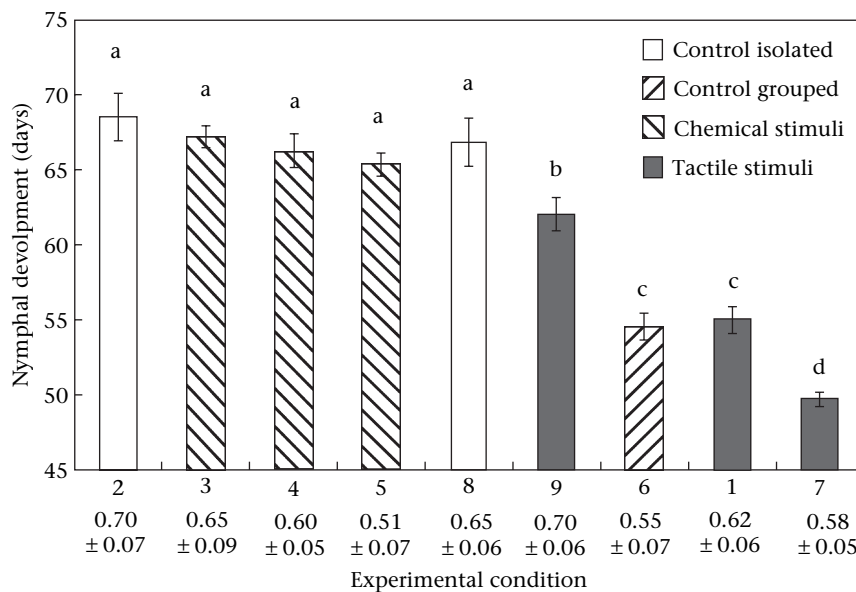

Figure 3. Sensory stimuli involved in *B. germanica* nymphal development: nymphal developmental durations ($\overline{X} \pm$ SE, days) in the presence of olfactory or tactile stimuli. One *B. germanica* nymph was reared with: (1) nine *B. germanica* nymphs; (2) no other nymphs; (3) a paper conditioned with the odour of *B. germanica* nymphs; (4) a paper conditioned with cuticular hydrocarbons of *B. germanica* nymphs; (5) a flux of volatile odour from *B. germanica* nymphs; (6) nine *S. pallens* nymphs; (7) nine *S. gregaria* nymphs; (8) a nonrotating feather; (9) a rotating feather. Each experimental condition was replicated 50 times. Thermal gain in the experimental boxes is given as mean $\pm$ SE (°C) for each condition. Different letters (a, b, c, d) above bars indicate significant differences between nymphal developmental durations (Z tests).

subsequent to aggregation. Izutsu et al. (1970), using much higher CHC doses than ours (cuticular extracts of 20 males), were not able to induce group effects. Consequently, a different type of social stimulus is required to explain group effects. For the first time, our results show that tactile stimuli are responsible for group effects in *B. germanica*. All types of tactile stimuli (presence of conspecifics, presence of individuals of other insect species or tactile stimuli of a rotating feather) increased developmental rates. This shows that tactile stimuli need not be specific and can be artificially mimicked. The fact that locusts stimulated developmental rates more efficiently than a group of conspecifics can be explained by their larger size and their frequent jumping movements that probably produce supranormal tactile stimuli. Even though nymphs of other insect species and feathers could have been contaminated with CHCs of a test *B. germanica* nymph during our experiments, this CHC dose was much lower than the one we tested in condition 4 and consequently could not play a part in triggering the physiological response. Therefore, we assume that tactile stimuli are the only stimuli involved in the observed developmental group effect in conditions 6, 7 and 9. The implication of the tactile channel as the main sensory channel responsible for group effects has been suggested in aphids (Johnson 1965; Lees 1967; Sutherland 1969) and lepidopterans (Drooz 1966; Kazimirova 1992; Gunn 1998) and tactile stimulation of the outer face of the hind femur of *S. gregaria* is sufficient to induce behavioural gregarization (Roessingh et al. 1998; Hägele & Simpson 2000; Simpson et al. 2001; Rogers et al. 2003). As this growing evidence suggests, the influence of tactile stimuli in insect group effects has probably been underestimated.

Our results for *B. germanica* do not allow us to establish whether tactile stimuli act directly on the physiology of individuals or whether they induce levels of restlessness that could increase whole animal metabolic rate (Stephenson et al. 2007). The question of how tactile stimuli trigger the increase in metabolic rate is thus still not completely understood. In *B. germanica*, social isolation is thought to lead to the brain inhibiting the corpora allata (Gadot et al. 1989; Holbrook et al. 2000). Tactile stimuli would thus have a disinhibitory effect on the corpora allata, enhancing juvenile hormone production and thereby an increase in developmental rate. The next step would be to map the tactile receptors able to trigger the physiological chain. Ishii (1971) suggested that antennae were involved in the perception of other individuals, and that the bristles on the antennae act as mechanoreceptors. The tactile receptors on the outer surfaces of the femur and tibia could also be good candidates to transmit information about the presence of conspecifics in resting cockroach aggregations, as in *S. gregaria* (Simpson et al. 2001; Rogers et al. 2003). Although cockroaches maintain a specific interindividual distance (Boyer & Rivault 2004), small modifications in position may lead to resting neighbours touching their outer leg surfaces, which are well positioned to indicate the presence of conspecifics.

To conclude, our data show that tactile stimuli perceived through contact with conspecifics are the main stimuli responsible for group effects in cockroach species that live in social aggregations. Chemical stimuli (CHCs) induce formation of aggregates and then tactile stimuli trigger acceleration of developmental rates of group members. Studying tactile communication and its implication in group effects should offer a fruitful line of research for a better understanding of gregariousness and sociality in insects (Costa 2006).

References

Bell, W. J. & Adiyodi, K. G. 1982. *The American Cockroach*. London: Chapman & Hall.

Boyer, S. & Rivault, C. 2004. Interspecific competition among urban cockroach species. *Entomologia Experimentalis et Applicata*, **113**, 15–23.

Bradley, J. T. 1985. Interactions between social factors and ovarian development in the European house cricket *Acheta domesticus*. *Entomologia Experimentalis et Applicata*, **38**, 249–254.

Chauvin, R. 1946. Notes sur la physiologie comparée des Orthoptères. V. L'effet de groupe et la croissance larvaire des blattes, des grillons et du Phanéroptère. *Bulletin de la Société Zoologique de France*, **71**, 39–48.

Clark, B. & Faeth, S. H. 1997. The consequences of larval aggregation in the butterfly *Chlosyne lacinia*. *Ecological Entomology*, **22**, 408–415.

Costa, J. T. 2006. *The Other Insect Societies*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.

Drooz, A. T. 1966. Color studies of reared elm spanworm larvae and pupae. *Annals of the Entomological Society of America*, **59**, 568–573.

Gadot, M., Burns, E. & Schal, C. 1989. Juvenile hormone biosynthesis and oocyte development in adult female *Blattella germanica*: effects of grouping and mating. *Archives of Insect Biochemistry and Physiology*, **11**, 189–200.

Grassé, P. P. 1946. Sociétés animales et effet de groupe. *Experientia*, **2**, 77–82.

Gunn, A. 1998. The determination of larval phase coloration in the African armyworm, *Spodoptera exempta* and its consequences for thermoregulation and protection from UV light. *Entomologia Experimentalis et Applicata*, **86**, 125–133.

Hägele, B. F. & Simpson, S. J. 2000. The influence of mechanical, visual and contact chemical stimulation on the behavioural phase state of solitarious desert locusts (*Schistocerca gregaria*). *Journal of Insect Physiology*, **46**, 1295–1301.

Harlow, H. F. 1965. Total social isolation: effects on macaque monkey behavior. *Science*, **148**, 666.

Highnam, G. L. & Haskell, P. T. 1964. The endocrine systems of isolated and crowded *Locusta* and *Schistocerca* in relation to oöcyte growth, and the effects of flying upon maturation. *Journal of Insect Physiology*, **10**, 849–864.

Holbrook, G. L., Armstrong, E., Bachmann, J. A. S., Deasy, B. M. & Schal, C. 2000. Role of feeding in the reproductive 'group effect' in females of the German cockroach *Blattella germanica* (L.). *Journal of Insect Physiology*, **46**, 941–949.

House, J. S. 2001. Social isolation kills, but how and why? *Psychosomatic Medicine*, **63**, 273–274.

Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

Ishii, S. 1971. Structure and function of the antenna of the German cockroach *Blattella germanica* L. (Orthoptera; Blattellidae). *Applied Entomology and Zoology*, **6**, 192–197.

Ishii, S. & Kuwahara, Y. 1967. An aggregation pheromone of the German cockroach *Blattella germanica* (Orthoptera: Blattellidae): 1. Site of the pheromone production. *Applied Entomology and Zoology*, **2**, 203–217.

Iwanaga, K. & Tojo, S. 1986. Effects of juvenile hormone and rearing density on wing dimorphism and oöcyte development in the brown planthopper, *Nilaparvata lugens*. *Journal of Insect Physiology*, **32**, 585–590.

Izutsu, M., Ueda, S. & Ishii, S. 1970. Aggregation effects on the growth of the German cockroach *Blattella germanica* (L.) (Blattaria: Blattellidae). *Applied Entomology and Zoology*, **5**, 159–171.

Johnson, B. 1965. Wing polymorphism in aphids. II: Interaction between aphids. *Entomologia Experimentalis et Applicata*, **8**, 49–64.

Kazimirova, M. 1992. The role of physical contact in the induction of phase polymorphism of *Mamestra brassicae* (Lepidoptera: Noctuidae). *Acta Entomologica Bohemoslovaca*, **89**, 87–95.

Krause, J. & Ruxton, G. 2002. *Living in Groups*. Oxford: Oxford University Press.

Kunkel, J. G. 1981. A minimal model of metamorphosis: fat body competence to respond to juvenile hormone. In: *Current Topics in Insect Endocrinology and Nutrition* (Ed. by G. Bhaskaran, S. Friedman & G. J. Rodriguez), pp. 107–129. New York: Plenum.

Lees, A. D. 1967. The production of the apterous and alate forms in the aphid *Megoura viciae* Buckton, with special reference to the role of crowding. *Journal of Insect Physiology*, **13**, 289–318.

Lefeuvre, J. C. 1966. Sur une espèce nouvelle du genre *Gromphadorhina* (Dictyoptère, Perisphaerinae). *Annales de la Société Entomologique de France*, **2**, 1–16.

Leoncini, I. & Rivault, C. 2005. Could species segregation be a consequence of aggregation processes? Example of *Periplaneta americana* (L.) and *P. fuliginosa* (Serville). *Ethology*, **111**, 527–540.

Long, D. B. 1953. Effects of population density on larvae of Lepidoptera. *Transactions of the Royal Entomological Society of London*, **104**, 543–585.

McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models*. London: Chapman & Hall.

Nakai, Y. & Tsubaki, Y. 1986. Factors accelerating the development of German cockroach *Blattella germanica* nymphs reared in groups. *Japanese Journal of Applied Entomology and Zoology*, **30**, 1–6.

Parrish, J. K. & Hamner, W. M. 1997. *Animal Groups in Three Dimensions*. Cambridge: Cambridge University Press.

Parrish, J. K., Hamner, W. M. & Prewitt, C. T. 1997. Introduction: from individuals to aggregations: unifying properties, global framework, and the holy grails of congregation. In: *Animal Groups in Three Dimensions* (Ed. by J. K. Parrish & W. M. Hamner), pp. 1–14. Cambridge: Cambridge University Press.

Perellóa, M., Chaconb, F., Cardinalic, D. P., Esquifinob, A. I. & Spinedi, E. 2006. Effect of social isolation on 24-h pattern of stress hormones and leptin in rats. *Life Sciences*, **78**, 1857–1862.

Rivault, C. & Cloarec, A. 1998. Cockroach aggregation: discrimination between strain odours in *Blattella germanica*. *Animal Behaviour*, **55**, 177–184.

Rivault, C., Cloarec, A. & Sreng, L. 1998. Cuticular extracts inducing aggregation in the German cockroach, *Blattella germanica* (L.). *Journal of Insect Physiology*, **44**, 909–918.

Roessingh, P., Bouaïchi, A. & Simpson, S. J. 1998. Effects of sensory stimuli on the behavioural phase state of the desert locust, *Schistocerca gregaria*. *Journal of Insect Physiology*, **44**, 883–893.

Rogers, S. M., Matheson, T., Despland, E., Dodgson, T., Burrows, M. & Simpson, S. J. 2003. Mechanosensory-induced behavioural gregarization in the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology*, **206**, 3991–4002.

Roth, L. & Willis, E. R. 1960. The biotic associations of cockroaches. *Smithsonian Miscellaneous Collections*, **141**, 1–470.

Rust, M. K., Owens, J. M. & Reierson, D. A. 1995. *Understanding and Controlling the German Cockroach*. Oxford: Oxford University Press.

Simpson, S. J., Despland, E., Hägele, B. F. & Dodgson, T. 2001. Gregarious behavior in desert locusts is evoked by touching their back legs. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 3895–3897.

Slone, D. H. & Gruner, S. V. 2007. Thermoregulation in larval aggregations of carrion-feeding blow flies (Diptera: Calliphoridae). *Journal of Medical Entomology*, **44**, 516–523.

Stephenson, R., Chu, K. M. & Lee, J. 2007. Prolonged deprivation of sleep-like rest raises metabolic rate in the Pacific beetle cockroach *Diploptera punctata*. *Journal of Experimental Biology*, **210**, 2540–2547.

Sutherland, O. R. W. 1969. The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. *Journal of Insect Physiology*, **15**, 1385–1410.

Tschinkel, W. R. & Wilson, C. D. 1971. Inhibition of pupation due to crowding in some tenebrionid beetles. *Journal of Experimental Zoology*, **176**, 137–146.

Weaver, D. K. & McFarlane, J. E. 1990. The effect of larval density on growth and development of *Tenebrio molitor*. *Journal of Insect Physiology*, **36**, 531–536.

Wharton, D. R. A., Lola, J. E. & Wharton, M. L. 1967. Population density, survival, growth, and development of the American cockroach *Periplaneta americana*. *Journal of Insect Physiology*, **13**, 699–716.

Wharton, D. R. A., Lola, J. E. & Wharton, M. L. 1968. Growth factors and population density in the American cockroach *Periplaneta americana*. *Journal of Insect Physiology*, **14**, 637–653.

Wilson, E. O. 1971. *The Insect Societies*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.

Woodhead, A. P. & Paulson, C. R. 1983. Larval development of *Diploptera punctata* reared alone and in groups. *Journal of Insect Physiology*, **29**, 665–668.

Zeigler, H. P. & Marler, P. 2004. *Behavioral Neurobiology of Birdsong*. New York: New York Academy of Sciences.