

# *The social biology of domiciliary cockroaches: colony structure, kin recognition and collective decisions*

**M. Lihoreau, J. T. Costa & C. Rivault**

## **Insectes Sociaux**

International Journal for the Study of  
Social Arthropods

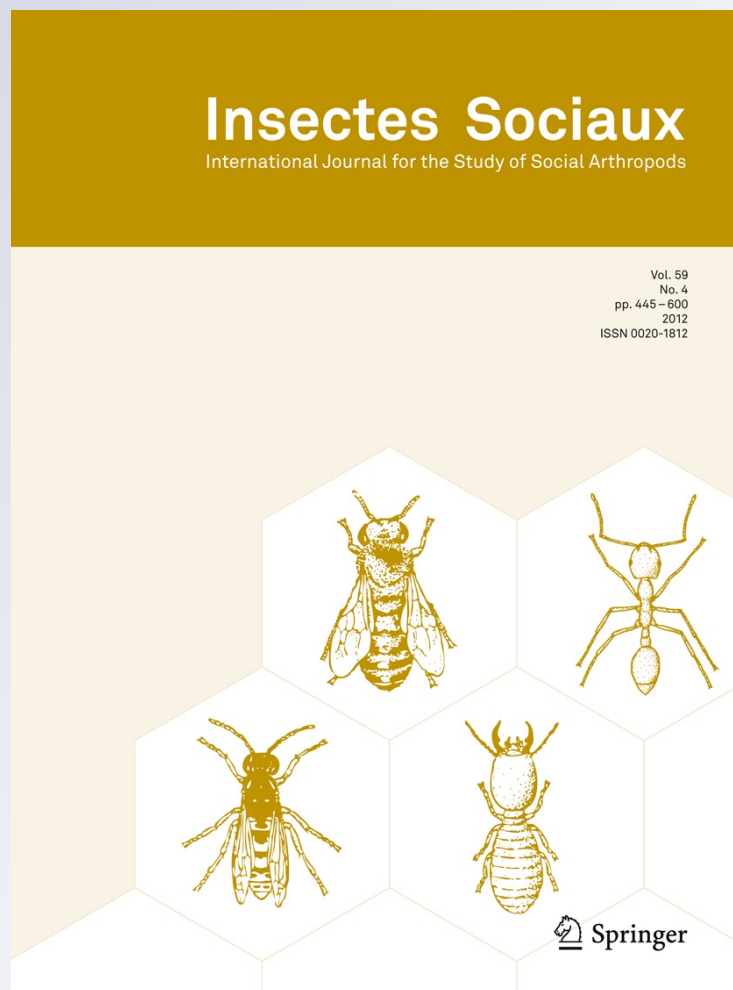
ISSN 0020-1812

Volume 59

Number 4

Insect. Soc. (2012) 59:445-452

DOI 10.1007/s00040-012-0234-x



**Your article is protected by copyright and all rights are held exclusively by International Union for the Study of Social Insects (IUSI). This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

# The social biology of domiciliary cockroaches: colony structure, kin recognition and collective decisions

M. Lihoreau · J. T. Costa · C. Rivault

Received: 3 December 2011 / Revised: 24 March 2012 / Accepted: 27 March 2012 / Published online: 8 April 2012  
© International Union for the Study of Social Insects (IUSI) 2012

**Abstract** A substantial body of research on eusocial insects seen in the last decades has gone hand-in-hand with the development of social evolution theory. In contrast, little attention has been given to the non-eusocial insect species that nevertheless exhibit a rich spectrum of social behaviours, thus effectively skewing our vision of insect sociality. Recent studies on the behaviour, ecology and genetic of “gregarious” cockroaches (Blattodea) have revealed a diversity of social structures and group dynamics unique among insects, providing an important comparative model for the broader understanding of insect social evolution. Here, we present an overview of the social biology of the domiciliary cockroaches (ca. 25 species adapted to human habitats) based on research on two model species, *Blattella germanica* and *Periplaneta americana*. We discuss the evolution of these domiciliary cockroaches, considering them in the context of “social herds” within the insect sociality framework.

**Keywords** Domiciliary cockroaches · Isolation syndromes · Kin recognition · Collective decisions · Social insects · Pathway pluralism

## Introduction

Since the formalisation of inclusive fitness theory (Haldane, 1955; Hamilton, 1964), substantial research on eusocial ants, bees, wasps and termites has improved our understanding of insect sociobiology (Gadau and Fewell, 2009), emphasising the importance of genetic factors (relatedness) in the evolution of advanced animal societies (Bourke, 2011). However, despite the strong ecological success they exemplify, eusocial insects represent only a limited fraction of the insect species where sociality occurs (sensu Wilson, 1971; Costa and Fitzgerald, 1996). Many insect species do not meet the three criteria defining eusociality (i.e. reproductive division of labour, overlapping generations, cooperative care of young) but nevertheless live in groups, interact and exhibit various levels of cooperation (Costa, 2006). Broadening the scope of insect sociobiology to include these simpler social forms is an important step to characterising the diversity of insect social behaviour and clarifies the relative contribution of genetic and ecological factors in their evolution (Eickwort, 1981; Tallamy and Wood, 1986; Choe and Crespi, 1997; Costa, 2006).

In recent years, cockroaches have emerged as a group of fundamental interest for the study of insect social evolution due to their phylogenetic proximity to eusocial termites within the Blattodea (Inward et al., 2007; Davis et al., 2009; Roth et al., 2009). Many of the ca. 4,000 described cockroach species were initially described as “gregarious” based on their tendency to live in groups at various stages of their developmental cycle (Roth and Willis, 1960; Bell et al.,

---

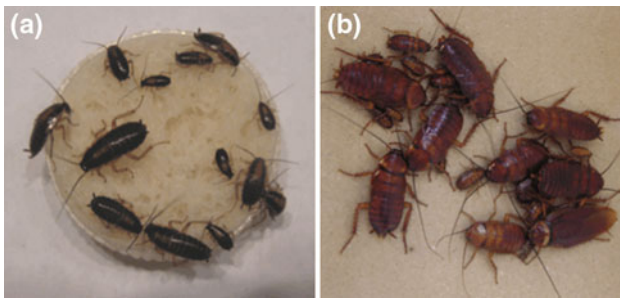
M. Lihoreau · C. Rivault  
Unité Mixte de Recherche 6552, Centre National  
de la Recherche Scientifique, Université de Rennes 1,  
Campus de Beaulieu, 35042 Rennes, France

*Present Address:*

M. Lihoreau (✉)  
School of Biological Sciences and the Charles Perkins Centre,  
The University of Sydney, Heydon-Laurence Building, Sydney,  
NSW 2006, Australia  
e-mail: mathieu.lihoreau@sydney.edu.au

J. T. Costa  
Department of Biology, Western Carolina University,  
Cullowhee, NC 28723, USA

J. T. Costa  
Highlands Biological Station, Highlands, NC 28741, USA



**Fig. 1** **a** Feeding aggregate of German cockroaches (*Blattella germanica*). Nymphs of various developmental stages feed collectively on a piece of bread. **b** Resting aggregate of American cockroaches (*Periplaneta americana*). Adults and nymphs at various developmental stages rest in group inside a cardboard shelter. Photographs by ML

2007). However, the structure, organisation, and functioning of these cockroach aggregates remain poorly characterised. While cockroaches are intensively studied in the fields of molecular biology, physiology and neurosciences, their social biology has received little attention (Web of Science search 25/11/2011: of 9,466 references containing the word “cockroach” in their title or abstract, 291 (3 %) were behavioural or ecological studies, and 187 (2 %) contained the word ‘social’).

Growing interest in the domiciliary cockroach species, which include ca. 25 Blattellidae, Blattidae and Blaberidae species that have adapted to human habitats (see Cornwell, 1968), has revealed surprisingly complex social organisations, communication systems and group dynamics. Here, we present an overview of the social biology of these domiciliary cockroaches based largely on studies of *Blattella germanica* (Fig. 1a) and *Periplaneta americana* (Fig. 1b), two model species exemplifying the unique “herding” social structure found in cockroaches. We then consider these societies in the broader framework of insect sociality and discuss the ecological constraints that may have favoured their evolution.

### Social structure

All domiciliary cockroach species have been described as gregarious (Roth and Willis, 1960; Cornwell, 1968). These cockroaches rest in groups during the light phase of the photocycle in dark shelters (e.g. pipes, cracks or crevices) and forage at night in search of food and water. In *B. germanica* and *Periplaneta* species, resting aggregates are composed of adults and nymphs at all developmental stages with a balanced sex ratio (Bell and Adiyodi, 1982; Appel and Smith, 1996; Ross and Mullins, 1995). Once established, groups remain faithful to their shelter as long as individuals can exploit enough resources in their surroundings to grow and reproduce

(Bell and Adiyodi, 1982; Rivault, 1989). Group size thus increases exponentially and can vary from as few as a dozen to millions of individuals depending on the holding capacity of the shelter (Ross et al., 1984; Appel and Rust, 1985).

The organisation of cockroach aggregates has been best characterised in *B. germanica* (Rust et al., 1995). In this species, there is no long-term social structure such as dominance hierarchies or a division of labour. Agonistic interactions are frequent but seem to be directed indiscriminately towards all group members (Breed et al., 1975; Olomon et al., 1976; Rivault and Cloarec, 1992). In addition, every individual can potentially reproduce (Lihoreau and Rivault, 2010). *B. germanica* females mate once in their lifetime and invest in the production of several successive oothecae (i.e. egg clutches), which they carry for extended periods prior to hatching. In contrast, *B. germanica* males can mate up to 20 times and do not provide parental care. Such asymmetry in the parental investment by sexes generates a male-biased operational sex ratio (i.e. the ratio of males to females available for mating) resulting in males competing for virgin females based on the vigour of their courtship display (Lihoreau and Rivault, 2010).

### Genetic structure

Resting aggregates are open and fluid entities in which genetically diverse individuals can transit without eliciting aggression or rejection from the residents (Ross et al., 1981; Amé et al., 2004; Sempo et al., 2009). In urban habitats such as buildings or sewers, aggregates form networks (or metapopulations) within which individuals disperse at multiple spatial scales. Data describing the genetic structure of cockroach populations are limited and have long been based on low-resolution mark-recapture techniques (Owens and Bennett, 1982; Appel and Rust, 1985; Rivault, 1990; Tee et al., 2011). However, recent usage of microsatellite markers in *B. germanica* has revealed a clear pattern of genetic differentiation by distance based on active dispersal of individuals and isolation (Crissman et al., 2010). In this species, populations usually develop at the scale of a human dwelling from a single colonising aggregate that gradually expands. Over time, new aggregates establish in different locations (e.g. adjacent rooms and apartments) through the dispersal, settlement and reproduction of only few individuals. These small founding populations are susceptible to genetic bottlenecks and may diverge from spatially distant aggregates through genetic drift (Crissman et al., 2010). At larger spatial scales, however, in the absence of contiguous suitable habitat through which active dispersal can occur between buildings, genetic differentiation is mainly driven by human-mediated transport and is less predictable (Booth et al., 2011). Because the rates of

local population growth exceed migration fluxes at all spatial scales, members of an aggregate are expected to share relatively high relatedness levels (Cloarec et al., 1999; Crissman et al., 2010). However, future analyses at the scale of the aggregate will be critical to clarify such genetic structure.

### Isolation syndromes

The social context is a key to the development and reproduction of domiciliary cockroaches. It has long been established that cockroaches maintained in social isolation for several days exhibit important developmental disorders known as 'isolation syndromes' (Chauvin, 1946; Roth and Willis, 1960; Lihoreau et al., 2009). Detailed studies of isolation syndromes in *Blattella*, *Periplaneta* and *Symptoe* species suggest that all domiciliary species suffer from isolation, thus highlighting the strong dependence of these cockroaches on a group-living lifestyle throughout their life.

In *B. germanica* and *P. americana*, social isolation delays the imaginal moult in nymphs and sexual maturation in adults (Holbrook et al., 2000; Lihoreau and Rivault, 2008). In *B. germanica*, isolation also impacts behaviour through a reduction of exploration and foraging activities (Lihoreau et al., 2009). Social interactions such as courting behaviour and aggregation are also profoundly affected, suggesting that the lack of social contacts during early development precludes the learning of cues essential for the assessment of mate quality and social recognition (Lihoreau et al., 2009). Although isolation-reared cockroaches can survive out of any social context and complete their entire physiological development, costs incurred by physiological and behavioural changes might seriously handicap their competitiveness against group-reared conspecifics for foraging and reproductive opportunities.

Isolation experiments in *B. germanica* and *P. americana* have demonstrated that the mechanisms responsible for these isolation syndromes are multiple. A primary factor affecting nymphal development is the frequency with which individuals interact physically with each other in resting aggregates. Hence, isolated nymphs provided with regular tactile stimulation grow faster than conspecifics entirely deprived of contacts (Lihoreau and Rivault, 2008). Although the precise nature of these tactile cues has not yet been identified, physical stimulation is non-specific and can be provided by other insects (e.g. locusts) or even applied artificially (e.g. with a feather) (Lihoreau and Rivault, 2008). Physical contact may therefore affect the activity of the corpora allata and control the production of juvenile hormone responsible for nymphal development and sexual maturation (Gadot et al., 1989; Holbrook et al., 2000). Neither olfactory nor visual communication is involved (Izutsu et al., 1970; Nakai and Tsubaki, 1986).

Another important socially mediated factor responsible for isolation syndromes is the effect of grouping on the shelter's microclimatic conditions. For instance, the metabolic heat produced by an aggregate of *B. germanica* cockroaches can increase the ambient temperature by up to 0.6 °C for large colony densities (2 individuals/cm<sup>3</sup>), which, in turn, stimulates nymphal development (Lihoreau and Rivault, 2008). Aggregated cockroaches also modulate ambient hygrometry by adjusting their inter-individual distances in response to decreased relative humidity, thus minimising water loss by evaporation (Dambach and Goehlen, 1999). The amplitude of these 'group effects' (sensu Grassé, 1946) is independent of group composition and increases with the density of individuals.

### Chemical ecology

Many cockroach species use chemical signals such as volatile sex pheromones to attract potential mating partners (Okada et al., 1990; Charlton et al., 1993; Nojima et al., 2005) or alarm pheromones to trigger group dispersion when a predator attacks (Nakayama et al., 1984; Ross and Tignor, 1986; Faulde et al., 1990; Farine et al., 1997). Growing evidence shows that domiciliary cockroach species also rely extensively on inadvertent social information (sensu Danchin et al., 2004), using cuticular hydrocarbons secreted on the body surface or deposited on the substrate.

In *B. germanica* and *Periplaneta* species, cuticular hydrocarbons operate as short-range cues mediating aggregation and the selection of new shelters (Rivault et al., 1998; Saïd et al., 2005a; Sempo et al., 2006). Cockroaches given a choice between a shelter free of chemical marking and a shelter scented with cuticular hydrocarbons join and settle under the scented shelter (Amé et al., 2004; Saïd et al., 2005a; Sempo et al., 2006). These cuticular hydrocarbons are low-volatility compounds with a high molecular weight, and are therefore perceived at very short distances through antennal contacts between conspecifics (Saïd et al., 2005b; Lihoreau and Rivault, 2009). However, when a shelter has long been occupied by a group, cockroaches can relocate their aggregate by following cuticular hydrocarbon marks passively deposited on the substrate by tarsal contact or in accumulated faecal extracts (Miller and Koehler, 2000; Jeanson and Deneubourg, 2006).

Cockroach cuticular hydrocarbon profiles consist of a fixed number of compounds (e.g. *Blattella* sp.: Jurenka et al., 1989; Carlson and Brenner, 1988; Rivault et al., 1998; *Periplaneta* sp.: Jackson, 1972; Saïd et al., 2005a; *Blatta* sp.: Lockey and Dularay, 1986). However, their relative abundance varies significantly among individuals of the same population, thus providing potential cues for intra-specific discrimination. In *B. germanica*, individual profiles



co-vary with genetic relatedness (Lihoreau and Rivault, 2009). These quantitative chemical variations are used for kin recognition, enabling cockroaches to discriminate full-siblings from less closely related group members (Lihoreau et al., 2007), or from conspecifics of different populations (Rivault and Cloarec, 1998) in binary choice experiments. Individual profiles are stable over time and are not affected by long periods of contact with unrelated conspecifics (Lihoreau and Rivault, 2009). This chemical signature thus constitutes a reliable source of information for discrimination of relatives from different kin classes in genetically diverse groups, where individuals regularly interact with familiar group members that do not necessarily share high levels of relatedness.

Kin recognition in *B. germanica* shapes an important part of the social life within resting aggregates, allowing cockroaches to adjust their behaviour towards other group members in relation to the context. In a sexual context, individuals avoid mating with their siblings, thus minimising fitness costs associated with inbreeding depression (Lihoreau et al., 2008; Lihoreau and Rivault, 2010). Conversely, in a social context nymphs and adults preferentially interact with close kin, which may lead to a subgroup structure of kin classes in large resting aggregates (Lihoreau and Rivault, 2009). Whether these kin associations provide indirect fitness benefits to individuals through kin selection has not yet been determined.

### Collective decisions

Domiciliary cockroaches are not only faithful to the shelter in which they rest and mate but also commonly engage in collective behaviour to localise and exploit resources in their home range. As observed in ants or honeybees, cockroaches make consensus decisions (sensu Conradt and Roper, 2005) whereby all or most individuals choose the same option among multiple alternatives when selecting shelters (Fig. 1b) or feeding sites (Fig. 1a).

In *B. germanica* and *P. americana*, consensus decisions occur during the selection of a new shelter—for instance, if the previous shelter is overcrowded or if food resources are locally depleted. An individual's decision to settle in a new place depends on the shelter's physical properties, such as darkness, size, height, temperature, or hygrometry (Canonge et al., 2009), as well as on the presence of conspecifics already resting in it (Amé et al., 2006; Canonge et al., 2011). Hence, groups of cockroaches given a choice between two or more identical shelters in a homogenous environment aggregate in one of the shelters selected at random (Jeanson et al., 2005). In both species, aggregation dynamics are driven by mutual inter-attraction mediated by short-range perception of cuticular hydrocarbons (Rivault

et al., 1998; Saïd et al., 2005a; Sempo et al., 2006) and can be replicated in agent-based models implementing simple interactions between individuals (Jeanson et al., 2005; Amé et al., 2006; Jeanson and Deneubourg, 2007; Sempo et al., 2009). When an exploring cockroach perceives an occupied shelter, it switches from a search mode to joining and settling. The larger the group in this shelter, the higher the probability that the newcomer will join and stay. Based on this “retention effect” resting individuals exert on newcomers, an aggregate gradually develops, eventually leading to the selection of a unique shelter by the entire group.

Consensus decisions also occur in *B. germanica* during the selection of feeding sites (Lihoreau et al., 2010). As with shelter choice, an individual's decision to exploit a food source depends on its inherent properties, such as its nutritional value (Jones and Raubenheimer, 2001) or its distance from the shelter (Durier and Rivault, 2001), but also in the presence of conspecifics already feeding on it (Lihoreau et al., 2010; Lihoreau and Rivault, 2011). Aggregation at food sources is based on a social facilitation process for feeding (Holbrook et al., 2000), so that cockroaches in large groups feed longer than those in small groups (Lihoreau et al., 2010). Socially foraging cockroaches feed on site but do not collect or retrieve food for other members of the group. Feeding aggregates are therefore transient phenomena that rapidly develop and erode as individuals become satiated (Lihoreau et al., 2010).

Interestingly, collective decisions in both contexts are self-organised phenomena relying on a similar positive feedback rule (i.e. retention effect) and potentially similar contact cues (i.e. cuticular hydrocarbons). These collective dynamics are density dependent and a decision is taken only when a critical size (i.e. quorum) is reached (Sempo et al., 2009; Lihoreau et al., 2010). Such behaviour yield mutual benefits to all group members and can be seen as emergent forms of cooperation (sensu West et al., 2007). First, aggregation processes tend to synchronise the resting and feeding activities of individuals. Such behavioural synchronisation maintains group cohesion over time and provides cockroaches with the various benefits of group effects (e.g. thermal gain, stable hygrometry, and/or reduced predation risks) as mentioned in earlier sections. Second, social information transfer allows grouped cockroaches to make faster and more accurate decisions than isolated conspecifics (Halloy et al., 2007; Canonge et al., 2011), an emergent property of swarm intelligence (Sumpter and Pratt, 2009).

### Domiciliary cockroaches as “social herds”

During the last decade, Blattodea has emerged as a key group for the study of insect social evolution, offering a considerable range of social lifestyles. Among the best-

studied social species are the eusocial termites (Bignell et al., 2010) and the subsocial wood roaches of the families Cryptocercidae and Blaberidae (Nalepa, 1984; Nalepa and Bell, 1997; Maekawa et al., 2008). As illustrated throughout this review, the domiciliary “gregarious” species (families Blattellidae, Blattidae and Blaberidae) present yet another form of sociality where individuals of all developmental stages and from various genetic lineages co-exist in open and more or less fluid (yet integrated) aggregates. Based on data from two model species (*B. germanica* and *P. americana*), the social biology of domiciliary cockroaches so far can be characterised by a common shelter, overlapping generations, non-closure of groups, equal reproductive potential of group members, an absence of task specialisation, high levels of social dependence, central place foraging, social information

transfer, kin recognition, and a meta-population structure (see Table 1 and references therein).

Accordingly, domiciliary cockroaches are much more than merely gregarious as previously assumed (Roth and Willis, 1960; Cornwell, 1968), but constitute social species in a broad sense (sensu Wilson, 1971; Costa and Fitzgerald, 1996) characterised by sophisticated communication and emergent forms of cooperation. The social system we describe here fits the definition of “mixed-family herds” applied by Costa (2006) to describe societies of caterpillars, sawflies, beetles, treehoppers, lubber grasshoppers, barklice, thrips, and others. As with larval societies of Lepidoptera or Coleoptera, these “herding” cockroach species form cohorts of individuals that arise from communal oviposition and/or the merging of initially discrete family groups (Costa, 2006). Group size is

**Table 1** Key references illustrating the main characteristics of the social biology of domiciliary cockroaches

Characteristics	Supporting arguments	Species	Key references
Common shelter with overlapping generations	Individuals show a high fidelity to their group	<i>Blattella germanica</i>	Rivault, 1990
		<i>Periplaneta fuliginosa</i> ; <i>Periplaneta americana</i>	Appel and Rust, 1985; Appel and Smith, 1996
Non-closure of group	Individuals from different strains aggregate in a common shelter	<i>Blattella germanica</i>	Amé et al., 2004
Meta-population structure	Genetic differentiation by distance	<i>Blattella germanica</i>	Crissman et al., 2010; Booth et al., 2011
Totipotency of individuals	All group members can become breeders	<i>Blattella germanica</i>	Lihoreau and Rivault, 2010
	Absence of a stable dominance hierarchy	<i>Blattella germanica</i> <i>Periplaneta americana</i>	Breed et al., 1975; Rivault and Cloarec, 1992 Olomon et al., 1976
Isolation syndromes	Social isolation delays imaginal moult	<i>Blattella germanica</i> ; <i>Symploce pallens</i> <i>Blatta orientalis</i> ; <i>Eurycotis floridana</i> ; <i>Gromphadorhina portentosa</i> ; <i>Periplaneta americana</i> ; <i>Periplaneta australasiae</i> ; <i>Periplaneta brunnea</i> ; <i>Periplaneta fuliginosa</i> ; <i>Suppella longipalpa</i>	Izutsu et al., 1970; Nakaï and Tsubaki, 1986; Lihoreau et al., 2008 Roth and Willis, 1960
	Social isolation delays sexual maturation	<i>Blattella germanica</i>	Gadot et al., 1989; Holbrook et al., 2000
	Social isolation induces behavioural disorders	<i>Blattella germanica</i>	Lihoreau et al., 2009
Central place foraging	Exploitation of resources in proximity to the resting site	<i>Blattella germanica</i>	Durier and Rivault, 2001
Information transfer and collective decisions	Collective selection of a shelter	<i>Blattella germanica</i>	Amé et al., 2004; Jeanson et al., 2004; Amé et al., 2006; Jeanson and Deneubourg, 2007
		<i>Periplaneta americana</i>	Sempo et al., 2009; Canonge et al., 2011
	Collective selection of feeding sites	<i>Blattella germanica</i>	Lihoreau et al., 2010; Lihoreau and Rivault, 2011
Kin recognition	Inbreeding avoidance during mate choice	<i>Blattella germanica</i>	Lihoreau and Rivault, 2008; Lihoreau and Rivault, 2010
	Kin associations in resting aggregates	<i>Blattella germanica</i>	Lihoreau and Rivault, 2009

primarily determined by the spatio-temporal distribution of resources in the environment, including shelter number and capacity, and nutritional resources. However, whether social herds observed in *B. germanica* and *P. americana* represent an ancestral trait to cockroaches or is a convergent adaptation unique to domiciliary species critical to colonising and surviving in human habitats is difficult to determine given the limited knowledge about the social biology of non-domiciliary cockroach species. This question constitutes an exciting line of research for future comparative studies among Blattodea species, essential in order to interpret the adaptive value of the social traits observed.

## Perspectives

We believe that assessing the domiciliary cockroach species within the broader framework of insect sociality is a positive step towards both a better understanding the social evolutionary processes in a remarkably diverse insect group, as well as in insects generally, by considering their unique and shared social traits alongside those of other social taxa. Social herds are useful models to address questions of general interest in sociobiology. For instance, domiciliary cockroaches have provided insights into the simple mechanisms whereby kin recognition and a range of collective behaviours arise through inadvertent information transfer. Their unique social structure, characterised by multiple aggregation site “nodes” and a fluid recruitment and interaction dynamic, also make them potential models for future investigation of social network theory—an increasingly valuable approach in the study of social evolution (Croft et al., 2007; Wey et al., 2008).

Perhaps more importantly, a comprehensive investigation of the social biology of insect herds, using cockroaches as model species, might help clarify the interplay between evolutionary forces leading to the emergence of insect societies. As with other mixed-family herds, cockroach herds are expected to arise primarily in response to ecological pressures (Costa, 2006). Herds may develop because of the need for collective defence, for sharing social information to localise vital resources, or for improving micro-climatic conditions to favour resource assimilation and metabolic rates, all independently of the genetic structure of groups. The idea of a preponderant role for ecological pressures in the evolution of insect societies contrasts with the focus on subsocial evolutionary pathways seen in recent decades (Hamilton, 1964; Bourke and Franks, 1995; Choe and Crespi, 1997). However, so-called parasocial pathways, where animals gain ecological benefits of group-living, are much cited in the vertebrate literature to explain the occurrence of cooperation and sociality between non-kin (Krause and Ruxton, 2002; Korb and Heinze, 2008; Clutton-

Brock, 2009; Sumpter, 2010). This is likely to be true in some arthropod societies as well. Indeed, varied combinations of ecological and genetic factors are expected to yield different evolutionary pathways to sociality, in some cases converging on the same social structure or expression. Biparental care, for example, is thought to arise via very different pathways, driven in varying degrees by some combination of nutritional resource, competition, and predation vulnerability factors (reviewed in Costa, 2006).

*Pathway pluralism* (Costa, 2006) expresses the idea that social diversity is broad and arises via multiple pathways, reflecting sets of such circumstances as life history, type, availability, and distribution of resources (from nest sites to nutritional resources), mating system, predation pressure, etc. In recent years social insect biologists have explored an ever-greater range of social forms, and in so doing increasingly recognise the important role of ecological pressures and context as a major evolutionary force in social evolution. Further broadening the scope of sociobiology discussions is a necessary step towards a more general framework for understanding social evolution. We hope this review of the social biology of domiciliary cockroaches and their unique social attributes will contribute to this goal by helping flesh out the spectrum of social systems encountered in insects and other arthropods.

**Acknowledgments** M.L. was supported by a postgraduate grant from the French Ministry of Research and a postdoctoral fellowship from the Australian Research Council. J.T.C.’s work on insect social evolution was supported by Western Carolina University, the US Department of Agriculture, and the Radcliffe Institute for Advanced Study, Harvard University. C.R. was funded by the Centre National pour la Recherche Scientifique.

## References

- Amé J.M., Halloy J., Rivault C., Detrain C. and Deneubourg J.L. 2006. Collegial decision making based on social amplification leads to optimal group formation. *Proc. Natl Acad. Sci. U.S.A.* **103**: 5835-5840
- Amé J.M., Rivault C. and Deneubourg J.L. 2004. Cockroach aggregation based on strain odour recognition. *Anim. Behav.* **68**: 793-801
- Appel A.G. and Rust M.K. 1985. Outdoor activity and distribution of the smokybrown cockroach, *Periplaneta fuliginosa* (Dictyoptera: Blattellidae). *Environ. Entomol.* **14**: 669-673
- Appel A.G. and Smith L.M. 1996. Harborage preferences of American and smokybrown cockroaches (Dictyoptera: Blattellidae) for common landscape materials. *Environ. Entomol.* **25**: 817-824
- Bell W.J. and Adiyodi K.G. 1982. *The American Cockroach*. Chapman & Hall, London.
- Bell W.J., Roth L.M. and Nalepa C.A. 2007. *Cockroaches: Ecology, Behavior, and Natural History*. John Hopkins University Press, Baltimore London.
- Bignell D.E., Roisin Y. and Lo N. 2010. *Biology of Termites: a Modern Synthesis*. Springer, Heidelberg.
- Booth W., Santangelo R.G., Vargo E.L., Mukha D.V. and Schal C. 2011. Population genetic structure in German cockroaches



- (*Blattella germanica*): differentiated islands in an agricultural landscape. *J. Hered.* **102**: 175-183
- Bourke A.F.G. 2011. *Principles of Social Evolution*. Oxford University Press, Oxford.
- Bourke A.F.G. and Franks N.R. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton.
- Breed M.D., Hinkle C.M. and Bell W.J. 1975. Agonistic behavior in the German cockroach, *Blattella germanica*. *Z. Tierpsychol.* **39**: 24-32
- Canonge S., Deneubourg J.L. and Sempo G. 2011. Group living enhances individual resources discrimination: the use of public information by cockroaches to assess shelter quality. *PLoS ONE* **6**: e19748
- Canonge S., Sempo G., Jeanson R., Detrain C. and Deneubourg J.L. 2009. Self-amplification as a source of interindividual variability: shelter selection in cockroaches. *J. Insect Physiol.* **55**: 976-982
- Carlson D.A. and Brenner R.J. 1988. Hydrocarbon-based discrimination of three North American *Blattella* cockroach species (Orthoptera: Blattellidae) using gas chromatography. *Ann. Entomol. Soc. Am.* **81**: 711-723
- Charlton R.E., Webster F.X., Zhang A., Schal C., Liang S.D., Sreng L. and Roelofs W.L. 1993. Sex pheromone for the brownbanded cockroach is an unusual dialkyl-substituted alpha-pyrone. *Proc. Natl Acad. Sci. U.S.A.* **90**: 10202-10205
- 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. *Bull. Soc. Zool. France* **71**: 39-48
- Choe J.C. and Crespi B.J. 1997. *The Evolution of Social Behaviour in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Cloarec A., Rivault C. and Cariou L. 1999. Genetic population structure of the German cockroach, *Blattella germanica*: absence of geographical variation. *Entomol. Exp. Appl.* **92**: 311-319
- Clutton-Brock T. 2009. Cooperation between non-kin in animal societies. *Nature* **462**: 51-57
- Conradt L. and Roper T.J. 2005. Consensus decision making in animal. *Trends Ecol. Evol.* **20**: 459-456
- Cornwell P.B. 1968. *The Cockroach. Vol. I*. Hutchinson, London.
- Costa J.T. 2006. *The Other Insect Societies*. Harvard University Press, Cambridge.
- Costa J.T. and Fitzgerald T.D. 1996. Developments in social terminology: semantic battles in a conceptual war. *Trends Ecol. Evol.* **11**: 285-289
- Crissman J.R., Booth W., Santangelo R.G., Mukha D.V., Vargo E.L. and Schal C. 2010. Population genetic structure of the German cockroach (Blattodea: Blattellidae) in apartment buildings. *Med. Vet. Entomol.* **47**: 553-564
- Croft D.P., James R. and Krause J. 2007. *Exploring Animal Social Networks*. Princeton University Press, Princeton.
- Dambach M. and Goehlen B. 1999. Aggregation density and longevity correlate with humidity in first-instar nymphs of the cockroach (*Blattella germanica* L., Dictyoptera). *J. Insect Physiol.* **45**: 423-429
- Danchin E., Giraldeau L.A., Valone T.J. and Wagner R.H. 2004. Public information: from nosy neighbors to cultural evolution. *Science* **305**: 487-491
- Davis R.B., Badaulf S.L. and Mayhew P.J. 2009. Eusociality and the success of the termites: insights from a supertree of dictyopteran families. *J. Evol. Biol.* **22**: 1750-1761
- Durier V. and Rivault C. 2001. Effects of spatial knowledge and feeding experience on foraging choices in German cockroaches. *Anim. Behav.* **62**: 681-688
- Eickwort G.C. 1981. Presocial insects. In: *Social Insects* (Hermann H.R., Ed), Academic Press, New-York. pp 199-280
- Farine J.P., Everaerts C., Le Quere J.L., Semon E., Henry R. and Brossut R. 1997. The defensive secretion of *Eurycotis floridana* (Dictyoptera, Blattidae, Polyzoisteriinae): chemical identification and evidence of an alarm function. *Insect Biochem. Mol. Biol.* **27**: 577-586
- Faulde M., Fuchs M.E.A. and Nagl W. 1990. Further characterization of a dispersion-inducing contact pheromone in the saliva of the German cockroach, *Blattella germanica* L. (Blattodea, Blattellidae). *J. Insect Physiol.* **36**: 353-359
- Gadau J. and Fewell J. 2009. *Organization of Insect Societies: from Genome to Sociocomplexity*. Harvard University Press, Cambridge.
- Gadot M., Burns J.G. and Schal C. 1989. Juvenile hormone biosynthesis and oocyte development in adult female *Blattella germanica*: effects of grouping and mating. *Arch. Insect Biochem. Physiol.* **11**: 189-200
- Grassé P.P. 1946. Sociétés animales et effet de groupe. *Experientia* **2**: 77-82
- Haldane J.B.S. 1955. Population genetics. *New Biol.* **18**: 34-51
- Halloy J., Sempo G., Caprari G., Rivault C., Asadpour M., Tâche F., Saïd I., Durier V., Canonge S., Amé J.M., Detrain C., Correll N., Martinoli A., Mondada F., Siegwart R. and Deneubourg J.L. 2007. Social integration of robots into groups of cockroaches to control self-organized choices. *Science* **318**: 1055-1058
- Hamilton W.D. 1964. The genetical evolution of social behaviour, I & II. *J. Theor. Biol.* **7**: 1-52
- Holbrook G.L., Armstrong E., Bachmann J.A.S., Deasy B.M. and Schal C. 2000. Role of feeding in the reproductive "group effect" in females of the German cockroach *Blattella germanica* (L.). *J. Insect Physiol.* **46**: 941-949
- Inward D., Beccaloni G. and Eggleton P. 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol. Lett.* **3**: 331-335
- Izutsu M., Ueda S. and Ishii S. 1970. Aggregation effects on the growth of the German cockroach *Blattella germanica* (L.) (Blattaria: Blattellidae). *Appl. Entomol. Zool.* **5**: 159-171
- Jackson L.L. 1972. Cuticular lipids of insects. IV: Hydrocarbons of the cockroaches *Periplaneta japonica* and *Periplaneta americana* compared to other cockroach hydrocarbons. *Comp. Biochem. Physiol. B.* **41**: 331-336
- Jeanson R. and Deneubourg J.L. 2006. Path selection in cockroaches. *J. Exp. Biol.* **209**: 4768-4775
- Jeanson R. and Deneubourg J.L. 2007. Conspecific attraction and shelter selection in gregarious insects. *Am. Nat.* **170**: 47-58
- Jeanson R., Rivault C., Deneubourg J.L., Blanco S., Fournier R., Jost C. and Theraulaz G. 2005. Self-organized aggregation in cockroaches. *Anim. Behav.* **69**: 169-180
- Jones S.A. and Raubenheimer D. 2001. Nutritional regulation in nymphs of the German cockroach, *Blattella germanica*. *J. Insect Physiol.* **47**: 1169-1180
- Jurenka R.A., Schal C., Burns E., Chase J. and Blomquist G.J. 1989. Structural correlation between cuticular hydrocarbons and female contact sex pheromone of German cockroach *Blattella germanica* L. *J. Chem. Ecol.* **15**: 939-949
- Korb J. and Heinze J. 2008. *Ecology of Social Evolution*. Springer, Heidelberg.
- Krause J. and Ruxton G.D. 2002. *Living in Groups*. Oxford University Press, Oxford.
- Lihoreau M. and Rivault C. 2008. Tactile stimuli trigger group effect in cockroach aggregations. *Anim. Behav.* **75**: 1965-1972
- Lihoreau M. and Rivault C. 2009. Kin recognition via cuticular hydrocarbons shapes cockroach social life. *Behav. Ecol.* **20**: 46-53
- Lihoreau M. and Rivault C. 2010. German cockroach males maximize their inclusive fitness by avoiding mating with kin. *Anim. Behav.* **20**: 303-309
- Lihoreau M. and Rivault C. 2011. Local enhancement promotes cockroach feeding aggregations. *PLoS ONE* **6**: e22048
- Lihoreau M., Brepson L. and Rivault C. 2009. The weight of the clan: even in insects, social isolation can induce a behavioural syndrome. *Behav. Proc.* **82**: 81-84

- Lihoreau M., Deneubourg J.L. and Rivault C. 2010. Collective foraging decision in a gregarious insect. *Behav. Ecol Sociobiol.* **64**: 1577-1587
- Lihoreau M., Zimmer C. and Rivault C. 2008. Mutual mate choice: when it pays both sexes to avoid inbreeding. *PLoS ONE* **3**: e3365
- Lihoreau M., Zimmer C. and Rivault C. 2007. Kin recognition and incest avoidance in a group-living insect. *Behav. Ecol.* **18**: 880-887
- Lockey K.H. and Dularay B. 1986. Cuticular methylalkanes of adult cockroaches *Blatta orientalis* and *Periplaneta americana*. *Comp. Biochem. Physiol. B.* **85**: 567-572
- Maekawa K., Matsumoto T. and Nalepa C.A. 2008. Social biology of the wood-feeding cockroach genus *Salganea* (Dictyoptera, Blaberidae, Panesthiinae): did ovoviviparity prevent the evolution of eusociality in the lineage? *Insect. Soc.* **55**: 107-114
- Miller D.M. and Koehler P.G. 2000. Trail-following behavior in the German cockroach (Dictyoptera: Blattellidae). *J. Econ. Entomol.* **93**: 1241-1246
- Nakayama Y., Suto C. and Kumada N. 1984. Further studies on the dispersion-inducing substances of the German cockroach *Blattella germanica* (L.) (Blattaria: Blattellidae). *Appl. Entomol. Zool.* **19**: 227-236
- Nakai Y. and Tsubaki Y. 1986. Factors accelerating the development of German cockroach *Blattella germanica* nymphs reared in groups. *Jpn. J. Appl. Entomol. Zool.* **30**: 1-6
- Nalepa C.A. 1984. Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav. Ecol.* **14**: 273-279
- Nalepa C.A. and Bell W.J. 1997. Postovulation parental investment and parental care in cockroaches. In: *Evolution of Social Behaviours in Insects and Arachnids* (Choe J.C. and Crespi B.J., Eds), Cambridge University Press, Cambridge. pp 26-51
- Nojima S., Schal C., Webster F.X., Santangelo R.G. and Roelofs W.L. 2005. Identification of the sex pheromone of the German cockroach, *Blattella germanica*. *Science* **307**: 1104-1106
- Okada K., Mori M., Shimazaki K. and Chuman T. 1990. Behavioral responses of male *Periplaneta americana* L. to female sex pheromone components, periplanone-A and periplanone-B. *J. Chem. Ecol.* **16**: 2605-2614
- Olomon C.M., Breed M.D. and Bell W.J. 1976. Ontogenetic and temporal aspects of agonistic behavior in a cockroach *Periplaneta americana*. *Behav. Biol.* **17**: 243-248
- Owens J.M. and Bennett G.W. 1982. German cockroach (Orthoptera, Blattellidae) movement within and between urban apartments. *J. Econ. Entomol.* **75**: 570-573
- Rivault C. 1989. Spatial distribution of the cockroach, *Blattella germanica*, in a swimming-bath facility. *Entomol. Exp. Appl.* **53**: 247-255
- Rivault C. 1990. Distribution dynamics of *Blattella germanica* in a closed urban environment. *Entomol. Exp. Appl.* **57**: 85-91
- Rivault C. and Cloarec A. 1992. Agonistic interactions and exploitation of limited food sources in *Blattella germanica* (L.). *Behav. Proc.* **26**: 91-102
- Rivault C. and Cloarec A. 1998. Cockroach aggregation: discrimination between strain odours in *Blattella germanica*. *Anim. Behav.* **55**: 177-184
- Rivault C., Cloarec A. and Sreng L. 1998. Cuticular extracts inducing aggregation in the German cockroach, *Blattella germanica* (L.). *J. Insect Physiol.* **44**: 909-918
- Ross R.H. and Mullins D.E. 1995. Biology. In: *Understanding and Controlling the German Cockroach* (Rust M.K., Owens J.M. and Reiersen D.A., Eds). Oxford University Press, Oxford. pp 21-47
- Ross M.H. and Tignor K.R. 1986. Response of German cockroaches to aggregation pheromone emitted by adult females. *Entomol. Exp. Appl.* **41**: 25-31
- Ross M.H., Bret B.L. and Keil C.B. 1984. Population growth and behavior of *Blattella germanica* (L.) in experimentally established shipboard infestations. *Ann. Entomol. Soc. Am.* **77**: 740-752
- Ross M.H., Keil C.B. and Cochran D.G. 1981. The release of sterile males into natural populations of the German cockroach *Blattella germanica*. *Entomol. Exp. Appl.* **30**: 241-253
- Roth L. and Willis E.R. 1960. The biotic associations of cockroaches. *Smith. Misc. Coll.* **141**: 1-470
- Roth S., Fromm B., Gäde G. and Predel R. 2009. A proteomic approach for studying insect phylogeny: CAPA peptides of ancient taxa (Dictyoptera, Blattoptera) as a test case. *BMC Evol. Biol.* **9**: 1-12
- Rust M.K., Owens J.M. and Reiersen D.A. 1995. *Understanding and Controlling the German Cockroach*. Oxford University Press, Oxford.
- Said I., Costagliola G., Leoncini I. and Rivault C. 2005a. Cuticular hydrocarbon profiles and aggregation in four *Periplaneta* species (Insecta: Dictyoptera). *J. Insect Physiol.* **51**: 995-1003
- Said I., Gaertner C., Renou M. and Rivault C. 2005b. Perception of cuticular hydrocarbons by the olfactory organs in *Periplaneta americana* (L.) (Insecta: Dictyoptera). *J. Insect Physiol.* **51**: 1384-1389
- Sempo G., Canonge S., Detrain C. and Deneubourg J.L. 2009. Complex dynamics based on a quorum: decision-making process by cockroaches in a patchy environment. *Ethology* **115**: 1150-1161
- Sempo G., Depickère S., Amé J.M., Detrain C., Halloy J. and Deneubourg J.L. 2006. Integration of an autonomous artificial agent in an insect society: experimental validation. *Lect. Notes Artif. Int.* **4095**: 703-712
- Sumpter D.J.T. 2010. *Collective Animal Behaviour*. Princeton University Press, Princeton.
- Sumpter D.J.T. and Pratt S.C. 2009. Quorum responses and consensus decision making. *Phil. Trans. R. Soc. B.* **364**: 743-753
- Tallamy D.W. and Wood T.K. 1986. Convergence patterns in subsocial insects. *Annu. Rev. Entomol.* **31**: 369-390
- Tee H.S., Saad A.R. and Lee C.Y. 2011. Population ecology and movement of the American cockroach (Dictyoptera: Blattidae) in sewers. *J. Med. Entomol.* **48**: 797-805
- West S.A., Griffin A.S. and Gardner A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**: 415-432
- Wey T., Blumstein D.T., Shen W. and Jordán F. 2008. Social network analysis of animal behavior: a promising tool for the study of sociality. *Anim. Behav.* **75**: 333-344
- Wilson E.O. 1971. *The Insect Societies*. Belknap Press, Cambridge