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The role of individuality in collective group movement

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How different levels of biological organization interact to shape each other's function is a central question in biology. One particularly important topic in this context is how individuals' variation in behaviour shapes group-level characteristics. We investigated how fish that express different locomotory behaviour in an asocial context move collectively when in groups. First, we established that individual fish have characteristic, repeatable locomotion behaviours (i.e. median speeds, variance in speeds and median turning speeds) when tested on their own. When tested in groups of two, four or eight fish, we found individuals partly maintained their asocial median speed and median turning speed preferences, while their variance in speed preference was lost. The strength of this individuality decreased as group size increased, with individuals conforming to the speed of the group, while also decreasing the variability in their own speed. Further, individuals adopted movement characteristics that were dependent on what group size they were in. This study therefore shows the influence of social context on individual behaviour. If the results found here can be generalized across species and contexts, then although individuality is not entirely lost in groups, social conformity and group-size-dependent effects drive how individuals will adjust their behaviour in groups.

1. Introduction

How the behaviour of individuals and the interactions between them produce group-level behaviour is at the heart of collective behaviour research [1]. Group-level properties, such as the collective movements of animal groups, emerge when individuals respond to the location and movements of their near neighbours [2–4]. This responsiveness to the behaviour of neighbours allows consensus to be reached over the timing and direction of group movements [5,6]. This in turn allows groups to maintain their coherence and enables group members to realize the benefits of group living [7]. To date, however, most studies of collective behaviour have assumed that group members are identical in their movements and responses to their neighbours [2–4] (but see [8–10] for theoretical predictions and [11,12] for empirical observations about individual differences in groups). This common assumption of homogeneity contrasts with a large and growing body of work documenting consistent inter-individual differences in behaviour [13–18] and evidence that differences in the social affiliations between group members, and individual differences, can affect leadership and the collective decision-making process [12,19,20].

But if groups composed of heterogeneous agents are to function effectively and cohesively, then group members may need to limit or even sacrifice some of their individuality in order to align their behaviour with that of their group mates. In some groups, for example, subordinate group members conform to the decisions of lead individuals, thereby suffering consensus costs [21], while in others, individuals alternate between leadership roles [22]. This

pressure to conform is likely to increase with group size, as the number of interactions with different individuals increases over time. However, complete conformity can stifle innovation and detract from the advantages of group living [23], hence maintenance of some individuality is likely to be advantageous [24,25]. So how do group members balance their own individuality against the need to conform, and how is this balance affected by group size and group composition? Understanding this inter-relationship of the individual and the group is fundamental to our appreciation of the mechanisms of collective behaviour.

Using a combination of fine-scale movement data of a shoaling species of fish (mosquitofish, *Gambusia holbrooki*), we tested whether fish retained individuality in their movement patterns, a term we name 'movement signatures', in groups. We first demonstrate that these fish exhibit consistent individual movement signatures in an asocial context over time. We show this using classical linear statistics comparing quantifiable movement parameters such as the fish's median speed and median turning speed. In practice, however, an individual's movement signature is a combination of these movement parameters, and therefore we complement our analysis using Markov chain models to analyse how the movement signatures of individuals changed between trials. We go on to determine whether individuals retain these individual movement signatures when placed into groups and asked whether this was dependent on group size. We determined if individuals self-assorted to occupy specific positions in the group that were dependent on their individual signatures. Further, we asked whether individuals moved in particular ways depending on what group size they were in, even if they did retain some of their individual movement signatures. Finally, we determined whether the median speed of a group's centroid was correlated with the asocial speeds of its component group members.

2. Material and methods

(a) Study species and experimental methods

Female mosquitofish (*Gambusia holbrooki*) (22 mm ± 4; mean ± 1 s.d.) were collected from Lake Northam (33°53′07 S, 151°11′35 E), Sydney, Australia. For each day of trials, an experimental arena (730 × 730 × 150 mm) made of 10 mm acrylic was filled to a depth of 70 mm with dechlorinated water. A further 2 l of water, taken from a housing tank containing over 50 mosquitofish, was poured into the arena in an attempt to keep the amount of chemical cues between trials constant, although the presence or absence of conspecific cues has little effect on the exploratory behaviour of fish [26]. Two columnar stones were placed 240 mm from two corners of the arena. A frame with an opaque black plastic curtain visually isolated the arena to prevent external disturbances to the fish. The arena was lit using fluorescent lights. In one corner of the arena was a transparent door, which could be remotely lifted with a poly-nylon cord. Fish could therefore be held in this holding-corner (behind the door) prior to the start of trials. Above this holding-corner, we placed a Nikon G10 digital video camera, which filmed the fish as they left the holding-corner into the main arena. These films were of high quality (macro-setting; 640 × 480 pixels, 30 fps) so that we could individually identify each fish from their elastomer tags (see electronic supplementary material). For each trial, we placed fish (depending on the treatment, singularly, or in groups of two, four or eight; see below) in the holding-corner for 5 min in order to acclimate the fish to the arena. Following these 5 min, we raised the door allowing the fish to enter the arena. A web-cam (Logitech Pro 9000) placed directly over the centre of the arena filmed the fish as they explored the arena for 5 min.

An 'asocial trial' consisted of trialling an individual on its own in the arena. A first set of 65 fish were given two asocial trials each (with two weeks between trials) in order to determine how consistent an individual's movements were in the absence of conspecifics. Subsequently, we used a different set of fish to record individuals' behaviours in an asocial trial and a social trial (individuals in a group). No individuals from the first set of trials were reused for this second set of trials. We selected group sizes of two, four and eight fish (12 replicates of each group size, $n = 168$ fish). All individuals in each group had been trialled in asocial trials. To control for the order of trials, half of the replicates were done with groups tested first, and subsequently the individuals in these groups were trialled on their own. For the other half, we trialled the individuals first, and then subsequently placed these individuals into the different group sizes. Again, we left two weeks before re-trialling individuals. The same fish were not reused in different group sizes. Using the automated tracking software CTRAX (v. 0.1) and the associated manual correction package FIXERRORS GUI in MATLAB, we obtained consistent tracks and coordinates (x, y) of each individual in each trial. From these data, we calculated each fish's median speed, variance in speed and median turning speed across each trial (see electronic supplementary material, figure S1 for details of calculations and average values for different group sizes). We chose to measure these parameters (i) because they are associated with behaviours such as exploration, navigation and foraging [27,28], (ii) because they are important in the social interactions between shoaling fish [2,4], and (iii) because they are easily quantifiable between the two contexts of interest. We calculated each group's average polarization [9] over the course of the trial (see electronic supplementary material). When groups were reasonably aligned (individuals being normally distributed about the mean direction of travel with a standard deviation of approx. 38.3°), we calculated the mean normalized position score of each individual in a group. Individuals that were always at the front of the group would have a score of zero, while individuals always at the back of the group would have a score of one (see electronic supplementary material). We also calculated the speed of each group's centroid. Finally, we calculated the mean distance of group members to the group's centroid over the course of a trial, which we used as a measure of the group's cohesiveness.

(b) Generalized linear mixed models and PCA

To determine whether individuals were consistent in their movement signatures between asocial trials, we analysed whether an individual's first asocial movement score (e.g. its median speed, variance in speed or median turning speed) could predict that movement score in its second asocial trial using linear models in R v. 2.13.0 [29].

We hypothesized that when in groups, individuals would behave more uniformly together, compared with when those same individuals had been tested on their own. Hence, we predicted that the variance in median speeds of individuals within a group would be reduced in the social context relative to the variance in median speeds of those same individuals in an asocial context. We call this group-level conformity. To test this, we used a linear mixed-effects model to assess the effect of context (social or asocial) and group size (two, four or eight as a categorical variable), and their interaction on the overall log variance in speed of individuals within a group (i.e. one data point per group per context). Group ID was added as a random factor to control for the repeated-measures nature of the data.

The response variable (variance in speed) was logged to improve the normality of model residuals.

Next, we hypothesized that the variance in an individual's speed (i.e. variance measured at the level of the individual, not the group as above) would also decrease in a group compared with that individual's variance in speed when tested on its own. Hence, individuals would be swimming with more uniform speeds in groups than when on their own. We call this individual-level conformity. To test this, we analysed the effect of context (social or asocial), group size (two, four or eight as a categorical variable) and average nearest-neighbour distance (NND), and their two- and three-way interactions on individual variance in speed using a linear mixed-effects model. Neighbour distance was included to account for the possibility that the level to which an individual adjusts its behaviour may depend on its proximity to neighbours. Individual ID, nested within group ID, was added to the model as random factors to account for the repeated-measures nature of the data and non-independence of individuals within a group. Non-significant interactions were removed in a stepwise fashion following Crawley [30], leaving a model containing only main effects (all interaction terms were non-significant).

We then investigated whether fish maintained their asocial movement parameter preferences in their social trials. We predicted that if individual signatures were maintained, a fish's behaviour (median speed, variance in speed and median turning speed) in its asocial trial would predict the same signature in its social trial. To do this, we used general linear mixed-effects models, incorporating body size as a covariate and group size as a fixed factor (categorical variable), to investigate the effect of movement parameters in an asocial setting (median speed, variance in speed or median turning speed) on movement parameters in a social setting. Group ID was included as a random factor to account for the non-independence of individuals within a group. We removed all non-significant interactions in a stepwise manner, leaving all main effects, whether significant or not, and significant interactions [30]. It is important to note that although the different movement parameters are correlated, principle components analysis is not appropriate here, because the weighting for the principle components generated for one context (asocial or social) would not directly map to the other context. This means analysing each response variable separately is more appropriate in this case (G. Ruxton 2011, personal communication).

We hypothesized that if some individuals had consistent individual signatures between asocial and social contexts, this could be because of some individuals leaving the group and behaving independently of other group members. If this were the case, we predicted that individuals at greater distances from their group members should show greater similarity between their social and asocial movement scores. To test this, individual consistency scores were calculated and defined as the absolute value of the difference between movement score in the social and asocial trials. Two movement scores were investigated: median speed and median turning speed. We assessed the effect of mean nearest-neighbour distance and group size (fixed effect), and their interaction, on the square root of individual consistency scores (square root transformation was necessary to normalize the data), using linear mixed-effects models. Group ID was added as a random factor to account for the non-independence of individuals within groups. We predicted that, if individuals are leaving the group and behaving independently, we would see a significant correlation between consistency and mean nearest-neighbour distance, with those individuals showing the highest levels of consistency (smallest consistency values) to be those that were further from their neighbours and so isolated from the group.

Finally, we investigated whether swimming behaviour could be used to predict the position an individual occupied in a group. Here, we were able to use PCA to reduce the three swimming variables (and body size) to a single measure of behaviour as we are not comparing directly between the social and asocial context, and although the weightings of the variables on the components differed between contexts, this does not affect our analysis. PCA analysis on each context separately revealed one significant component for each context (see the electronic supplementary material). We investigated the effects of the social or asocial principle component, group size (categorical variable) and their interaction on normalized position score using linear mixed-effects models. Again, group ID was added as a random factor to account for non-independence of individuals in a group, and non-significant interactions were removed.

(c) Markov chain modelling technique

We also used a Markov chain modelling technique to detect individual signatures between asocial trials, individual signatures in social trials, and general movement signatures depending on the group size. Markov chain models allow the description and classification of dynamic patterns by assigning probabilities to sequences of events, where the probability of an event only depends on the immediately preceding event. If we assume that in a sequence of actions of an individual the probability of some action is largely determined by the preceding action, Markov chains can be used for the analysis and models of behaviour [11,31–33]. If for all pairs (a_i, a_j) of possible actions the conditional probability $P(a_j|a_i)$ is known, the probability of a whole sequence of actions can be computed by multiplying the probabilities of all pairs of consecutive actions in the sequence (see the electronic supplementary material for a definition of the actions). For each individual, a specific Markov chain can be constructed by estimating the probabilities of pairs of actions from observations of this individual's movements. When exploring, many fish will swim with a saltatory (stop–start) movement pattern [34–36]. Differences in the lengths and transitions between steps make two fish differ in their swimming speed and turning speed. This is included, together, in our Markov models. Therefore, these individual-specific models can be used to try to recognize the individual that produced a newly observed sequence of actions.

In order to properly use these Markov chain models for the detection of individual signatures, we applied Bayesian classification: given an observed sequence of actions O, we looked for the individual i that caused the sequence O with the highest probability, meaning the one that maximizes the conditional probability

$$P(i|O) = \frac{P(O|i)P(i)}{P(O)}.$$

Note that the maximization procedure does not depend on $P(O)$. Also, in our experimental set-up, $P(i)$, the probability for individual i to occur, is the same for all i. This means that we can find the individual we were looking for by determining the individual that maximizes $P(O|i)$. If we have a Markov chain model for each individual, this can be done in the following way: for each individual, we simply compute the probability of the observed sequence O based on the respective individual-specific model, and pick the individual that yields the highest probability. In the same way, we can compute the rank of a specific model M for an observed sequence O by determining how many other individual models yield a higher probability than M. Regardless of whether a Markov chain can completely explain the swimming patterns, these models can be used in the classification procedure described above because the decision is based on a simple comparison of values yielded by the models. Further, although it would be possible to make these models more complex by using higher-order Markov chains (which take a finite sequence of previous actions into consideration to

Table 1. Linear mixed-effects models investigating the effect of context (asocial or social) and groups size on (*a*) group-level conformity (the variance in median speed between individuals within a group) and (*b*) individual-level conformity (the variance in speed exhibited at an individual level). Intercept refers to the baseline parameters of the behaviour of individuals allocated to a group of two, in an asocial context. There is less variability between group members when in groups compared with when tested on their own, and individuals behave in a less variable manner when in a group. Group-level conformity decreases as group size increases, but this is not the case for individual-level conformity. Significant *p*-values at the 0.05 level are shown in bold.

fixed effect	value	s.e.	d.f.	*t*-value	*p*-value
(*a*) group-level conformity					
intercept	3.357	0.435			
context	−2.073	0.389	35	−5.327	**<0.001**
group size = 4	1.146	0.550	33	2.085	**0.045**
group size = 8	1.954	0.550	33	3.553	**0.001**
(*b*) individual-level conformity					
intercept	7.626	0.078			
context	−0.097	0.025	167	−3.876	**<0.001**
group size = 4	−0.029	0.074	33	−0.388	0.701
group size = 8	0.021	0.074	33	0.277	0.784
NND	−0.000	0.001	131	−0.003	0.998

predict the next action) or including location-dependent models (which specifically describe the behaviour, e.g. in corners or in the middle of the arena), this would require more data, and, as our findings indicate, such models are not required to test our specific hypotheses.

For the detection of individual signatures between asocial trials, we constructed a model M_i for each individual i based on the first trial. Using the data of the second trial for each individual i, we then determined the rank of M_i among all other models. A rank of 1 means 'perfect detection' of an individual (i.e. no other individual's models were better at predicting that individual than its own model). In the absence of any individual signatures, all ranks are equally probable and should be uniformly distributed with a mean of 33 (because there were 65 individuals in these asocial consistency trials). We used a one-tailed Wilcoxon signed-rank test to determine whether the mean of our recognized ranks was smaller than that of this null model.

We also applied this Markov chain model technique to investigate whether an individual's asocial behaviour could be used to detect that individual in a group. To do this, we determined the rank of each individual's model among all other models on the social trials. The expected mean rank in the absence of individual signatures was 84.5 (because there were 168 individuals in the social trials). In this analysis, we were interested in whether these scores were dependent on what group size an individual was in. Therefore, we analysed the scores for each group size separately against this null model, again using one-tailed Wilcoxon signed-rank tests.

Using this modelling technique for a third time, we also asked whether we could detect general differences between how individuals moved in asocial versus social contexts. This analysis was therefore not concerned with differences between individuals, but rather differences in movement signatures between contexts including differences between group sizes. To test this, we used the same Markov chain modelling approach as described previously to determine whether an individual's movements could be distinguished as 'an individual moving on its own' or 'an individual moving in a group'. This time, however, we did not construct models from single individual trials but from sets of asocial trials and of social trials, respectively. These models therefore do not represent the behaviours of specific individuals, but rather the general behaviour of an individual moving on its own or of an individual moving in a group.

3. Results

Fish were highly consistent in the movement parameters we recorded between their two asocial trials (median speed: $F_{1,63} = 20.74$, $p < 0.001$; variance in speed: $F_{1,63} = 12.83$, $p < 0.001$; median turning speed: $F_{1,63} = 23.47$, $p < 0.001$; electronic supplementary material, figure S2). We could also detect individual signatures between these two asocial trials using the Markov chain modelling technique. By comparing fish i's movement patterns in its first trial with those in its second trial (as compared with other randomly assigned individuals' movement patterns), we found more evidence that fish displayed consistent individual movement patterns between trials (Wilcoxon signed-rank test, $V = 582.5$, $p = 0.001$).

In groups, we found that the variance between individuals' median speeds was significantly lower in the social trial than in the asocial trial, demonstrating group-level conformity (table 1*a*). There was also a significant effect of group size on individuals' variance in speed (table 1*a*), indicating that individuals showed greater variability in larger groups. We also found that individuals exhibit individual-level conformity; the variance in an individual's speed decreased in a social context compared with an asocial context. In this case, however, individual-level conformity was independent of group size or the mean distance to a fish's nearest-neighbour over the trial (table 1*b*).

Conformity resulted in individuals adopting movement characteristics that were group-size-dependent. The Markov model was able to detect differences between the movements of a fish in asocial versus social trials, no matter what group size individuals were in (binomial test: $n = 74$, $N = 96$, $p = 0.5$, $p < 0.001$). In addition, it detected differences between the way a fish moved in asocial trials, the movement of a fish in smaller groups (two or four fish) and the

Table 2. Linear mixed-effects model investigating the effect of movement scores in the asocial trial ((a) median speed, (b) variance in speed and (c) turning speed), group size (as a categorical variable) and body size, on movement score in the social trial. Individuals are consistent in their median speeds and median turning speeds between contexts, but not their variance in speed. Significant p-values at the 0.05 level are shown in bold.

fixed effect	value	s.e.	d.f.	t-value	p-value
(a) median speed (mm s^{-1})					
intercept	59.140	5.460			
individual	0.062	0.028	130	2.210	**0.029**
group size = 4	−0.359	4.778	33	−0.075	0.941
group size = 8	6.059	4.755	33	1.274	0.211
body size	−0.642	0.705	130	−0.910	0.364
(b) variance in speed (mm^2 s^{-2})					
intercept	1541.963	229.261			
individual	0.069	0.042	130	1.655	0.100
group size = 4	−120.140	160.507	33	−0.749	0.460
group size = 8	14.820	158.844	33	0.093	0.926
body size	46.130	33.790	130	1.365	0.175
(c) median turning speed (rad s^{-1})					
intercept	1.129	0.082			
individual	0.144	0.028	130	5.117	**<0.001**
group size = 4	0.001	0.063	33	0.021	0.983
group size = 8	0.080	0.063	33	1.277	0.211
body size	−0.065	0.011	130	−5.719	**<0.001**

movement of a fish in larger groups of eight fish (binomial test: $n = 45$, $N = 72$, $p = 1/3$, $p < 0.001$). Individuals therefore adopted movement characteristics that were dependent on the group size they were in.

The level to which individuals conformed to each other's behaviour also affected some group-level characteristics. For groups of two or eight individuals, groups with a lower variance between group members' median social speeds were more cohesive than groups with a higher variance between group members' median social speeds (groups of two: Pearson correlation, $r = 0.71$, $p = 0.01$; groups of eight: Pearson correlation, $r = 0.62$, $p = 0.03$). However, this was not the case in groups of four (Pearson correlation, $r = 0.136$, $p = 0.673$). Instead, in groups of four, groups with lower average social turning speeds between shoal mates were correlated with higher shoal cohesiveness (Pearson correlation, $r = 0.62$, $p = 0.03$), while this trend was not evident for groups of two or eight (groups of two: Pearson correlation, $r = 0.33$, $p = 0.29$; groups of eight: Pearson correlation, $r = 0.40$, $p = 0.19$). There was no evidence that the level of conformity (again measured as the variance between individuals' social speeds) affected the median speed of the group in any group size (groups of two: Pearson correlation, $r = 0.07$, $p = 0.82$; groups of four: Pearson correlation, $r = 0.48$, $p = 0.12$; groups of eight: Pearson correlation, $r = 0.37$, $p = 0.24$). Nor was there any evidence that the level of conformity affected group polarization (variance between individuals' median social speeds; groups of two: Pearson correlation, $r = -0.47$, $p = 0.119$; groups of four: Pearson correlation, $r = 0.21$, $p = 0.51$; groups of eight: Pearson correlation, $r = -0.23$, $p = 0.47$; variance between individuals' median social turning speeds; groups of two: Pearson correlation, $r = -0.12$, $p = 0.72$; groups of four: Pearson

correlation, $r = 0.32$, $p = 0.31$; groups of eight: Pearson correlation, $r = -0.31$, $p = 0.32$).

Although individuals conformed to the behaviours of others, they also retained some key aspects of their movement signatures. There was no evidence that these consistent individual signatures were an artefact of individuals leaving the group and behaving independently of group members (linear mixed-effects model for speed: effect of average NND: $F_{1,131} = 1.483$, $p = 0.226$; linear mixed-effects model for effect of group size: $F_{2,33} = 1.093$, $p = 0.347$ turning speed: effect of NND: $F_{1,131} = 0.469$, $p = 0.495$; effect of group size: $F_{2,33} = 1.668$, $p = 0.204$). In particular, the characteristic median speed and median turning speed of fish in the asocial trials was retained to an extent in the social context, although their variance in speed signature was lost (table 2). Group size and individual body size had no effect on the maintenance of speed signatures, and there were no significant interaction effects between these variables (table 2a). Both body size and asocial turning speed (but not group size) predicted average turning speed in a group (table 2c). There was no evidence, however, that individuals occupied different positions within the group depending on their asocial movement preferences or their social movements preferences (linear mixed-effects model for asocial movement component: effect of behaviour: $F_{1,131} = 0.59$, $p = 0.45$; effect of group size: $F_{2,33} = 0.01$, $p = 0.99$; linear mixed-effects model for social movement component: effect of behaviour: $F_{1,131} = 0.47$, $p = 0.49$; effect of group size: $F_{2,33} = 0.007$, $p = 0.99$).

We also used the Markov models to detect an individual's movement signature in a group from its movement signature in its asocial trial. In group sizes of two and four, individuals' asocial trial models could successfully predict their own

movement signature in a group compared with other randomly assigned individuals' asocial models (groups of two: mean rank = 59.54, $V = 60$, $p < 0.01$; groups of four: mean rank = 73.90, $V = 429$, $p = 0.05$). In group sizes of eight, however, the models were unable to correctly identify individuals' movement signatures in groups from their asocial models (mean rank = 88.43, $V = 2532$, $p = 0.77$). As group size increased, therefore, our analysis suggests that individuals lost some aspects of their movement signatures.

Finally, we aimed to predict group-level properties—in this case, the median speed of the centroid of the group—from how a group's members had behaved asocially. In groups of two, the fastest individual's median asocial speed in the pair could predict the median speed of the centroid of the group (Pearson correlation, $r = 0.754$, $p = 0.005$). In groups of four and eight, on the other hand, the fastest asocial individual's median speed could not predict the group's median speed (Pearson correlation, $r = 0.324$, $p = 0.30$; Pearson correlation, $r = -0.038$, $p = 0.91$, respectively). In the largest group size, there was a trend, although non-significant, for the median of all individuals' median asocial speeds to predict the median centroid speed of the group (groups of two: Pearson correlation, $r = 0.311$, $p = 0.33$; groups of four: Pearson correlation, $r = 0.246$, $p = 0.44$; groups of eight: Pearson correlation, $r = 0.523$, $p = 0.08$).

4. Discussion

By recording the fine-scale movement characteristics of individual fish in both asocial and social contexts, we have determined how individual-level behaviour is maintained, but also adapted, according to the social context. We first showed that between asocial contexts, individuals exhibited repeatable aspects of their movement signature, including their median speed, variance in speed and median turning speed. In social contexts, we could detect an individual's asocial median speed and median turning speed signature in every group size, but not their asocial variance in speed signature. Using a different analytical method, our Markov models could also detect asocial individual movement signatures in groups of two or four individuals, but not in groups of eight. But although individuals maintained their movement signatures to some degree, they also adapted them, which led to group-level conformity. In particular, individuals behaved more similarly to each other in social rather than in asocial contexts. In group sizes of two and eight, groups with higher levels of conformity were also more cohesive. Individuals also reduced the variability of their own individual behaviour in groups and adopted group-level movement characteristics that were dependent on the group size they were in. In particular, there were specific differences in movement signatures between individuals on their own, individuals in group sizes of two or four and individuals in group sizes of eight, as demonstrated by our Markov model. We did not find any evidence, however, that individuals self-assorted into positions relating to either their asocial or social movement signatures. Finally, predicting group-level properties was group-size-specific, with the fastest individual's asocial speed of a pair predicting the median centroid of a group, while the median asocial speeds of all group members was a better predictor of group speed in groups of eight.

If individuals are to realize the benefits of group living, individuals should conform, at least to some extent, to the behaviour of their group members [16]. In our trials, individuals clearly demonstrated this process, as the variation between individuals' movement signatures decreased in groups compared with when those individuals were tested on their own. Furthermore, individuals reduced the variation in their own speed in groups, indicating individual-level conformity. Behavioural conformity such as this, both at the individual and group levels, stops individuals from 'standing out from the crowd', otherwise known as the oddity effect [37], or becoming isolated from the group. This in turn reduces an individual's likelihood of predation [37,38]. Total behavioural conformity, however, where individuals display no behavioural differences in groups, was not reached in the group sizes tested here and individuals maintained some aspects of their individual movement signatures in groups. This is important, because if some individuals conform completely to the behaviour of other group members, then they may suffer consensus costs under certain conditions [21]. Our results demonstrate that when individuals with different behavioural preferences are in the same group, these individuals can maintain group cohesion, while not abandoning their individuality by completely conforming to a subset of individuals or a despotic group member. By doing this, compromise over the timing and direction of collective movements can be reached, and individuality maintained, at least to some degree [22].

In the largest group size tested here (i.e. eight individuals), it became increasingly difficult to detect an individual's movement signature. This suggests that in larger group sizes still, individuals may not show any of their asocial behavioural preferences. Again, this is likely to be driven by the need to conform and, in particular, reduce an individual's likelihood of predation. But confusion effects, where predators find it more difficult to select an individual prey item in the group [37], do not necessarily require complete coordinated behaviour [39]. Therefore, this may allow individuals to maintain some aspects of individuality in larger groups, while not suffering oddity effect costs. Hence, individuality may be maintained in larger groups, but this remains to be tested.

Although conformity was clearly apparent in these groups, the mechanism behind the manifestation of conformity remains unclear. However, it must be driven by the interaction rules between individuals and the instances when an individual decides to follow or copy a neighbour's movements. Therefore, whether an individual maintains its individual signature is likely to scale with group size, as the number of potential interactions with group members increases over time. This in turn may lead individuals in groups to display group-size-dependent movement characteristics. Both these predictions are consistent with the findings in our study. Also, in certain contexts, such as in novel environments, the need to conform may be higher as individuals benefit from gathering social information from group members rather than relying on their own minimal private information [40]. In such cases, this may place more importance on conformity over individual signature retention. Future studies should investigate the role of conformity over longer time periods, where individuality may return after the amount of private information collected from the environment increases, and reliance on social information diminishes. Determining the instances when an individual decides to follow others and instances when an individual decides to ignore social interactions will

determine the mechanism underlying conformity and highlight its inter-relationship with individual signature retention.

As individuals conformed to the behaviour of their group members, they adopted movement characteristics that were group-size-dependent. Specifically, individuals had different movement characteristics depending on whether they were on their own, in groups of two or four, or in groups of eight. The ability to predict the behaviour of individuals as a function of the group size that they are in provides a powerful demonstration of the effect of social context in shaping behaviour [16]. Further, predicting how individuals will behave in groups, through both empirical and modelling work, is an important step towards predicting what properties these groups will display [41–43]. Our analysis of group-level properties, such as a group's median speed, shows that in small groups the asocial speed of the fastest individual is an important determinant, whereas in larger groups, the median asocial speed of all group members is more important. Our work provides a foundation for future investigations into this area, and will provide predictions and methods for investigating individuality in other animal groups, including human crowds [44]. We suggest the field of collective behaviour will benefit now from a new generation of collective movement models, including specific and consistent individual differences in agents, much as in the study by Romey [10]. Such models will aid in predicting what group-level properties may be affected by having individual differences between group members, leading empiricists to compose groups of specific behavioural phenotypes to test and validate model predictions.

Other studies have also demonstrated that individuals can maintain particular individual behavioural traits in social contexts. For example, in a recent study, individual fish in a decision-making task consistently occupied particular positions in the group, while experimenters controlled for satiation levels, size and sex [45]. Other studies also report that the maintenance of these traits depends on both the level of the trait and state dependencies. In perch (*Perca fluviatilis*), for example, traits such as time spent in open habitat are consistently expressed between asocial and social contexts (groups of four fish); however, bolder individuals changed their behaviour less between contexts [46]. Similarly, three-spined sticklebacks (*Gasterosteus aculeatus*) maintain their behavioural traits in a pair, where the bolder individual of the pair will initiate more foraging trips, while a shyer individual will follow [11,47]. However, when satiation levels are manipulated, and the bolder of two individuals is fed while the shyer individual is left unfed, then the shyer individual changes its behaviour and initiates more foraging trips [47]. State-dependent behavioural plasticity is an important component of individuality and would be particularly interesting to study in larger groups because our results suggest that as group size increases, individual signatures get weaker and become harder to detect. This may cause factors such as state dependence to play a more important role in shaping the structure and leadership of larger groups, rather than individual differences.

Belonging to a group exposes individuals to the behaviour or opinions of others, and results in costs and benefits associated with following or adopting others' decisions [48]. Retaining individuality in groups is important, therefore, as it allows individuals to balance the energetic demands and behavioural needs specific to each individual [49]. If individuals can retain some aspects of their individual behaviour, they may be better suited to group living than either total conformists, who lose all trace of individuality, or nonconformists, who maintain all or most aspects of their asocial behaviour. Trading off between these two behavioural strategies is likely to have been an important selective factor in the evolution of grouping behaviour.

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