



Rapid report

The weight of the clan: Even in insects, social isolation can induce a behavioural syndrome

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ABSTRACT

Social isolation has dramatic consequences on the development of individuals of many vertebrate species, and it induces a set of behavioural disturbances rendering them unable to process environmental as well as social stimuli appropriately. We hypothesized that isolation syndrome is a ubiquitous trait of social life that can be observed in a wide array of species, including invertebrates. Here we report that gregarious cockroaches (*Blattella germanica*) reared in isolation showed (i) stronger exploration-avoidance, (ii) reduced foraging activity, (iii) reduced willingness to interact socially, and (iv) reduced ability to assess mating partner quality than conspecifics reared in groups. We demonstrate the occurrence of a behavioural syndrome induced by social isolation, similar to syndromes described in vertebrates, revealing the importance of social interactions and group-living in this non-eusocial insect species. We suggest that investigating social isolation effects on individual development should provide interesting results to assess social cohesion of species and thus constitute an additional tool for comparative studies focusing on the evolution of social life.

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1. Introduction

Group-living, from loose aggregates to sophisticated eusocial colonies, is widespread and provides individuals fitness benefits (Krause and Ruxton, 2002). A wealth of information shows that social interactions have such a potent influence on individuals that isolation rearing induces dramatic consequences on the physiology and behaviour of many species (e.g. Harlow, 1965; Fuller, 1967; Nottebohm, 1970). Until now, studies investigating these isolation effects have focused mainly on social vertebrates (including humans) that present a variety of long-lasting behavioural impairments making them unable to process environmental and social stimuli appropriately. In particular, disturbances in exploratory, feeding, social and mating behaviours showed by rats lacking social interactions led to the formulation of an isolation syndrome, to describe anxiogenic, overly emotional individuals that reacted excessively to handling (Hall, 1998; Fone and Porkess, 2008).

Although these isolation syndromes have been described only in vertebrates, we predict that they could be ubiquitous traits characteristic of social life. In particular, the study of such inter-individual dependence could provide additional information to evaluate social cohesion of species and to characterize their sociality levels. While physiological impairments due to social deprivation have been

reported in many invertebrates for decades (Grassé, 1946; Wilson, 1971), behavioural disturbances have been studied only in eusocial insects and are still poorly documented (e.g. Champalbert and Lachaud, 1990; Cole, 1991; Boulay et al., 2000). Group-living cockroaches are good models to investigate these questions as rearing in isolation induces important developmental delays (Lihoreau and Rivault, 2008). Here, we investigated the influence of social isolation on the development of behavioural patterns in the cockroach *Blattella germanica* (L.), by testing the occurrence of behavioural disturbances in various contexts. We compared behavioural responses of cockroaches reared in total isolation to those of cockroaches reared in groups, in four different contexts: when (i) exploring, (ii) foraging, (iii) aggregating, and (iv) mating.

2. Materials and methods

Test individuals came from our laboratory *B. germanica* reference strain. They were reared in isolation (IR cockroaches) or in groups of 10 siblings (GR cockroaches) from hatching until being tested. They were tested either when in the middle of their sixth (last) nymphal instar (approximately 45 days old) or at the beginning of their adult life (approximately 65 days old). Behaviour of IR and GR individuals of the same developmental stage could be compared because social isolation does not induce differences in body size. To control for genetic differences, one IR individual and one of its GR siblings from each ootheca were tested in each experimental situation. As we used the same set-up in the different contexts,

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Table 1

Behaviour of nymphs reared in isolation (IR) and in groups (GR) tested in three contexts: exploration (bare arena), foraging (food on squares N–O) and aggregation (a group of conspecifics on squares N–O).

	Exploration			Foraging			Aggregation		
	GR	IR	<i>P</i>	GR	IR	<i>P</i>	GR	IR	<i>P</i>
Number of individuals leaving their shelter/number of replicates	27/30	16/30	0.003 ^a	27/32	27/32	1.000 ^a	26/32	29/32	0.285 ^a
Latency to leave their shelter	105.44 ± 31.52	233.18 ± 110.53	0.763 ^b	448.59 ± 125.03	339.56 ± 98.86	0.303 ^b	199.84 ± 71.71	191.03 ± 59.64	0.590 ^b
Exploration speed (s/squares)	3.46 ± 0.68	1.99 ± 0.49	0.020 ^b	4.34 ± 0.69	3.79 ± 0.63	0.559 ^b	2.97 ± 0.44	2.42 ± 0.45	0.161 ^b
Time spent near their shelter (%)	41.31 ± 1.47	51.69 ± 3.22	0.001 ^b	37.37 ± 4.96	62.62 ± 4.96	0.019 ^b	39.33 ± 3.11	50.38 ± 1.26	0.042 ^b
Number of individuals finding the resource/number of individuals leaving their shelter	–	–	–	27/27	27/27	1.000 ^a	26/26	29/29	1.000 ^a
Mean duration of a visit to the resource (s)	–	–	–	94.94 ± 12.77	49.08 ± 7.09	0.010 ^b	529.79 ± 103.50	340.75 ± 128.27	0.048 ^b
Total time at the resource (s)	–	–	–	637.08 ± 105.06	322.33 ± 55.48	0.048 ^b	661.30 ± 152.57	321.83 ± 112.61	0.018 ^b

Means are given with standard errors.

^a Chi square test of homogeneity.^b Wilcoxon test.

we tested each individual only once to avoid biases in exploration behaviour due to memory effects (Durier and Rivault, 2000). We investigated the behavioural traits of IR and GR individuals across large samples of individuals in each context.

In the exploration, foraging and aggregation contexts, IR and GR nymphs were tested individually in a square glass arena (680 mm × 680 mm). The floor was divided into 16 equal squares lettered from A to P and covered with a clean white paper renewed before each test (Table 1). Before a test, individuals were placed in a dark shelter (80 mm long × 30 mm large × 20 mm high) on the arena squares B–C. Tests lasted 45 min and started when the shelter was opened. The test arena (i) was bare in the exploration context, (ii) had a food source (bread) in the foraging context, and (iii) had a group of 15 conspecifics (enclosed in a box allowing antennal contacts and resting nearby) in the aggregation context. We recorded numbers of individuals leaving their shelter, latency to leave their shelter, their exploration speed, the time they spent near their shelter (in squares A, D, E–H), numbers of individuals that found the resource (food or conspecifics) and time spent near it.

In the mating context, IR and GR males were observed in pairs to test inter-male competition for one receptive virgin female. The three individuals were colour-marked and tested in plastic boxes (80 mm in diameter × 50 mm high). To control for genetic bias in mate choice, the males of a pair were siblings but not related to the female. Triads were observed with scan sampling at 30 min intervals from their formation until mating occurred (see Lihoreau et al., 2008). We recorded male assessment of female quality (latency before first antennal contact, numbers of antennal contacts), numbers of courting attempts and identity of the mating male. After mating, females were isolated to record the total number of viable nymphs they produced.

3. Results

In the exploration context, IR and GR nymphs left their shelter with similar latencies, but significantly less IR nymphs than GR nymphs left their shelter (Table 1). The overall activity level of IR nymphs that explored the arena was lower than that of GR nymphs, as they walked at significantly slower speeds. In addition, they stayed longer near their shelter whereas GR nymphs explored further away.

In the foraging context, although the presence of food improved IR nymphs' exploration activity, they still remained near their shelter (Table 1). Consequently, they spent significantly less time feeding than did GR nymphs, each of their feeding bouts being shorter.

In the aggregation context, exploration patterns of IR nymphs were similar to those observed in the foraging context (Table 1). They spent significantly less time in contact with conspecifics than did GR nymphs and each contact was also shorter.

In the mating context, IR males contacted females quicker and more often than did GR males (Table 2). However, females mated as often with both types of males. As previously demonstrated (Lihoreau et al., 2008), they preferred to mate with males that

performed the most vigorous courtships whatever their rearing condition (courting attempts: mated males 4.71 ± 0.61 , non-mated males 3.05 ± 0.40 , $W = 1316.5$, $P = 0.0417$). The total number of viable nymphs produced by females was significantly influenced by their lifespan, but not by the rearing conditions of their mates (ANCOVA, lifespan: $F_{1,54} = 68.94$, $P < 0.001$; rearing condition: $F_{1,54} = 1.62$, $P = 0.208$, lifespan × rearing condition: $F_{1,54} = 0.18$, $P = 0.669$).

4. Discussion

Cockroaches reared in isolation showed (i) stronger exploration-avoidance, (ii) reduced foraging activity, (iii) reduced willingness to interact socially and (iv) reduced ability to assess mating partner quality compared to group-reared cockroaches. The main consequence of social deprivation can be described as a global decrease in individual activity level. The higher tendency of cockroaches reared in isolation to stay in their shelter and to restrict exploration to near their shelter reveals risk aversion and neophobia. Their motivation to feed or to interact with conspecifics seems to be counterbalanced by their apprehension to leave the protection of their shelter. Our results thus reveal a strong social influence on the development of individual behavioural patterns and the importance of social cohesion in this species. The question remains of whether the changes in behaviour documented here are reversible or not. Although social isolation decreases the probability to find a mate by inducing developmental delays, reluctance to explore their environment and to interact with conspecifics, it does not affect reproductive capacities. The fact that isolated cockroaches survive and are still able to reproduce could be one of the reasons for the ecological success of this species.

Our results raise the question of the mechanisms involved in these behavioural changes and allow us to consider two non-mutually exclusive hypotheses. First, the general decrease of activity level could be a consequence of the decrease in metabolic and developmental rates described in individuals lacking social interactions in this species (Lihoreau and Rivault, 2008). Second, the fact that they seek conspecifics less might be due to a lack of learning social codes. Cockroaches assess the quality of their partners through antennal contacts before engaging in a behavioural interaction (Lihoreau and Rivault, 2009; Lihoreau et al., 2008). The fact that, after a first contact, individuals reared in isolation interrupted social contacts more rapidly than did group-reared individuals, means that they do not interpret positively the presence of conspecifics as group-reared cockroaches do when they decide to rest in aggregates (Amé et al., 2006). In addition, sexually stimulated males reared in isolation engaged antennal contacts quicker because they perceived a new olfactory stimulus, but required longer antennal contacts before initiating courtship, indicating their difficulties to recognize receptive females. In both cases their difficulties to analyse the species' communication code suggest the occurrence of a learning phase in contact with conspecifics during ontogeny.

Whatever the mechanisms involved in these isolation effects, the novelty of our study is that isolation can induce important

Table 2
Mating and reproductive success of males reared in isolation (IR) and in groups (GR).

	GR	IR	P
Latency before first antennal contact (min)	2711.54 ± 67.48	1305.71 ± 71.52	0.034 ^b
Number of antennal contacts	0.64 ± 0.12	1.60 ± 0.20	0.001 ^b
Number of courting attempts	3.88 ± 0.59	3.88 ± 0.45	0.526 ^b
Number of matings	24	34	0.121 ^a
Number of viable nymphs sired	132.92 ± 5.45	134.44 ± 6.23	0.619 ^b

Means are given with standard errors. Number of replicates: 58

^a Chi square test of homogeneity.

^b Wilcoxon test.

behavioural changes in non-eusocial invertebrates. The fact that changes are observed in several contexts suggests the occurrence of a behavioural syndrome (Sih et al., 2004) and allows us to draw parallels with isolation syndromes of social vertebrates. Comparative studies in rodents suggest that the effects of social deprivation are more pronounced in species living in closed social units than in species living in looser structures (Syme, 1973; Einon et al., 1981; Shapiro and Insel, 1990; Stowe et al., 2005). We assume that isolation syndrome is a ubiquitous trait of social species and that the importance of this syndrome reveals the strength of social cohesion. Therefore, social isolation effects could be an additional criterion to evaluate sociality level of species, as for example reproductive skew or the occurrence of cooperative tasks, and could be used in comparative studies (see discussions in; Costa and Fitzgerald, 2005; Crespi, 2005; Lacey and Sherman, 2005; Wcilslo, 2005). Considering the large diversity of group-living forms in arthropods, we suggest that investigating these effects, both at the physiological and the behavioural level, should bring interesting data to compare species and to study the arousal of sociality within invertebrates.

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