



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. Hescok^{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.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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 & Edelman, 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 & Weindenmüller, 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.

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.debvort.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

on arrival. We selected 60 males from a mixed-sex population that were free of conspicuous external damage and used them as experimental individuals. Cockroaches were housed in opaque black plastic containers with translucent white perforated lids. Houses contained egg-carton cardboard enrichment. Food pellets (Rat and Mouse Food, Carolina Biological Supply, Burlington, NC, U.S.A.) and water-soaked paper towels were replaced weekly. Containers were cleaned weekly.

The test cockroaches were tagged with BEEtag codes for automated video tracking (Crall et al., 2015). Tags were printed on waterproof paper and measured $\sim 8 \times 8$ mm. Each cockroach was anaesthetized using CO₂. While anaesthetized, we abraded the pronotum of the cockroach with fine grit sandpaper and attached the BEEtags to the pronotum using cyanoacrylate glue. Cockroaches were given a minimum of 48 h to recover after anaesthetization before the start of experimental trials. During this time, two out of ~ 80 tagged individuals shed their tags, and were not retained for experiments.

Experimental Set-up and Stimulus

We constructed a circular arena with walls made from high-density polyethylene by cutting the top and bottom off a 5-gallon (18.93-litre) liquid waste container. The circular arena was 28.2 cm in diameter and ~ 30 cm tall. A mounting base for the arena was constructed with black 5.6 mm acrylic. The arena walls could be slotted into a ~ 5 mm wide circular groove cut into this base, holding the walls in place. For trials, we covered the base by a sheet of Absorbent Lab Paper (VWR-51138-500, VWR, Radnor, PA, U.S.A.), which was changed between trials, to minimize odorant contamination. An Optoma S316 DLP (digital light processing) projector and 5MP monochromatic digital camera with a global shutter (Blackfly model, Point Grey, Richmond, BC, Canada) were mounted on an aluminium extrusion rig above the arena. Recordings were collected at seven frames/s, with an exposure time of 8 ms. This exposure time was chosen to minimize motion blur within each frame, as well as to synchronize with the vertical scan of the DLP projector. The projector delivered a computer-controlled stimulus (at 30 frames/s) onto the base and the interior walls of the arena. The camera lens was covered by a 590 nm long-pass red filter (Thorlabs, Newton, NJ, U.S.A.). The camera recorded a video of the entire base of the arena for the duration of each trial.

For tagging control experiments (see [Supplementary Fig. S1](#)), the projected stimulus was magenta on the top half and red on the bottom half. Control experiments were conducted with individual cockroaches ($N = 21$ untagged, 19 tagged) and in groups of three randomly selected individuals ($N = 6$ untagged groups, 5 tagged groups). For all other experiments, the projected stimulus was alternating red and magenta quadrants ([Fig. 1](#)). The quadrants rotated at 0.05 Hz and randomly reversed rotation direction with a probability of 0.033 per frame, resulting in an average rotational direction persistence of 1 s. The stimulus also included two small black wedges at the centre of the red sectors, which allowed us to use machine vision to identify the position of the sectors in the same image that we used to track the BEEtags. These colours were chosen because cockroaches do not sense red light, so the red segments of the stimulus would appear to be dark to them, while the magenta stimulus would appear bright ([Walther, 1958](#)). Before each trial, we transferred experimental animals to an empty plastic container in darkness. We then initiated the stimulus and gently poured the cockroaches into the arena ([Supplementary Movie S1](#)). Recordings lasted either 10 min or 5 min.

Trial Structure

We conducted four different experiment phases (Rounds), varying the composition of housing and experimental groups (cohorts).

Round 1

In the first round of trials, we randomly placed 60 individuals into six cohorts of 10 cockroaches each. To ensure that cohort composition was not influenced by the relative ease of picking up some cockroaches compared to others, we took a population of 80 tagged cockroaches and divided them into five groups of equal size. Cockroaches were placed in these temporary groups in the order in which they were picked up (the first 16 cockroaches picked up went into group 1, the second 16 cockroaches went into group 2, etc.). From each group we randomly selected two cockroaches to be in each of the experimental cohorts. The cockroaches were allowed to acclimate to their new housing group for 48 h. Each 10-individual cohort then underwent one experimental trial each day on 6 consecutive days, in which the entire cohort was introduced into the arena for a 10 min trial ([Fig. 1c, d](#)). Here and in all analyses, tracking performance was defined as the percentage of time that each individual spent in the red zones. Only the first 5 min was considered because the cockroaches habituated to the stimulus (see below).

Round 2

After the last experiment of Round 1, we placed the cockroaches in new housing and experimental cohorts ('re-cohorted') based on their ranked individual tracking performance in the first round. Rank 1 individuals were all added to the first new cohort. Rank 2 individuals were randomly split between the first and second Round 2 cohorts, so that the first cohort had 10 members, etc. We continued this procedure to populate all Round 2 cohorts ([Fig. 1d](#)). We then gave the cockroaches 48 h to acclimate to their new housing groups. Experiments in Round 2 proceeded as in Round 1, with each cohort of 10 individuals being tested six times.

Round 3

After the last Round 2 experiment, the cockroaches were re-cohorted randomly into six new cohorts with the use of a six-sided die. The cockroaches were then given 48 h to acclimate to their new housing groups. For experiments, we introduced each individual into the arena alone ([Supplementary Movie S2](#)) and recorded its movements for 5 min. The stimulus presentation during trials was identical except for the random timing of quadrant reversals. Each day we tested cockroaches from two cohorts, and we repeated this until each individual was tested four times in this Round, which consequentially lasted for 12 days ([Fig. 1d](#)).

Round 4

After the last Round 3 experiment, the cockroaches were re-cohorted randomly into six new cohorts with the use of a six-sided die. The cockroaches were then given 48 h to acclimate to their new housing groups. These cohorts underwent group trials similar to the trials described in the first and second rounds of trials. Each cohort of 10 individuals was tested three times each over the course of Round 4.

Thus, in terms of fully independent units (i.e. the sample sizes), we tested six cohorts of 10 roaches each in Rounds 1, 2 and 4, and 60 individual roaches in Round 3. The number of replicate experiments per Round 1–4 was, respectively, 6, 6, 4 and 3. During the 31 days of experiments, three cockroaches died, the first between trials 1 and 2 of the first round of experiments. This individual was replaced with a randomly chosen individual from the remaining pool of tagged cockroaches. The subsequent cockroaches were not replaced, so at any time, up to two experimental and housing cohorts had nine individuals rather than 10 individuals.

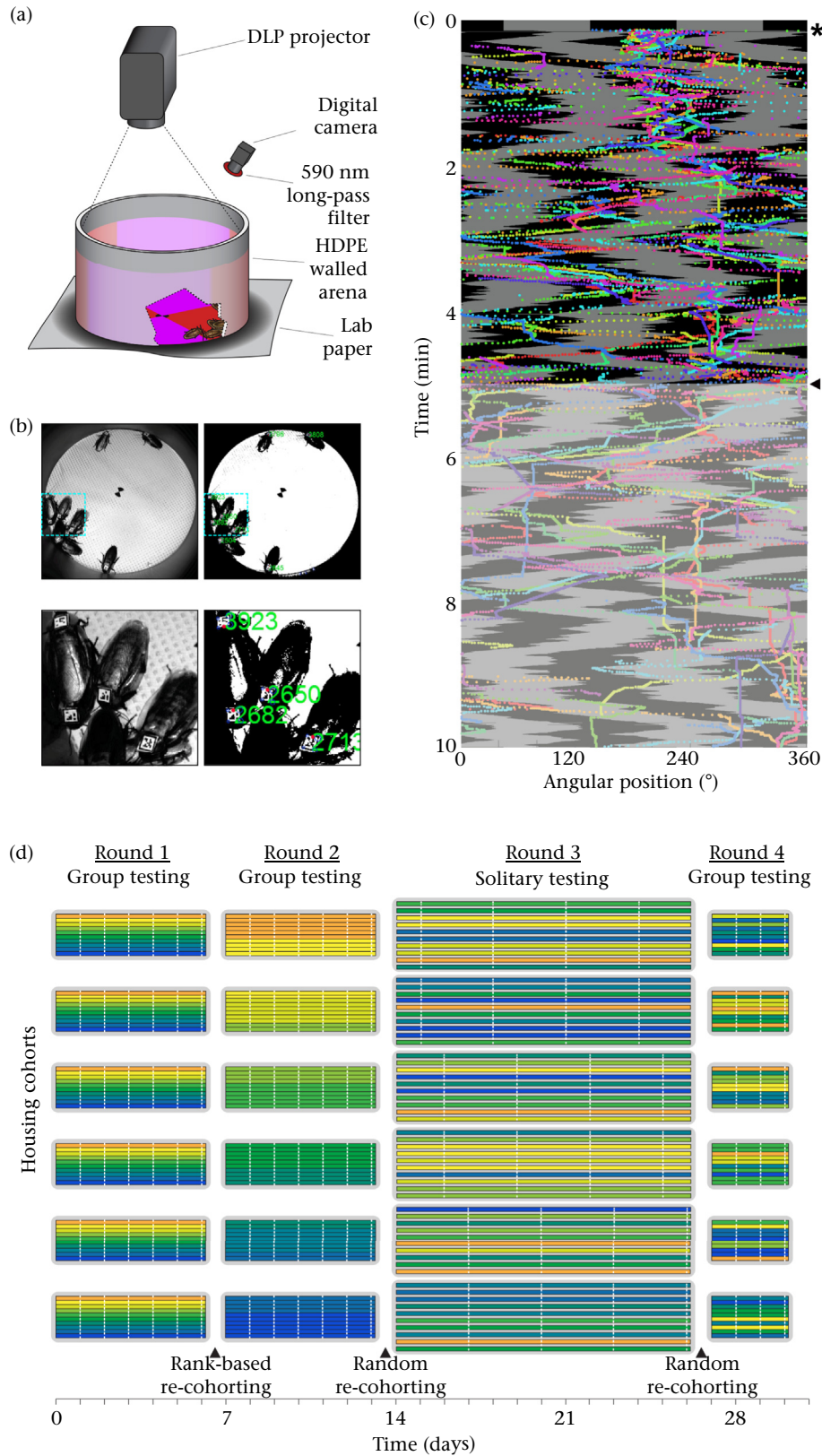


Figure 1. An automated tracking system monitored individual cockroach behaviour during group phototaxis. (a) Diagram of experimental set-up. Circular arena resting on absorbent laboratory paper directly under a projector that projected the moving stimulus onto the arena. A digital camera was positioned to capture the entire arena; the camera was filtered with a 590 nm long-pass filter to allow digital tracking through both light conditions. (b) Upper row: a still frame of the tracking video during a group trial (left) and the same image showing the number and location of identified tags. Lower row: inset images from each of the upper-row panels. (c) Kymograph with time running along the vertical axis, depicting cockroach angular position in the arena as it relates to the angular position of shaded and lit regions over time. The black region corresponds to the red zone of the arena and the grey region corresponds to the magenta zone. Each cockroach has a unique colour trail throughout the timeline of the kymograph. Note that only the top half, or the first 5 min, of the kymograph was used in the analysis. (d) Cohort composition during each of the four rounds of trials. Round 2 cohorts were determined based on tracking performance in Round 1; cohorts for Rounds 1, 3 and 4 were randomly selected. Colours illustrate hypothetical tracking performance.

Automated Behavioural Analysis

All recordings were saved in raw monochromatic .avi format and processed using custom scripts in MatLab (Mathworks, Natick, MA, U.S.A.). For control experiments comparing tagged and untagged cockroaches, we imported movies and collected 50 evenly spaced frames throughout the recording. We combined the frames using a median filter to generate an image of the empty arena for background subtraction. We thresholded the subtracted images and reduced noise by eroding and dilating above threshold pixels until only the outlines of the cockroaches remained. In solitary control trials, we considered the centre of a convex hull surrounding the cockroach's outline to be the animal's position. In three animal trials, we calculated the aggregation index as the area enclosed by the convex hull surrounding all outlines.

We extracted BEEtag positions from thresholded images using published code (Crall et al., 2015). For each trial, we marked the centre of the arena manually upon running the MATLAB script. To determine an optimal image threshold for tag identification, we chose a sample of frames from throughout the recording and then systematically varied the thresholds. The threshold identifying the greatest number of tags from those sample frames was used for the whole movie. Based on the indicated centre of the arena, we translated the cockroach positions into polar coordinates, and chose the angular coordinate as the focus for analysis. Sometimes tracking of the position of the red sectors generated errors (e.g. when a cockroach walked over the small black targeting sectors). To address this, we used an interpolation script to make a 'best guess' estimate of the sector positions for each frame. Individuals were untrackable on some frames due to motion blur, foreshortening of the BEEtags, being obscured by other cockroaches, being flipped upside down, or (rarely) walking through the unilluminated black targeting sectors. We replaced these missing values with values linearly interpolated across the gap of missing values (Movie S3). We calculated average instantaneous speeds for each cockroach as a proxy for activity. Average velocity within a trial was highly correlated with portion of time spent moving, since cockroaches had a relatively characteristic speed when moving, and we therefore only included average speed in our analyses here.

Statistics

We calculated ANOVAs and regression analyses in MatLab or R (R Foundation for Statistical Computing, Vienna, Austria) with built-in functions. For all ANOVAs, individual cockroaches provided the independent grouping variables. We estimated repeatability of individual behaviour within rounds with the intraclass correlation coefficient (ICC) in the ICC package in R (Wolak, Fairbairn, & Paulsen, 2011).

RESULTS

In control experiments, we found that both tagged and untagged cockroaches preferred the shaded portion of the arena, showing no conspicuous differences in either tracking performance (Fig. S1a) or speed (Fig. S1b). The tagging treatment caused no significant differences in the distribution of aggregation index scores of groups of three animals (Fig. S1c). Thus, the application of BEEtags did not appear to significantly alter naturalistic behaviour.

We measured the shade-tracking performance of each of the six experimental cohorts in Round 1 six times each over successive days (Fig. 1d). Cockroaches tracked the shaded sectors (Fig. 1c, Movie S1), although they exhibited habituation to the stimulus over the course of 10 min (Supplementary Fig. S2). We chose a cutoff of

5 min for further trials to capture the highest shade-tracking performance.

Cockroaches showed significant interindividual variation in tracking performance (one-way ANOVA: $F_{60,291} = 3.599$, $P < 10^{-6}$; repeatability (estimated ICC (95% CI)) = 0.31 (0.20–0.44); Fig. 2a, Supplementary Table S1). The best-tracking cockroaches avoided the light ~75% of the time, while the poorest trackers avoided it ~55% of the time. The distribution of tracking performance appeared to be roughly Gaussian. Individual shade-tracking performance was stable across the six trials within Round 1, which spanned 6 days (Fig. 2b). Notably, individual tracking performance, averaged across trials, was not correlated with the speed of individuals, averaged across trials (Pearson correlation: $r_{60} = 0.13$, $P = 0.31$; Supplementary Fig. S3). Because of this individual variation in tracking performance, cohorts also varied in their mean tracking performance across trials (Fig. S4).

For Round 2, the cockroaches were placed in new experimental cohorts, based on their ranked tracking performance within their respective Round 1 cohorts (Fig. 1d). The best-performing individuals from each Round 1 cohort were placed together into a single Round 2 cohort, etc. As in Round 1, consistent interindividual variation in tracking was observed in Round 2 (one-way ANOVA: $F_{58,295} = 2.443$, $P < 10^{-6}$; repeatability (95% CI) = 0.20 (0.10–0.32); Supplementary Fig. S5a, Table S1), which persisted across days (Supplementary Fig. S5b). Likewise, cohorts in Round 2 varied in their average tracking performance (Supplementary Fig. S4b). Individual tracking performance in Round 2 was significantly correlated with individual tracking performance in Round 1 (Pearson correlation: $r_{58} = 0.58$, $P < 0.0001$; Fig. 3a). Individuals that tracked well in Round 1 continued to track well in Round 2, and individuals that tracked poorly in Round 1 continued to track poorly in Round 2. The overall tracking performance of each cohort in Round 2 was not significantly different from a prediction based on the average performance of its members in Round 1 (multiple comparisons corrected t test: $2.37 > t_{18} > 0.062$, $0.16 < P < 0.99$; Fig. 3b). Thus, individual tracking performance in a group context appears to be robust to group composition.

In Round 3, individuals were tested alone to see if the observed idiosyncratic behaviour, evident in groups, appears in a solitary context. All individuals were randomly assigned to six new housing groups of 10 individuals (Fig. 1d). From these housing cohorts, individuals were removed and tested alone under the same stimulus conditions as the earlier group tests (Movie S2). Concordant with previous results on collective light-avoidance behaviour in cockroaches, the average tracking performance in solitary trials was significantly lower than in-group trials (Supplementary Fig. S6).

Cockroaches in Round 3 demonstrated consistent interindividual variation in tracking performance in the solitary trials (one-way ANOVA: $F_{58,176} = 1.821$, $P = 0.0015$; repeatability (95% CI) = 0.17 (0.05–0.32); Fig. 4a, Supplementary Table S1), which persisted over days (Supplementary Fig. S5c). Individual tracking performance (average of four Round 3 trials) in the solitary context was uncorrelated with tracking performance in the group context (average of six Round 2 trials) (Pearson correlation: $r_{58} = 0.094$, $P = 0.48$; Fig. 4b). Thus, the individual shade-tracking performance observed in group contexts disappeared during solitary trials. In its place, new, consistent individual tracking performance levels appeared during solitary trials. As expected, the average tracking performance was lower in the solitary context than in the group context (Fig. 4a).

The final experiments (Round 4) examined whether individual tracking performance levels would re-emerge when animals were restored to the group context during experiments. This was an important control when considering the possibility that over time and repeated manipulation the behaviour of the cockroaches may

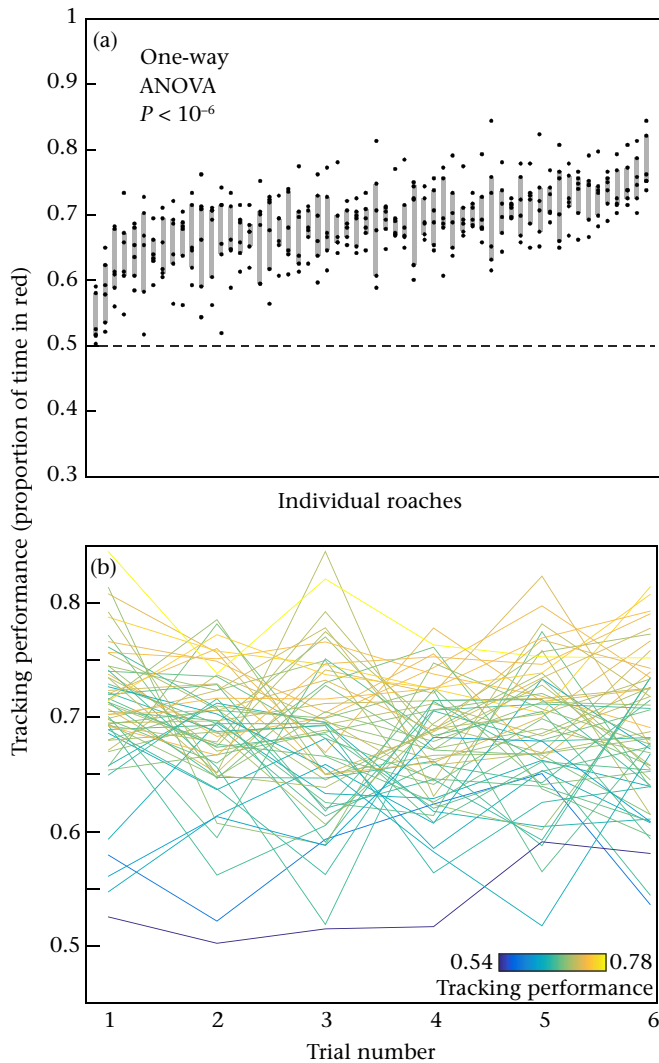


Figure 2. (a) Proportion of time that each cockroach spent in the shaded region (i.e. tracking performance) for each of the six Round 1 trials. A shaded region indicates the interquartile range. The cockroaches are sorted by average tracking performance. Dotted line shows the null expectation of a tracking performance of 0.5. (b) Each cockroach's tracking performance across all six trials of Round 1. Line colours indicate average tracking performance for that individual.

have drifted (Ridgel, Ritzmann, & Schaefer, 2003), which could trivially explain the lack of correlation between tracking performance between Round 3 and earlier Rounds. When individuals were randomly assigned to new experimental cohorts (Fig. 1d), the observed individual tracking performances from Round 2 re-emerged. Average tracking performance was significantly correlated between Rounds 2 and 4 across individuals ($r_{57} = 0.39$, $P = 0.0023$; Fig. 5). Individual tracking performance in Round 4 was significantly correlated with Round 1 performance as well. Thus, all pairwise comparisons between Rounds of individual tracking performance in the group context were significantly correlated (Table 1). Conversely, the individual tracking performance in the solitary context was not significantly correlated with individual performance in any other Rounds (Table 1). As before, tracking performance showed significant interindividual variation (one-way ANOVA: $F_{1,57} = 1.834$, $P = 0.0032$; repeatability = 0.22 (0.06–0.40); Supplementary Fig. S5d, Table S1) and persistence across days (Supplementary Fig. S5e). As expected, cohorts in Round 4 differed in their average tracking performance (Supplementary Fig. S4c).

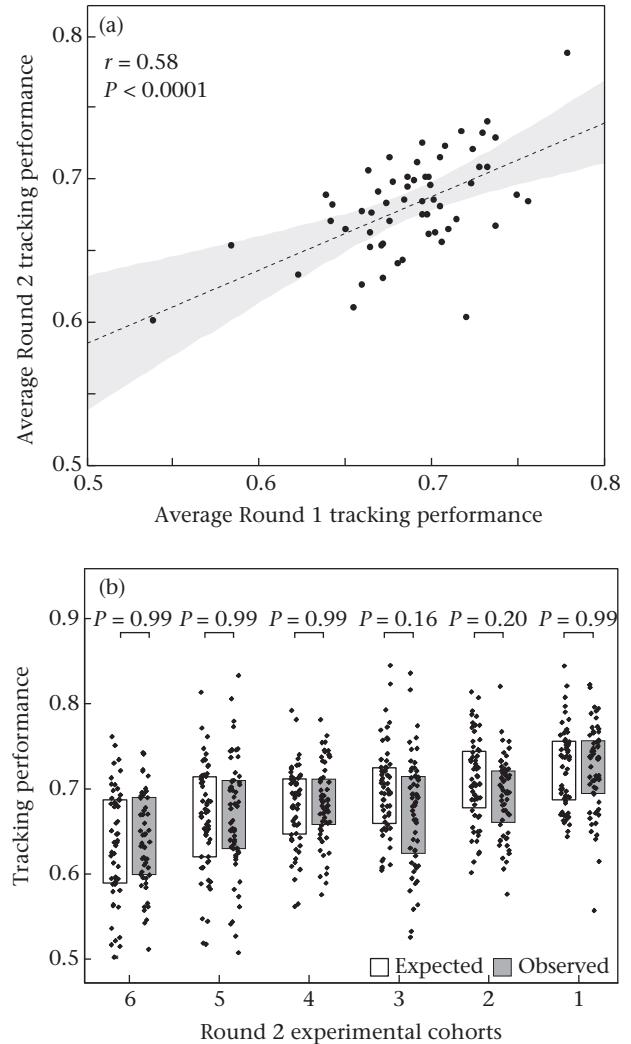


Figure 3. (a) Scatterplot of average individual performance in Round 2 versus Round 1. Dotted line indicates linear fit. Shaded region indicates the 95% confidence interval on the linear regression. (b) Expected (white) and observed (grey) distributions of individual trial tracking performance, by experimental cohort. Expected values are based on the per-trial performance of each cohort's members in Round 1. P values were corrected for $k = 6$ multiple comparisons using the formula $p^* = 1 - (1 - p)^k$.

DISCUSSION

Our results demonstrate that cockroaches have individually consistent variation in shade-tracking performance (Figs. 1 and 2). We show that this idiosyncratic cockroach behaviour is robust to group composition (Fig. 3) and is consistent over the course of several weeks (Fig. 5), but surprisingly does not persist when cockroaches are tested in isolation from a group (Fig. 4). Overall, these findings show that idiosyncratic behaviour is modulated by social context in cockroaches. While previous work has investigated how individual behavioural variation affects group performance in different classes of organisms (Briffa, 2013; Burns, Herbert-Read, Morrell, & Ward, 2012; Marras & Domenici, 2013; Millor, Amé, Halloy, & Deneubourg, 2006; Pruitt & Keiser, 2014), it is less well understood how group membership influences individual behavioural performance.

These results have important implications for understanding the dynamics of collective decision making in animals. Despite increasing focus on both collective decision making (Arganda, Pérez-Escudero, & de Polavieja, 2011; Planas-Sitjà et al., 2015)

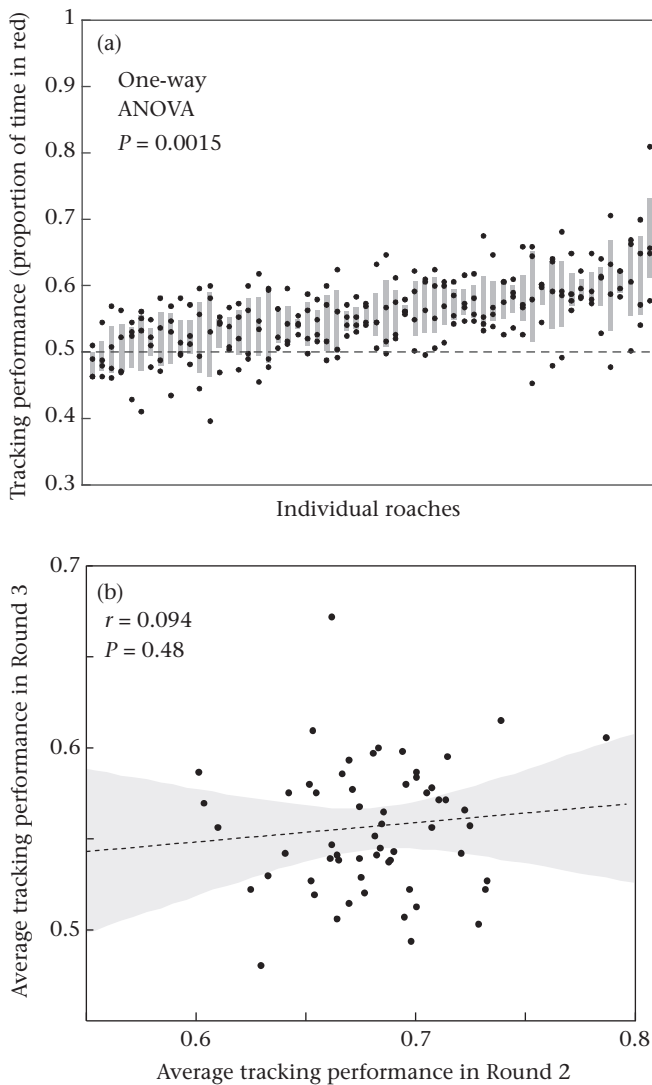


Figure 4. (a) Tracking performance for each of the six Round 3 trials. Shaded regions show interquartile range. (b) Scatterplot of average individual performance in Round 3 versus Round 2. Dotted line indicates linear fit. Shaded region indicates the 95% confidence interval on the linear regression.

and consistent interindividual variation (i.e. personality; Burns et al., 2012; Santos, Neupert, Lipp, Wikelski, & Dechmann, 2014) in animals, the role of group heterogeneity in collective decision making of animals, particularly in gregarious insects, remains a nascent research area. Where attempts have been made to understand the role of group heterogeneity in collective behaviour, this has typically been done by measuring personalities when individuals are separated (Briffa, 2013; Brown & Irving, 2013; Pruitt & Keiser, 2014). This approach might not always be valid, however, because our results show that individual differences can be substantially modified by group context.

What drives individual behavioural variation in cockroach groups? One hypothesis for this variation could be the dichotomy between bold and shy (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007; Sinn, Gosling, & Moltshaniwskyj, 2008) or sitter–rover (de Belle & Sokolowski, 1987) personalities present in a wide variety of animals (Sih, Bell, & Johnson, 2004), since both higher activity level and higher portion of time in light could be considered characteristics of bold individuals. Especially for a mobile stimulus as used here, it is possible that more active individuals would perform

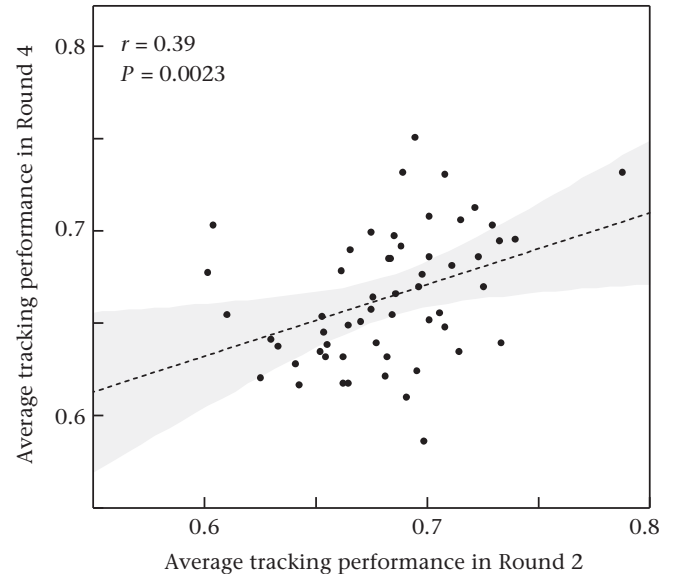


Figure 5. Scatterplot of average individual tracking performance in Round 4 versus Round 2. Dotted line indicates linear fit. Shaded region indicates the 95% confidence interval on the linear regression.

Table 1

Pairwise Pearson correlation coefficients (r) across tracking performances of individual cockroaches (averaged across trials) between all rounds

	Round 2	Round 3	Round 4
Round 1			
r	0.58	0.10	0.38
P	<0.001	0.45	0.003
Round 2			
r		0.094	0.39
P		0.48	0.002
Round 3			
r			0.19
P			0.15

better at tracking since they must actively search out the preferred stimulus. In our experiments, however, there was no relationship between activity level (i.e. velocity) and tracking performance (Supplementary Fig. S3, Movie S2).

Individual variation may also be produced dynamically in the presence of a social group, either by the presence of social hierarchies (Chase, 1980), or by social niche differentiation (Bergmüller & Taborsky, 2010). However, this does not appear to be the case in the experiments described here, since individuals did not shift behaviour in response to group composition shuffling (Fig. 3) as would be expected from individual behavioural variation that emerges dynamically from the establishment of social hierarchies (Bell, Gorton, Tourtellot, & Breed, 1979).

Although it is still possible that social niche differentiation plays a role in increasing behavioural variation among individual cockroaches, this effect would have to occur on a timescale of at least several weeks, since cockroaches housed together in new groups with lower behavioural variation (Round 2 above) for 1 week continuously showed no significant shift in their individual tracking performance. Alternatively, there may be a critical window for social niche construction, so that if an individual joins a niche sufficiently early in life, it will stay in that niche permanently even if re-grouped among individuals in the same niche. Even in this case, however, this social niche construction would seem to apply only in social contexts, since it disappeared when individuals were tested in isolation.

Another potential source of individual variation could be individual experience (Ravary et al., 2007), for example arising from microenvironmental differences. However, for two reasons, we believe that environmental differences are unlikely to explain the sudden change in individual behaviours seen when animals were transferred to the solitary context. First, we were careful to match their environmental circumstances during the experiments (i.e. matching their social conditions with constant group size housing; matching their visual experience by storing them in dark containers when not conducting experiments; making sure that all experimental handling was done by each experimenter across the whole cohort, rather than across subsets of animals). Second, the re-emergence in Round 4 of the individual behaviours observed in Rounds 1 and 2 would be statistically improbable if environmental fluctuations explained the behavioural differences that occurred between Rounds 3 and 4.

As we observed, the correlation in individual shade-tracking performance between solitary and group contexts was very weak, and could plausibly be less than zero ($r_{58} = 0.094$ between rounds 2 and 3; bootstrap resampling: 95% CI = -0.19 – 0.37). The weaker correlation between solitary and group performance cannot be explained by sampling error alone, as all within-condition correlations (e.g. between pairs of Rounds 1, 2, 4) were above the 95% CI of the solitary * group correlation.

A possible mechanism at play is that individuals vary in social cohesion (i.e. are more or less likely to stay next to other cockroaches), and this drives interindividual variation in tracking performance, but only in the group context. Attraction to conspecifics is important in many aspects of social behaviour (e.g. collective motion: Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; habitat selection: Stamps, 1988), and interindividual variation in social cohesion can be important in structuring social behaviour (see, e.g. Wey & Blumstein, 2010). Since group-tracking performance was generally much higher than tracking performance of separated individuals (Supplementary Fig. S6), individuals that are more likely to stay with a group are also more likely to have higher average tracking performance than individuals that ignore the presence of others. However, the intensity of social cohesion among individual cockroaches would have no necessary bearing on performance when alone. This might explain the lack of correlation between individual performance levels in the solitary and group contexts (Fig. 4). One way of testing this hypothesis in future work might be to examine interindividual variation in levels of social cohesion, for example by measuring the amount of time cockroaches spend in proximity to a constrained group of other cockroaches in a behavioural arena. This test could be done in either the presence or the absence of a light stimulus to investigate the interaction between social and visual stimuli.

This hypothesis highlights an important result of our experiments, namely that parameters driving individual behavioural performance in isolation may not have simple relationships to the parameters relevant for the same task when performed in a group. For example, in the group context, the probability of stopping next to another cockroach might be the single most important factor in determining tracking performance, while in isolation other behavioural parameters (e.g. velocity differences when in versus out of the shade stimulus, etc.) may be much more relevant. If the correlation between individual performance in the group and solitary contexts is strictly zero, or negative, this implies that the cues driving shade tracking in both the solitary and group contexts (such as visual information) interact nonlinearly with the cues present only in the group context (such as conspecific odour or tactile cues). If the interaction were linear, better-than-average exploitation of solitary cues would invariably be helpful in the group context, imparting a positive correlation. A slightly positive correlation

could arise if significantly more linear weight were given to group-only cues; alternatively, the presence of group-only cues could gate the processing of solitary cues. In humans, social context modulates numerous sensory channels including nociception (Krahé, Springer, Weinman, & Fotopoulou, 2013) and vision–touch integration (Heed, Habets, Sebanz, & Knoblich, 2010).

In agreement with previous findings (Canonge et al., 2011; Salazar et al., 2013), we found that cockroach groups outperformed individuals at tracking a shade stimulus (Supplementary Fig. S6). We hypothesize that this difference is due to the lack of information sharing typically associated with the presence of conspecifics and aggregation behaviour. The presence of conspecifics enhances public information sharing, which has been shown to be important for a variety of collective decision-making tasks (Miller, Garnier, Hartnett, & Couzin, 2013), including locating shelters in cockroaches (Canonge et al., 2011).

One important consideration when interpreting the results of any longitudinal behaviour study in animals is the potential for time and physical injury to have influenced behaviour. Ageing has been associated with neural degradation that affects not only gait mechanics but also the neural pathways associated with escape behaviours (Ridgel et al., 2003). While not statistically significant, our experiments showed a tendency towards lower tracking performance in Round 4 when compared to Rounds 1 and 2 (Fig. S6), as well as weaker correlations between individual performance in Round 4 and Rounds 1 and 2 than was first observed between experimental Rounds 1 and 2 (Fig. 5). These results suggest there may be at least weak levels of both behavioural drift and performance degradation.

Interestingly, cockroaches displayed the least individual consistency (i.e. the lowest repeatability) in the solitary context (Supplementary Table S1). This result is consistent with the emergence of more stable individual behavioural patterns within a group context, as has been observed in solitary ant queens and suggested to play an important role in division of labour in insect colonies (Fewell & Page, 1999).

Most broadly, our results highlight the importance of considering group context when examining behaviour in animals. For animals exhibiting any degree of social behaviour, from occasionally gregarious animals to the highly eusocial insects, groups are not only composed of individuals of different types, but may also play an active role in modulating and creating individual variation in collective behaviours.

Acknowledgments

We thank Clark Magnan, Ed Soucy and Joel Greenwood for help with implementing experiments.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.10.032>.

References

- Arganda, S., Pérez-Escudero, A., & de Polavieja, G. G. (2011). A common rule for decision making in animal collectives across species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(50), 20508–20513.
- Bell, W. J., Gorton, R. E., Tourtellot, M. K., & Breed, M. D. (1979). Comparison of male agonistic behaviour in five species of cockroaches. *Insect Socialia*, *26*(3), 252–263.
- de Belle, J. S., & Sokolowski, M. B. (1987). Heredity of rover/sitter: alternative foraging strategies of *Drosophila melanogaster* larvae. *Heredity*, *59*, 73–83.

- Bengston, S. E., & Jandt, J. M. (2014). The development of collective personality: the ontogenetic drivers of behavioural variation across groups. *Frontiers in Ecology and Evolution*, 2, 81. <http://dx.doi.org/10.3389/fevo.2014.00081>.
- Berdahl, A., Torney, C. J., Ioannou, C. C., Faria, J. J., & Couzin, I. D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science*, 339(6119), 574–576. <http://dx.doi.org/10.1126/science.1225883>.
- Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9), 504–511.
- Briffa, M. (2013). The influence of personality on a group-level process: shy hermit crabs make longer vacancy chains. *International Journal of Behavioral Biology*, 119(11), 1014–1023.
- Brown, C., & Irving, E. (2013). Individual personality traits influence group exploration in a feral guppy population. *Behavioral Ecology*, 25(1), 95–101.
- Buchanan, S. M., Kain, J. S., & de Bivort, B. L. (2015). Neuronal control of locomotor handedness in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 6700–6705. <http://dx.doi.org/10.1073/pnas.1500804112>.
- Burns, A., Herbert-Read, J., Morrell, L., & Ward, A. (2012). Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. *PLoS One*, 7(5), e36567.
- Canonge, S., Deneubourg, J. L., & Sempo, G. (2011). Group living enhances individual resources discrimination: the use of public information by cockroaches to assess shelter quality. *PLoS One*, 6(6), e19748.
- Canonge, S., Sempo, G., Jeanson, R., Detrain, C., & Deneubourg, J. L. (2009). Self-amplification as a source of interindividual variability: shelter selection in cockroaches. *Journal of Insect Physiology*, 55(11), 976–982.
- Chase, I. (1980). Social process and hierarchy formation in small groups: a comparative perspective. *American Sociological Review*, 45(6), 905–924.
- Crall, J., Gravish, N., Mountcastle, A. M., & Combes, S. A. (2015). BEtag: a low cost image based tracking system for the study of animal behaviour and locomotion. *PLoS One*, 10(9), e0136487.
- Fewell, J. H., & Page, R. E., Jr. (1999). The emergence of division of labour in forced associations of normally solitary ant queens. *Evolutionary Ecology Research*, 1, 537–548.
- Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Krüger, A., et al. (2013). Emergence of individuality in genetically individual mice. *Science*, 340(6133), 756–759.
- Frost, J., Winrow-Giffen, A., Ashley, P., & Sneddon, L. (2007). Plasticity in animal personality traits: does prior experience alter the degree of boldness. *Proceedings of the Royal Society B: Biological Sciences*, 274, 333–339.
- Gepe, T., Stach, S., Bienefeld, K., & Beye, M. (2012). Mixing of honeybees with different genotypes affects individual worker behaviour and transcription of genes in the neuronal substrate. *PLoS One*, 7(2), e31653.
- Heed, T., Habets, B., Sebanz, N., & Knoblich, G. (2010). Others' actions reduce cross-modal integration in peripersonal space. *Current Biology*, 20(15), 1345–1349.
- Hoffman, R. L. (1958). Homogeneity of member personality and its effect on group problem-solving. *58(1)*, 27–32.
- Hui, A., & Pinter-Wollman, N. (2014). Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. *Animal Behaviour*, 93, 261–266.
- Hunt, G. J., Guzman-Novoa, E., Uribe-Rubio, J. L., & Prieto-Merlos, D. (2003). Genotype–environment interactions in honeybee guarding behaviour. *Animal Behaviour*, 66, 459–467.
- Jandt, J. M., Bengston, S., Pinter-Wollman, N., Pruitt, J. N., Raine, N. E., Dornhaus, A., et al. (2014). Behavioural syndromes and social insects: personality at multiple levels. *Biological Reviews*, 89, 48–67.
- Jeanson, R., & Weindemüller, A. (2014). Interindividual variability in social insects: proximate causes and ultimate consequences. *Biological Reviews*, 89, 671–687.
- Kain, J. S., Stokes, C., & de Bivort, B. L. (2012). Phototactic personality in fruit flies and its suppression by serotonin and white. *Proceedings of the National Academy of Sciences of the United States of America*, 109(48), 19834–19839.
- Keiser, C. N., Modlmeier, A. P., Singh, N., Jones, D. K., & Pruitt, J. N. (2014). Exploring how a shift in the physical environment shapes individual and group behavior across two social contexts. *Ethology*, 120(8), 825–833. <http://dx.doi.org/10.1111/eth.12256>.
- Keiser, C. N., & Pruitt, J. N. (2014). Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 281(1796), 20141424.
- Krahé, C., Springer, A., Weinman, J., & Fotopoulou, A. (2013). The social modulation of pain: others as predictive signals of salience, a systematic review. *Frontiers in Human Neuroscience*, 7, 386.
- Laskowski, K. L., & Pruitt, J. N. (2014). Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B: Biological Sciences*, 281(1783), 20131666. <http://dx.doi.org/10.1098/rspb.2013.1666>.
- LeBoeuf, A. C., & Grozinger, C. M. (2014). Me and we: the interplay between individual and group behavioural variation in social collectives. *Current Opinion in Insect Science*, 5, 16–24.
- Marras, S., & Domenici, P. (2013). Schooling fish under attack are not all equal: some lead, others follow. *PLoS One*, 8(6), e65784.
- Miller, N., Garnier, S., Hartnett, A., & Couzin, L. (2013). Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, 110(13), 5263–5268.
- Millor, J., Amé, J. M., Halloy, J., & Deneubourg, J. L. (2006). Individual discrimination capability and collective decision-making. *Journal of Theoretical Biology*, 239(3), 313–323.
- Modlmeier, A. P., Keiser, C. N., Shearer, T. A., & Pruitt, J. N. (2014). Species-specific influence of group composition on collective behaviors in ants. *Behavioral Ecology and Sociobiology*, 68(12), 1929–1937. <http://dx.doi.org/10.1007/s00265-014-1799-3>.
- Modlmeier, A. P., Keiser, C. N., Watters, J., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: an ecological and evolutionary overview. *Animal Behaviour*, 89, 53–62.
- Modlmeier, A. P., Laskowski, K. L., DeMarco, A. E., Coleman, A., Zhao, K., Brittingham, H. A., et al. (2014). Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. *Biology Letters*, 10(8), 20140419. <http://dx.doi.org/10.1098/rsbl.2014.0419>.
- Modlmeier, A. P., Liebmam, J. E., & Foitzik, S. (2012). Diverse societies are more productive: a lesson from ants. *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2142–2150.
- O'Donnell, S. (1998). Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). *Annual Review of Entomology*, 43, 323–346.
- van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, 16(4), 716–723.
- Parrish, P. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, 284(5411), 99–101.
- Petrovskii, S., Mashanova, A., & Jansen, V. A. A. (2011). Variation in individual walking behavior creates the impression of a lévy flight. *Proceedings of the National Academy of Sciences of the United States of America*, 108(21), 8704–8707.
- Planas-Sitjà, I., Deneubourg, J. L., Gibon, C., & Sempo, G. (2015). Group personality during collective decision-making: a multi-level approach. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142515. <http://dx.doi.org/10.1098/rspb.2014.2515>.
- Pruitt, J. N., & Keiser, K. N. (2014). The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Animal Behaviour*, 93, 87–95.
- Pruitt, J. N., & Riechert, S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B: Biological Sciences*, 278(1709), 1209–1215.
- Ravary, F., Lecoutey, E., Kaminski, G., Châline, N., & Jaisson, P. (2007). Individual experience alone can generate lasting division of labor in ants. *Current Biology*, 17(15), 1308–1312.
- Ridgel, A., Ritzmann, R., & Schaefer, P. (2003). Effects of aging on behaviour and leg kinematics during locomotion in two species of cockroaches. *Journal of Experimental Biology*, 206(24), 4453–4465.
- Salazar, M. O. L., Deneubourg, J. L., & Sempo, G. (2013). Information cascade ruling the fleeing behaviour of a gregarious insect. *Animal Behaviour*, 85(6), 1271–1285.
- Santos, C. D., Neupert, S., Lipp, H. P., Wikelski, M., & Dechmann, D. K. N. (2014). Temporal and contextual consistency of leadership in homing pigeon flocks. *PLoS One*, 9(7), e10277.
- Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77, 1041–1050.
- Schuett, W., Dall, S. R. X., Baeumer, J., Kloesener, M. H., Nakagawa, S., Beinlich, F., et al. (2011). 'Personality' variation in a clonal insect: the pea aphid, *Acyrtosiphon pisum*. *Developmental Psychobiology*, 53(6), 631–640.
- Sempo, G., Canonge, S., Detrain, C., & Deneubourg, J. L. (2009). Complex dynamics based on a quorum: decision-making process by cockroaches in a patchy environment. *Ethology*, 115, 1150–1161.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.
- Sinn, D. L., Gosling, S. D., & Moltchanivskiy, N. A. (2008). Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. *Animal Behaviour*, 75, 433–442.
- Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. *American Naturalist*, 131(3), 329–347.
- Stamps, J. A., Saltz, J. B., & Krishnan, V. V. (2013). Genotypic differences in behavioural entropy: unpredictable genotypes are composed of unpredictable individuals. *Animal Behaviour*, 86, 641–649.
- Treherne, J. E., & Foster, W. A. (1980). The effects of group size on predator avoidance in a marine insect. *Animal Behaviour*, 28(4), 1119–1122.
- Uzsák, A., & Schal, C. (2013). Social interaction facilitates reproduction in male German cockroaches, *Blattella germanica*. *Animal Behaviour*, 85, 1501–1509.
- Vindenes, Y., Engen, S., & Sæther, B. E. (2008). Individual heterogeneity in vital parameters and demographic stochasticity. *American Naturalist*, 171(4), 455–467.
- Walther, J. B. (1958). Changes induced in spectral sensitivity and form of retinal action potential of the cockroach eye by selective adaptation. *Journal of Insect Physiology*, 2(2), 142–151.
- Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, 79, 1343–1352.
- Winston, M. L., & Michener, C. D. (1977). Dual origin of highly social behaviour among bees. *Proceedings of the National Academy of Sciences of the United States of America*, 74(3), 1135–1137.
- Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2011). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, 3(1), 129–137. <http://dx.doi.org/10.1111/j.2041-210X.2011.00125.x>.