Animal Behaviour 111 (2016) 297–305

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Social context modulates idiosyncrasy of behaviour in the gregarious cockroach *Blaberus discoidalis*

James D. Crall [a, b, *, 1], André D. Souffrant [a, 1], Dominic Akandwanaho [a, 1], Sawyer D. Hescock [a, 1], Sarah E. Callan [a, 2], W. Melissa Coronado [a, 2], Maude W. Baldwin [a], Benjamin L. de Bivort [a, c, *]

[a] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.
[b] Concord Field Station, Harvard University, Bedford, MA, U.S.A.
[c] Center for Brain Science, Harvard University, Cambridge, MA, U.S.A.

ARTICLE INFO

Article history:
Received 24 June 2015
Initial acceptance 21 July 2015
Final acceptance 29 September 2015
Available online 12 December 2015
MS. number: A15-00542R

Keywords:
animal personality
behaviour
cockroach
collective behaviour
group composition
individuality
phototaxis
sociality

Individuals are different, but they can work together to perform adaptive collective behaviours. Despite emerging evidence that individual variation strongly affects group performance, it is less clear to what extent individual variation is modulated by participation in collective behaviour. We examined light avoidance (negative phototaxis) in the gregarious cockroach *Blaberus discoidalis*, in both solitary and group contexts. Cockroaches in groups exhibited idiosyncratic light-avoidance performance that persisted across days, with some individual cockroaches avoiding a light stimulus 75% of the time, and others avoiding the light just above chance (i.e. ~50% of the time). These individual differences were robust to group composition. Surprisingly, these differences did not persist when individuals were tested in isolation, but returned when testing was once again done in groups. During the solo testing phase cockroaches exhibited individually consistent light-avoidance tendencies, but these differences were uncorrelated with performance in any group context. Therefore, we have observed not only that individual variation affects group-level performance, but also that whether or not a task is performed collectively can have a significant, predictable effect on how an individual behaves. That individual behavioural variation is modulated by whether a task is performed collectively has major implications for understanding variation in behaviours that are facultatively social, and it is essential that ethologists consider social context when evaluating individual behavioural differences.

In animal groups, individuals with different phenotypes can nevertheless coordinate their behaviours to solve problems and increase individual fitness. Group living increases the chance of encountering a mate (Uzsák & Schal, 2013), provides security from predators (Treherne & Foster, 1980; Uzsák & Schal, 2013), and enhances access to other key resources such as food and shelter (Parrish & Edelstein-Keshet, 1999). Group dynamics are important for understanding how animals use collective decision making to solve problems and attain high levels of fitness.

To understand group dynamics, we need to examine the relationship between individual variation and collective behaviour. This relationship is complex, however, and is currently a frontier of research in animal behaviour (Bengston & Jandt, 2014; Jandt et al., 2014; Jeanson & Weindenmuller, 2014; LeBoeuf & Grozinger, 2014). It is clear that individual variation (arising through a number of mechanisms, including genetic diversity (Bengston & Jandt, 2014), or differences in experience (Ravary et al., 2007)) can give rise to variation between groups through a variety of processes, such as founder effects or interactions with conspecifics, etc. (Bengston & Jandt, 2014; LeBoeuf & Grozinger, 2014). Increasingly, however, there is also evidence that the presence of conspecifics can drive individual behavioural variation (LeBoeuf & Grozinger, 2014), for example through social niche differentiation (Bergmüller & Taborsky, 2010). Individual variation can thus affect, but also be affected by, group behaviour.

* Correspondence: J. D. Crall, B. L. de Bivort, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, U.S.A.
E-mail addresses: james.crall@gmail.com (J. D. Crall), debivort@oeb.harvard.edu (B. L. de Bivort).
[1] These authors contributed equally.
[2] These authors contributed equally.

http://dx.doi.org/10.1016/j.anbehav.2015.10.032

There is strong empirical evidence for individual variation in collectively behaving animals. Schools of fish (Marras & Domenici, 2013), flocks of homing pigeons (Hoffman, 1958), and even human groups (Vindenes, Engen, & Sæther, 2008) are populated by highly varied individuals, which can have important effects on group performance (Brown & Irving, 2013). Among invertebrates, castes within eusocial insects are a classical example of behavioural differentiation within a group context (O'Donnell, 1998; Winston & Michener, 1977). These differences can emerge even when all individuals are genetically identical (Freund et al., 2013), suggesting that individual variation in behaviour could be an emergent property of group membership. Yet, eusociality is not a prerequisite for behavioural differences between individuals. Indeed, several non-eusocial insects exhibit conspicuous individual differences even when genetically identical (Buchanan, Kain, & de Bivort, 2015; Kain, Stokes, & de Bivort, 2012; Petrovskii, Mashanova, & Jansen, 2011; Schuett et al., 2011; Stamps, Saltz, & Krishnan, 2013), probably reflecting developmental noise rather than an emergent property.

As an intermediate case between eusocial and solitary lifestyles, gregarious insects represent an interesting case for the consideration of individuality in the group context. Clonal, gregarious aphids exhibit individuality in both escape (Schuett et al., 2011) and exploratory locomotion behaviours (Petrovskii et al., 2011). Canonge, Sempo, Jeanson, Detrain, and Deneubourg (2009) showed that American cockroaches, *Periplaneta americana*, exhibit individual differences in resting site preferences. Planas-Sitjà, Deneubourg, Gibon, and Sempo (2015) found (in the same species) that behavioural variation between individuals can affect group dynamics and collective shelter-seeking behaviour. However, the interplay between individual variation and collective behaviour in gregarious insects remains a nascent research area.

There is emerging evidence that such individual variation plays an important role in determining collective behaviour (Hui & Pinter-Wollman, 2014; Modlmeier, Keiser, Shearer, & Pruitt, 2014) and group success (Modlmeier, Liebmann, & Foitzik, 2012; Pruitt & Riechert, 2011). Individual variation in social spider groups (*Stegodyphus dumicola*) plays a larger role in determining group success than the size of the group (Keiser & Pruitt, 2014). Hoffman (1958) showed that even in humans, the individual variation within a group significantly contributes towards that group's success. The effect of individual differences on group behaviour can be distributed evenly across individuals or concentrated in specific members. Key individuals in a group can have a particularly strong influence on the collective behaviour of their group (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014).

Despite increasing evidence that individuality plays a large role in determining collective behaviour, we have only recently begun to understand the potential effects of group membership in modulating individual variation. In social spiders, group membership can increase individual behavioural variation (Laskowski & Pruitt, 2014; Modlmeier, Laskowski, et al., 2014). In social insects, there has been increasing interest in understanding how feedback between individual behaviour and social context may dynamically produce stable, individually specific behavioural patterns (Bengston & Jandt, 2014; Jandt et al., 2014; Jeanson & Weindenmuller, 2014; LeBoeuf & Grozinger, 2014). In honeybees, for example, colony context has a clear effect on at least some behaviours, with clonal subpopulations of bees exhibiting different behavioural patterns depending on the genetic homogeneity of the entire colony (Gempe, Stach, Bienefeld, & Beye, 2012; Hunt, Guzman-Novoa, Uribe-Rubio, & Prieto-Merlos, 2003). Outside of social insects, there is also evidence that social context can modulate behavioural traits typically associated with ‘personality’ (i.e. risk-taking behaviour: Schuett and Dall, 2009; van Oers, Klunder, & Drent, 2005; ‘boldness’: Keiser, Modlmeier, Singh, Jones, & Pruitt, 2014). However, the extent to which such group effects are pervasive outside of highly social arthropods is largely unknown.

Our broad goal was to use cockroach light-avoidance behaviour to examine (1) how individual behavioural differences correlate with collective behaviour in a system that allows rapid quantification and robust tracking of individuals across contexts and (2) the effect that group membership has on individual variation. Cockroach light-avoidance is likely a predator-evasion and shelter-seeking response. Performance (defined as the fraction of time spent in the shade) of this behaviour improves with the size of the group, and thus can be considered a collective behaviour (Canonge, Deneubourg, & Sempo, 2011; Salazar, Deneubourg, & Sempo, 2013; Sempo et al., 2009). When searching for a suitable shelter, cockroaches are able to use social cues to reach a consensus and aggregate in a single suitable shelter (Sempo et al., 2009). However, the consensus decision is influenced by the individual variation within a group (Sempo et al., 2009). Thus we also expected to find that individual variation in light-avoidance performance contributes to differences at the group level.

Using a new two-dimensional bar-coding system (Crall, Gravish, Mountcastle, & Combes, 2015), we tracked individual cockroaches as they performed a collective light-avoidance behaviour, in a variety of group configurations, to test the following hypotheses. First, we hypothesized that individual animals would display different behaviours with respect to the light stimulus. Specifically, some individuals would be better at avoiding the light than others. We also hypothesized that these differences between individuals would emerge from social niche construction occurring after the formation of those experimental groups. We reassigned individual roaches from their original random groups to groups based on similarity in their individual light-avoidance performance. If social niche construction acts on days-long timescales, individual variation in performance would re-emerge even in groups initially composed of individuals with little variation. These experiments assess the stability of individual differences across changes in group membership. Next, using solitary light-avoidance assays, we tested the hypothesis that any stable individual differences observed across the first two experiments would persist when animals were assayed individually. Finally, by restoring the animals to experimental groups, we tested the hypothesis that any discrepancy between individual behaviours in the group and solitary contexts could be explained by drift in individual behavioural biases over time.

METHODS

We developed a system for automatically tracking cockroach position in a circular arena, in which a downward-facing projector delivered a moving light/shade stimulus, and cockroach position was imaged using light invisible to the cockroaches. Cockroaches were permanently tagged with optical codes whose positions could be extracted from the frames of a video using pattern recognition software (Crall et al., 2015). Combining these two techniques, we were able to determine a cockroach's position and speed, and whether it was in the light or in the shade. The use of permanent tags enabled us to track the performance of individual cockroaches over a month of successive experiments, even while varying the membership of the groups.

Scripts and processed cockroach position data are available at: http://lab.debivort.org/social-context-modulates-idiosyncrasy and Zenodo (doi:10.1101/028571).

Study Organism and Animal Care

Blaberus discoidalis animals were purchased from Backyard Brains (Ann Arbor, MI, U.S.A.) and were approximately 8 months old