Personality variation is eroded by simple social behaviours in collective foragers

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ABSTRACT

The movement of groups can be heavily influenced by ‘leader’ individuals who differ from the others in some way. A major source of differences between individuals is the repeatability and consistency of their behaviour, commonly considered as their 'personality', which can influence both position within a group as well as the tendency to lead. However, links between personality and behaviour may also depend upon the immediate social environment of the individual; individuals who behave consistently in one way when alone may not express the same behaviour socially, when they may be conforming with the behaviour of others. Experimental evidence shows that personality differences can be eroded in social situations, but there is currently a lack of theory to identify the conditions where we would expect personality to be suppressed. Here, we develop a simple individual-based framework considering a small group of individuals with differing tendencies to perform risky behaviours when travelling away from a safe home site towards a foraging site, and compare the group behaviours when the individuals follow differing rules for aggregation behaviour determining how much attention they pay to the actions of their fellow group-members. We find that if individuals pay attention to the other members of the group, the group will tend to remain at the safe site for longer, but then travel faster towards the foraging site. This demonstrates that simple social behaviours can result in the repression of consistent inter-individual differences in behaviour, giving the first theoretical consideration of the social mechanisms behind personality suppression.

INTRODUCTION

How groups move collectively can depend upon which individuals have influence (Conradt and Roper, 2005; MacGregor et al., 2020; Sumpter, 2010). Much attention has been paid to the behaviour of groups when individuals can behave autonomously but also respond to the actions of their neighbours, and models have been successful at simulating group behaviour that corresponds to natural patterns of flocking and shoaling. These models typically consider individuals making movement decisions based on the presence or absence of local neighbours and their proximity (Aoki, 1982; Bernardi and Scianna, 2020; Calovi et al., 2015; Couzin et al., 2002; Gueron et al., 1996; Huth and Wissel, 1992; Viscido et al., 2002; Wood and Ackland, 2007), where individuals in close proximity may copy, or be strongly influenced by, each other's behaviour (*e.g.* Evans et al., 2018; Hoyle et al., 2021; Lecheval et al., 2018; Rands et al., 2014). The behaviour of individuals in a group can be disproportionately influenced by a few individuals, who act as leaders (Biro et al., 2006; King and Cowlishaw, 2009; Pettit et al., 2015; Watts et al., 2017). These individuals may hold useful information (Dall et al., 2005; Danchin et al., 2004; McComb et al., 2011; Rands, 2010) and influence the movement of the group solely through their actions (Bernardi et al., 2021; Couzin et al., 2005; Ioannou et al., 2015; Lachlan et al., 1998), or through the imposition of social hierarchies (Hemelrijk, 2000; Rands et al., 2006). Physical differences between individuals may cause some individuals to take specific positions within a group (Killen et al., 2012; Reebs, 2001). Leadership decisions may also be made by individuals who are in a specific behavioural or physical state at a given moment in time (Garland et al., 2018; Niemelä and Dingemanse, 2018; Rands et al., 2008, 2003). Consistent with this, behavioural and physiological state can influence the position of individuals within groups where hungry individuals position themselves at the front of the group where they are more likely to find food (Balaban-Feld et al., 2019; Krause, 1993; Romey, 1995), trading an increased chance of energetic gain for an increased risk of predation (Ioannou et al., 2019). The movement of individual fish in shoals is influenced by their nutritional state, and it is likely that the behaviours of single fish is dependent not only on their own state, but also that of their neighbours (Hansen et al., 2015a).

These mechanisms demonstrate that the movement of groups can be heavily influenced by individuals who differ in some way, regardless of whether this inter-individual variation is long-term or transient. Apart from physical differences such as size, a major source of long-term differences between individuals is in the repeatability and consistency of their behaviour. This is commonly considered to be the 'personality' of an individual animal (Carere and Maestripieri, 2013; Dall et al., 2004; Sih et al., 2004). The personalities of

individuals can influence both their position within a group (Aplin et al., 2014; McDonald et al., 2016; Tang and Fu, 2020), and their tendency to lead (Beauchamp, 2000; Harcourt et al., 2009). For example, consistently 'bold' individuals are willing to accept greater risk in the same manner that leaders in many animal groups do, and hence bold individuals often lead group decisions (Harcourt et al., 2009; Ioannou and Dall, 2016). However, even if individuals are behaviourally consistent over time and contexts, their behaviour may still be influenced by their social environment (Webster and Ward, 2011). Individuals who behave consistently on their own may not express this behaviour in a group when they conform to other group members' behaviour (Herbert-Read et al., 2013; McDonald et al., 2016), and this conformity effect can be stronger in more sociable individuals who are more likely to be influenced by others' behaviour (Bevan et al., 2018).

While these experimental results show that strong personality differences can be eroded in social situations, there is a lack of modelling to establish under what conditions we would expect inter-individual (*i.e.* personality) variation to be suppressed, or still be expressed, when individuals interact in groups. The study by McDonald *et al.* (2016) considered the group decisions made by small fish (three-spined sticklebacks, *Gasterosteus aculeatus*) choosing to cross an open space between a refuge and a known food source. These fish could be seen as making a typical trade-off between perceived predation risk (elevated when crossing the open space and at the foraging site) and starvation (Houston et al., 1993; Houston and McNamara, 1993; Lima and Dill, 1990). When travelling this short distance on their own, the behaviour of solitary fish reflects this risk-taking trade-off (Rands, 2017) and was shown to be repeatable, *i.e.* the fish demonstrated personality variation in boldness (McDonald et al., 2016). However, when in groups, the fish were influenced by social factors as well: being in a group reduced the time taken to travel between the refuge and the food source for the average individual, but it also suppressed personality variation. Here, we present a model motivated by the experiment conducted by McDonald *et al.* (2016) that considers what happens when we create groups from individuals who would be consistently different if they were behaving on their own. Assuming that there are benefits for reducing predation risk from remaining in close proximity to other group members, we also explore the effects of simple social interaction rules that may influence the behaviour of individuals, echoing previous models considering social herding behaviour under predation risk (Hamilton, 1971; Morrell et al., 2015; Morrell and James, 2008; Morton et al., 1994; Rands et al., 2004). Using this model, we explore whether simple social interaction rules are sufficient to erode consistent behavioural differences between individuals.

METHODS

The models

The models consider a linear (one dimensional) environment, consisting of a home refuge site, a foraging site located in the region greater or equal to d_{food} distance units away from the home site in one direction, and a continuous strip of food-free space between them. Within the environment, there are n individuals, and at a given time period t each individual i is located at a point $d_{i,t}$ distance units away from the home site. All individuals are assumed to have constant personal speeds, so if an individual moves during a period, it moves s_i distance units towards or away from the home site. Whether and where to move is dependent upon the individual's probability of moving outward to the foraging site, which is characterised by two parameters. The first of these is a time-dependent probability of moving outward $p_{i,t}$, which increases as time passes and represents a growing need by an individual to move to the site where food is available. Secondly, individuals are characterised by a personal outward probability adjustment ω_i, which represents the boldness if the individual. If the model includes social behaviour, the decision is also influenced by the current position of the other individuals within the environment.

At the start of a simulation $t = 0$, n individuals are created. Each individual $i = 1 \ldots n$ has a time-dependent probability of moving outward $p_{i,t}$, which is initially set at a baseline common to all individuals, $p_{i,0} = p_{baseline}$. At the same time, the individual's personal outward probability adjustment is set at $\omega_i = (i–1).\omega_{difference}$. Individual 1 has a personal outward probability adjustment set at 0, and the other individuals have personal outward probability adjustment values that increase regularly by $\omega_{difference}$. This means that the identity i of an individual defines its likelihood of choosing to move outwards, falling on a movement hierarchy where individuals with low values of i are less likely to move. The speed s_i of individual i is independently sampled from a uniform distribution $U(0.95, 1.0)$. The initial location of all individuals is at the home site, so $d_{i,0} = 0$.

Subsequent periods are then considered sequentially, starting at $t = 1$. During a period, each individual makes a single decision, and the order that the different individuals make and then act on their decision is randomised at the start of each period. Firstly, the time-dependent probability of moving outward is adjusted to $p_{i,t} = p_{i,t-1} + \omega_i$ (so at each timestep, each individual becomes more likely to move outward, and the difference between individuals in

their values of ω_i means that outward movement probability increases faster for bolder individuals). The individual then makes its movement decision: if the refuge site lies between itself and the foraging site (so $d_{i,t-1} < 0$), it moves towards to foraging site such that $d_{i,t} = d_{i,t-1} + s_i$; if it is at the foraging site ($d_{i,t-1} \geq d_{food}$), it does not move (so $d_{i,t} = d_{i,t-1}$); whereas if it is positioned between the refuge and foraging site ($0 \leq d_{i,t-1} < d_{food}$), it draws a random value from a uniform distribution $U(0,1)$. If this random value is below $p_{i,t}$, it moves towards the foraging site ($d_{i,t} = d_{i,t-1} + s_i$), otherwise it conducts a social action dependent upon which of the four social rules it uses.

The social interaction rules all calculate a metric that allows the individual to choose between two positions (moving to $d_{i,t-1} + s_i$ or $d_{i,t-1} - s_i$), or staying put at $d_{i,t-1}$. They are:

1) **central**: move towards the weighted centre of group. Here, the two positions that could be moved to (either towards or away from the foraging site) are assessed for how 'central' they are to the group, using a summed weighting function that gives lower weight to closer neighbours

$$w(d_{i,t}) = \sum_{\forall j \neq i} \left[k_{max} - (k_{max} - k_0) e^{-a|d_{i,t} - d_{j,t}|} \right] / n, \qquad (1)$$

where k_{max}, k_0 and a are constant terms (set in calculations at 0.1, 0.15 and 0.1 respectively, although these exact values have no effect on the behaviour, as all results are quantitatively identical provided $k_{max} > k_0$). The focal individual then moves to the point that has the lowest summed weight, or remains where it is if the weights of both travel locations are identical.

2) **nearest-neighbour**: move towards the nearest neighbour. The focal individual identifies its closest neighbour (or randomly chooses a nearest neighbour, if there are more than one), and then moves s_i units in the direction towards (or past) the identified neighbour. If the nearest neighbour occupies $d_{i,t-1}$ the focal individual does not move.

3) **majority**: move towards majority of group. The focal individual identifies whether there are more colleagues towards the foraging site or the refuge. It then moves s_i units in the direction of the majority. If there are equal numbers of individuals in either direction, the focal individual does not move.

4) **non-social** behaviour. Here, the focal individual does not move if the 'social' behaviour is chosen.

All individuals act on a single movement decision once during a period. A simulation continues until all individuals are within the foraging site at the end of a period.

Model exploration: effects of model parameters

Two parameters were identified that could affect the behaviour of the modelled group: the baseline time-dependent probability of moving outward $p_{baseline}$ (where an increasing value means that individuals are going to start moving outwards after a shorter period of time, *i.e.* are bolder), and the outward probability adjustment parameter $\omega_{difference}$ (where a larger value means that there is an increase in the separation in probabilities that individual group members move outward, *i.e.* they become more different from one another). The distance to the foraging site d_{food} and the size of the group n were also assumed to affect group behaviour. Using baselines of $\omega_{difference}$ = 0.001, $p_{baseline}$ = 0.001, d_{food} = 100 units and n = 10, we explored the effects of altering these target parameters by systematically changing a single parameter away from its baseline and running 10,000 simulations for each resulting parameter set for each of the four social interaction rules (including the non-social behaviour). These single parameter explorations considered $p_{baseline}$ = (0.0001, 0.0002, … 0.0020), $\omega_{difference}$ = (0.0001, 0.0002, … 0.0020), d_{food} = (20, 30, … 200 units), and n = (5, 10, … 50). Simulations were built and run using *NetLogo* 5.3.1 - 6.2 (Wilensky, 2003, 1999).

Six statistics were recorded from each simulation to measure group behaviour. The number of periods until the end of each simulation was recorded to measure the number of timesteps taken for all group members within the simulation to reach the foraging site. One individual from each simulation was also chosen at random to be a focal individual to collect statistics from. As well as the identity of this individual (corresponding to its position within a movement hierarchy), we recorded the time it took to first move past a threshold distance (taken to be ten distance units from the refuge, referred to as its 'departure' time) and the latency between this individual's time and that of the first individual to pass this threshold within the simulation. We also recorded the time it took the focal individual to reach the foraging site, and the latency between this time and that of the first individual to reach the foraging site within the simulation. Because each individual in a group was equally likely to be the randomly chosen focal individual, recorded latency values therefore represent an

average latency after the first individual to pass the threshold or arrive at the foraging site (where if the first individual to arrive is being tracked, it is assumed to have a latency of zero). From these statistics, we also calculated the time each focal individual took to travel between crossing the threshold and arriving at the foraging site.

Data were explored within *R* 3.3.0-4.1.2 (R Development Core Team, 2017). Exploratory graphs were generated using *ggplot2* 3.3.5 (Wickham, 2009) both for the average of a simulated group (calculated as the mean value for all individuals followed for a given parameter value, regardless of the hierarchical identity of those individuals), and for focal individuals with a known position within a movement hierarchy (although the latter was not considered when changing n, due to the confounding effects of increasing the size of the group). In order to quantify the difference in variation within and between the increments of target parameters during the exploration, we ran standard ANOVA tests with the altered parameter as the explanatory variable and the behavioural measure as the response. We extracted the resulting F values as a measure of the ratio of variance between and within each of the increments of the target parameter. Larger F values indicate larger effects of changing the target parameter relative to the variation between replicates of the simulation with identical parameters.

Model exploration: variation between individuals

We also ran smaller sets of simulations where the travel time, departure time and arrival time of all individuals within a group of 10 individuals were recorded. This allowed quantification of how difficult it was to identify differences between interacting individuals within a simulation based on the inter-individual variation in their personal outward probability adjustment ω_i (equivalent to personality variation in boldness). We tested how the variation between individuals within a simulation was shaped by the four parameters ($\omega_{difference}$, $p_{baseline}$, d_{food} and n) considered in the models. To do this, we ran four sets of simulations where three of the parameters were held constant, and the fourth was systematically altered. Using baselines identical to the earlier model ($\omega_{difference}$ = 0.001, $p_{baseline}$ = 0.001, d_{food} = 100 units, n = 10), we systematically changed a single parameter away from its baseline, using $p_{baseline}$ = (0.0001, 0.0002, … 0.0020), $\omega_{difference}$ = (0.0001, 0.0002, … 0.0020), d_{food} = (20, 30, … 200 units), or n = (5, 10, … 50), and ran 200 simulations for each resulting parameter set for each of the four social interaction rules (including the non-social behaviour). This systematic alteration of a single parameter meant that we were able to generate four datasets where there was a large and evenly-spread

amount of variation in a single parameter, with no variation in the other three parameters. This meant that we could observe how individual differences in behaviours within a group could be affected if there was variation in a single parameter.

The travel time, departure time and arrival time for all individuals in the set were rescaled such that the minimum time within the group was set equal to 0 and the maximum to 1. In order to quantify how difficult it was to distinguish individuals within a group, we measured the variation between individuals within each group (*i.e.* within each run of the simulation) relative to the variation between groups (different runs of the simulation with the same set of parameters). This was done using repeated-measures ANOVA tests with the value of the single altered model parameter and the identity of the individuals (their position within the initial movement hierarchy) repeated within a simulation as the two explanatory variables, and the behavioural measure as the response (the rescaled timings for each individual), and extracted the resulting *F* values. Larger *F* values indicate greater between-group variation, so that individuals within the same group show more similar behaviour, and hence inter-individual variation within a group is more difficult to detect.

To explore the difference between social and non-social behaviours, for the simulation sets described above where $\omega_{difference}$, $p_{baseline}$, d_{food} and n were systematically altered we calculated the difference between the rescaled time parameters for each of the three social interaction rules and the non-social behaviour, giving a value between -1 (the focal individual took the minimum time when behaving socially and the maximum time when behaving non-socially) and +1 (the focal individual took the maximum time when behaving socially and the minimum time value when behaving non-socially).

RESULTS

figure 1 near here

In most cases and as expected, increasing either of the parameters generating outward movement ($\omega_{difference}$ and $p_{baseline}$) led to all measured behaviours happening faster or sooner (figures 1 and S1, where the transition from green to yellow indicates an increase the value of the target parameter), regardless of the social interaction rule being used. Similarly, increasing the distance to the foraging site tended to cause behaviours to take longer or

happen later (figure S2), whilst increasing group size meant behaviours tended to occur sooner or faster (figure S3).

For most of the parameter sets investigated, the groups with social interactions conducted the measured behaviours faster or sooner than the corresponding groups of independently-behaving non-social individuals (Figures 1 and S1-S3). Exceptions to this occurred when considering the time at which the first individual passed beyond the threshold distance from the starting point ('leave time' in Figure 1), particularly when the group was using the central social interaction rule where attraction was towards the weighted centre of the group. This was not the case, however, when the group was using the majority rule, and this was one of the few cases that the central and majority rules gave qualitatively different results, with the nearest neighbour rule being intermediate between these two rules. Confirming that the central and majority rules resulted in greater cohesion of the groups, the latencies between the first and other individuals to leave the refuge and to arrive at the foraging site (rows d and f, respectively, in Figures 1 and S1-S3) were much faster with these rules compared to the nearest neighbour and non-social rules, which were more similar to one another.

Direct pairwise comparisons between the social rules (figures S4-S7) demonstrate that the different social interaction rules have differing effects upon the behaviours observed. The total time until the end of the simulation was minimised by the central and (to a lesser extent) majority rules, and took the longest in the simulations with no social interactions between the individuals. While the central and majority rules resulted in similar times until the end of the simulation, the later departures by the groups using the central rule were compensated for by shorter travel times, thus groups using the central rule were exposed to risk between the refuge and foraging sites for less time. Compared to the majority rule, these shorter travel times for the average individual can be explained by the groups using the central rule being more cohesive, with shorter latencies between the first and other individuals when departing from the refuge.

Increasing $\omega_{difference}$ (the difference between individuals in their tendency to move toward the foraging site, figure S4), $p_{baseline}$ (the default level of boldness of individuals in each group, figure S5), d_{food} (the distance the group needed to travel, figure S6), and the group size n (figure S7) in general had little effect on the differences between the social rules. However, the benefit of having social interactions in reducing the time until all individuals had arrived at the foraging site increased as $\omega_{difference}$, d_{food} and group size increased and as $p_{baseline}$ decreased. These trends can be explained by social interactions allowing bolder individuals

to have social influence on the slowest individual in the group (which determines the time until the end of the simulation) by reducing the time taken by the slowest individual. $\omega_{difference}$ and group size increase the boldness of the bolder individuals in the group and if social interactions are present, their influence reduces the time taken by the slowest individual. In contrast, the slowest individual does not become bolder and hence faster as these parameters increase when there are no social interactions (figure 1a, S3). This also explains why increasing the boldness of the shyest individual (by increasing $p_{baseline}$) reduces the difference in the time taken between the social and non-social rules, as the time to the end of the simulation for groups with social interactions are much less affected by $p_{baseline}$ than groups without social interactions (figure S1a). Increasing d_{food} slows the time taken until the end of the simulation to a greater extent in non-social groups, thus as d_{food} increases, the benefit of social interactions increases as social influence acts a buffer on the speed of the slowest individual in the group. The figures S4-S7 also demonstrate that there are large variances around these results, and the different rules tend to overlap in their performance despite the obvious qualitative differences, suggesting that there is a lot of noise (from stochasticity within both individual behaviour and between simulations) in the behaviours recorded.

figure 2 near here

Thinking forward to empirical tests of the model predictions, it is important to quantify the amount of variation between runs of the simulations, as the overlap between the results generated for differing values of the same parameter dictates how easy it would be to successfully identify a true difference between experimentally manipulated groups. For example, in figure 1a, the vertical error bars (denoting the standard deviation of the measured end of simulations for groups using the central social behaviour, with the change in line colour representing a systematic increase in $\omega_{difference}$) show very little overlap. Conversely, looking at the horizontal (non-social) error bars in the same panel, there is nearly complete overlap for all values of $\omega_{difference}$, suggesting that it would be impossible to discern a difference regardless of the value of $\omega_{difference}$ used in a simulation. Higher values in figure 2 denote cases where most variation in a measured behaviour occurs between different values of the parameter rather than the variability being between replicates with the same parameter values. This suggests behaviours that would be useful to measure in empirical studies either manipulating these parameters (*e.g.* by manipulating group composition to vary $\omega_{difference}$) or relying on naturally occurring differences in these parameters, such as comparisons between populations under different selection pressures.

Low values denote cases where the amount of variation within responses to a given value of a parameter are similar to that seen from all values of the parameter. In general, the time until the end of the simulation, the travel time and the arrival time were sensitive measures allowing the effects of the manipulated parameters to be detected, although for the time to the end of the simulation in particular, this did depend on the social interaction rule being used (note the log scale). The leave time, leave latency and arrival latency did not perform as well, especially when testing for the effects of differing distances to the foraging site (also see figure S2c,d,f).

figure 3 and table 1 near here

Groups do not consist of individuals behaving in exactly the same way: the $\omega_{difference}$ parameter initialises the differences in movement probability between a group's members from the very start of the simulation. This imposed difference means that some individuals are behaviourally predisposed to leave the refuge and move to the foraging site earlier in the simulation than others. If we consider a group where its members are using the non-social behavioural rule, it is equivalent to the group's members moving on their own, without social interactions. If we compare these non-social results to the behaviour of identical groups following social rules in an identical environment, we can explore the effects of the social rules on group members. Figure 3 shows the (rescaled) movement times for individuals within a simulation. Individuals using the non-social rule behave as would be expected: those that were behaviourally predisposed to leave the refuge and move earlier (*i.e.* bold individuals) took less time to travel to their destination (as shown by travel times in figure 3a falling as the individual's identity – corresponding to the probability of it moving outwards – increases), with both their leave times (figure 3e) and arrival times (figure 3i) correspondingly falling. Adding social rules did not completely remove the effect of $\omega_{difference}$ on the order in which individuals arrived, but did make it much more difficult to discern between individuals. This is shown by the greater overlap in the distributions of times for all individuals within a simulation, especially between the 'shy' individuals least likely to start moving towards the foraging site (the lower numbered individuals in figures 3b-d, f-h and j-l). Table 1 quantifies this overlap in behavioural metrics for individuals, showing much lower overlap (higher *F* values) for the non-social rule. The behaviour being measured was also important; it would be very difficult to discern between individuals if using leaving time as a metric (as can be seen in figure 3d and the corresponding low *F* value in Table 1). Arrival time gives the best opportunity for discerning between individuals (the high *F* value in Table 1), although figure 3f demonstrates that this difference is probably going to be more visible in

the individuals that are predisposed to moving earlier (those individuals with higher values in figure 3). For the travel and leave times, individuals were easier to discern if they were using the nearest neighbour interaction rule compared to the other social interaction rules, although they were easier to discern when using the majority rule when arrival times were measured. Table 1 demonstrates that these trends are similar when systematically altering $p_{baseline}$ and d_{food}.

figure 4 near here

Differences between the behaviours shown by specific individuals within a group are most visible in those individuals that are most likely to move towards the foraging site, as can be seen in individual 1 in the social behaviours shown in figure 3: the behaviour of these individuals appears to be least influenced by other members of the group, with the smaller range of variation across the simulations showing that these individuals still tended to be last to conduct behaviours when they were moving within a socially-behaving group. If we look at how the behaviour of individuals changes between using the non-social rule and one of the social rules (figure 4), it is apparent in many cases that individual 10 shows little change in behaviour, with behavioural differences close to zero meaning that there is no difference when using non-social or social rules. This is not the case when considering the leave time (figures 4d and f, and 4e to a lesser extent), where a positive value indicates that even the most motivated individuals tend to take longer to move away from the start point when behaving socially compared to when they behave independently of other individuals. Most of the other individuals show this slower behaviour in travel time, leave time and arrival time when social, with the exception of individual 1 (the least likely individual to move away from the start point when behaving independently), which moves faster when behaving socially than when non-social.

For individuals who are neither the fastest or slowest to move to the foraging site when behaving independently (*i.e.* those with intermediate values of ω), there were moderate ordering changes when comparing social and non-social behaviours, with individuals tending to shift an observed behaviour to later in the hierarchy when behaving socially. This difference is greatest for individuals in the 'middle' of the group movement parameter set for central and majority social rules (*e.g*. figure 4a), or greatest for the second-most 'shy' individual (individual 2) for the nearest neighbour rule (*e.g*. figure 4b). Contrary to the other nine members of the group, the most 'shy' individual (individual 1) tended to shift its ordering to earlier in the hierarchy when behaving socially. This reflects the cohesive nature of the social group behaviours, where the individual that would normally take longest to travel to

safety is caught up within the group and consequently has an opportunity to conduct a measured behaviour before at least one other of its colleagues, dragging the values shown in figure 4 downwards from the zero values. Because figure 4 shows standardised values, caution should be taken to not interpret the trends shown as indications of behaviours becoming faster or slower. Instead, the broad message of this figure is that social behaviours mean that group members are more likely to be behaving together, and their individual behavioural identities become less easy to identify when observing the group behaving together.

DISCUSSION

It is well established in experimental studies that individuals in groups can forage more successfully than solitary individuals (Grand and Dill, 1999; Ioannou, 2017; Vanthournout et al., 2016). Our model replicates this effect in a simple, idealised scenario by comparing simulations of individuals with no social behaviour, *i.e.* where they acted independently, to simulations with social interaction rules. However, speeds were not always faster in social groups. The social rule of moving to the centre of the group actually increased the time taken to leave the refuge, but reduced the time taken to travel to the foraging site. McDonald *et al.* (McDonald et al., 2016) showed a similar trend, where the median time taken to leave the refuge was marginally longer in groups compared to solitary individuals, but the time taken to cross the arena was considerably faster in groups. The later departures from the refuge for groups using the central rule were more than compensated for by faster travel times between the refuge and foraging site, so that these groups arrived sooner than groups using the other rules. The central rule thus reduces exposure to predation risk during travel to a foraging site but still allows earlier access to the foraging site, and hence would be favoured by natural selection.

Our results also demonstrate that simple social behaviours can result in consistent inter-individual differences in behaviour (widely referred to as personality variation) being repressed. This echoes experimental results (Herbert-Read et al., 2013; McDonald et al., 2016), where behaving as part of a group reduces the expression of behaviours that are consistently shown when an individual is on its own. As McDonald *et al*. (McDonald et al., 2016) note, although social conformity suppressing personality variation is well documented (Koski and Burkart, 2015; Laubu et al., 2016; Webster and Ward, 2011), the mechanisms behind this conformity are not known. McDonald *et al*. (McDonald et al., 2016) provide evidence that quorum-like consensus decision-making might be driving this behaviour

(similar to the majority-movement rule that we consider), but the model we present here demonstrates that other social mechanisms can result in this effect as all three of the social behaviours considered led to social conformity occurring. It is likely that other social behaviours exist that will give similar behaviours (compare for example the various different rules suggested for selfish herding: (Hamilton, 1971; Morrell et al., 2015; Morrell and James, 2008; Morton et al., 1994; Viscido et al., 2002)), and careful experimentation would be required to identify whether these are appropriate for explaining the behaviour seen (such as the technique used by (de Vos and O'Riain, 2013)). The three social interaction rules we present consider an individual as paying attention to different individuals in the group. Huth and Wissel (1992) suggest that paying attention to many neighbours is important – just paying attention the nearest neighbour cannot realistically drive a group's behaviour. We demonstrate that personality erosion occurs both when individuals are considering a single neighbour (the nearest neighbour social rule) and when individuals are accounting for the behaviour of most or all of the group (the central and majority social rules), although the effect of conformity was stronger when a larger proportion of the group are considered. Not only do our results demonstrate that simple social interactions can make discerning between different personality types in groups difficult, but they also imply that selection pressures that would act on personality variation in non-social animals may have no, or a weakened, effect in social groups where conformity reduces the realised differences between individuals (Bevan et al., 2018).

Our model considers a simple drive to move from shelter to a food source, which we allow to differ between individuals. Personality variation can be based on differences in metabolic rate, where those with greater metabolic requirements will consistently show greater risk-taking behaviour which increases access to food (Biro and Stamps, 2010), although, conversely, satiation of bolder individuals after feeding can result in switching of leader-follower roles (Nakayama et al., 2012). Our model can thus represent a simple caricature of a group of individuals being driven by their energetic reserves, where those individuals moving sooner and with a faster increase in their probability to move could be seen as 'hungry' individuals. This is consistent with experiments where food-deprived individuals are mixed with satiated ones, and the hungrier individuals tend to move to food sooner and may drive the behaviour of the rest of the group (Balaban-Feld et al., 2019; Hansen et al., 2015b; James et al., 2004; Krause, 1993; Krause et al., 1998; Romey, 1995). Although in our simulations the predetermined requirement to move towards the food is shown by all individuals, the social interaction rules mean that the movement of individuals is determined not just by 'hunger' but also by the behaviour of the other members of the group. Furthermore, our results suggest that the lag shown by normally bold individuals (that is

revealed by comparing simulations with social and non-social behaviours) may be driven by the reluctance of less bold individuals to move, mirroring the large influences that individuals with specific personality traits may have on the group's behaviour (Brown and Irving, 2014).

Although our model considers a driving force that brings individuals to a food source, we do not explicitly consider energetic reserves or any other physiological processes (Killen et al., 2021). Movement and changing direction may be costly (as is considered by James et al., 2004). Nor do we consider a cost to associating closely together, where collision risk could be a danger (as is considered in the inner repulsion zone considered in many models of collective behaviour (Aoki, 1982; Couzin et al., 2002; Gueron et al., 1996; Huth and Wissel, 1992; Viscido et al., 2002; Wood and Ackland, 2007)). Similarly, we make no assumptions about predation in this model, although the social behaviours we consider echo those considered for social herding behaviour (Hamilton, 1971; Morrell et al., 2015; Morrell and James, 2008; Morton et al., 1994), and it has been demonstrated that individuals may use more complex social behaviour rules (Kimbell and Morrell, 2015), pay attention to more neighbours (Reluga and Viscido, 2005), and make more egalitarian collective decisions (Herbert-Read et al., 2019) when exposed to predation risk.

Given that the rules governing the behaviour of individuals relates to both their internal state and the behaviour of other individuals (where the behaviour of those other individuals is dictated by their own internal state), it would be possible to use modelling tools such as stochastic dynamic games (*e.g.* Rands et al., 2008, 2003) to calculate optimal social rules, which would mean that we could use a little less guess-work in suggesting the heuristics that individuals are using (Rands, 2011a). Following the experiment presented by McDonald *et al*. (2016), we implicitly assume here that all individuals are equally aware of the food source, and alternative assumptions would need to be made to consider the case where only a few individuals are informed (Couzin et al., 2005; Reebs, 2000). Similarly, careful experimental manipulation of the energetic state of individuals in groups may reveal further subtleties in how individuals alter their behaviour to suit their immediate personal condition (Hansen et al., 2016). Potentially confounding hierarchical differences, or differences in being able to compete for food (MacGregor et al., 2020), between individuals would also need to be accommodated (Rands, 2011b; Rands et al., 2008), as social hierarchies may directly confound the energetic states of interacting individuals (Giles et al., 2020, 2015; Jennings et al., 2010; Šárová et al., 2013). Regardless of these additional complexities, we have demonstrated here that simple social behavioural rules can drive conformity behaviour in groups, eroding consistent behavioural differences shown by individual animals.

Author contributions

SAR and CCI designed the model, and SAR coded and analysed it, with input from CCI. SAR wrote the initial draft of the paper, and the final draft was edited and approved by both authors.

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Software availability

Annotated *Netlogo* code is freely available on *figshare* at https://doi.org/10.6084/m9.figshare.19391651.

References

Aoki I. 1982. A simulation study on the schooling mechanism in fish. *Bulletin of the Japanese Society of Scientific Fisheries* **48**:1081–1088. doi:10.2331/suisan.48.1081

Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B* **281**:20141016. doi:10.1098/rspb.2014.1016

Balaban-Feld J, Mitchell WA, Kotler BP, Vijayan S, Tov Elem LT, Abramsky Z. 2019. State-dependent foraging among social fish in a risky environment. *Oecologia* **190**:37–45. doi:10.1007/s00442-019-04395-z

Beauchamp G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour* **137**:301–314.

Bernardi S, Eftimie R, Painter KJ. 2021. Leadership through influence: what mechanisms allow leaders to steer a swarm? *Bull Math Biol* **83**:69. doi:10.1007/s11538-021-00901-8

Bernardi S, Scianna M. 2020. An agent-based approach for modelling collective dynamics in animal groups distinguishing individual speed and orientation. *Phil Trans R Soc B* **375**:20190383. doi:10.1098/rstb.2019.0383

Bevan PA, Gosetto I, Jenkins ER, Barnes I, Ioannou CC. 2018. Regulation between personality traits: individual social tendencies modulate whether boldness and leadership are correlated. *Proc R Soc B* **285**:20180829. doi:10.1098/rspb.2018.0829

Biro D, Sumpter DJT, Meade J, Guilford T. 2006. From compromise to leadership in pigeon homing. *Curr Biol* **16**:2123–2128. doi:10.1016/j.cub.2006.08.087

Biro PA, Stamps JA. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol Evol* **25**:653–659. doi:10.1016/j.tree.2010.08.003

Brown C, Irving E. 2014. Individual personality traits influence group exploration in a feral guppy population. *Behav Ecol* **25**:95–101. doi:10.1093/beheco/art090

Calovi DS, Lopez U, Schuhmacher P, Chaté H, Sire C, Theraulaz G. 2015. Collective response to perturbations in a data-driven fish school model. *J R Soc Interface* **12**:20141362. doi:10.1098/rsif.2014.1362

Carere C, Maestripieri D. 2013. Animal personalities: behavior, physiology, and evolution. Chicago: University of Chicago Press.

Conradt L, Roper TJ. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution* **20**:449–456.

Couzin ID, Krause J, Franks NR, Levin SA. 2005. Effective leadership and decision-making in animal groups on the move. *Nature* **433**:513–516. doi:10.1038/nature03236

Couzin ID, Krause J, James R, Ruxton GD, Franks NR. 2002. Collective memory and spatial sorting in animal groups. *J Theor Biol* **218**:1–11. doi:10.1006/jtbi.2002.3065

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* **20**:187–193. doi:10.1016/j.tree.2005.01.010

Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* **7**:734–739. doi:10.1111/j.1461-0248.2004.00618.x

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH. 2004. Public information: from noisy neighbours to cultural evolution. *Science* **305**:487–491.

de Vos A, O'Riain MJ. 2013. Movement in a selfish seal herd: do seals follow simple or complex movement rules? *Behavioral Ecology* **24**:190–197. doi:10.1093/beheco/ars153

Evans MHR, Lihoe KL, Rands SA. 2018. Black-headed gulls synchronise their activity with their nearest neighbours. *Sci Rep* **8**:9978. doi:10.1038/s41598-018-28378-x

Garland J, Berdahl AM, Sun J, Bollt EM. 2018. Anatomy of leadership in collective behaviour. *Chaos* **28**:075308. doi:10.1063/1.5024395

Giles SL, Harris P, Rands SA, Nicol CJ. 2020. Foraging efficiency, social status and body condition in group-living horses and ponies. *PeerJ* **8**:e10305. doi:10.7717/peerj.10305

Giles SL, Nicol CJ, Harris PA, Rands SA. 2015. Dominance rank is associated with body condition in outdoor-living domestic horses (*Equus caballus*). *Appl Anim Behav Sci* **166**:71–79. doi:10.1016/j.applanim.2015.02.019

Grand TC, Dill LM. 1999. The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? *Anim Behav* **58**:443–451. doi:10.1006/anbe.1999.1174

Gueron S, Levin SA, Rubinstein DI. 1996. The dynamics of herds: from individuals to aggregations. *Journal of Theoretical Biology* **182**:85–98.

Hamilton WD. 1971. Geometry for the selfish herd. *J Theor Biol* **31**:295–311. doi:10.1016/0022-5193(71)90189-5

Hansen MJ, Schaerf TM, Krause J, Ward AJW. 2016. Crimson spotted rainbowfish (*Melanotaenia duboulayi*) change their spatial position according to nutritional requirement. *PLoS One* **11**:e0148334. doi:10.1371/journal. pone.0148334

Hansen MJ, Schaerf TM, Ward AJW. 2015a. The influence of nutritional state on individual and group movement behaviour in shoals of crimson-spotted rainbowfish (*Melanotaenia duboulayi*). *Behavioral Ecology and Sociobiology* **69**:1713–1722. doi:10.1007/s00265-015-1983-0

Hansen MJ, Schaerf TM, Ward AJW. 2015b. The effect of hunger on the exploratory behaviour of shoals of mosquitofish *Gambusia holbrooki*. *Behaviour* **152**:1659–1677. doi:10.1163/1568539X-00003298

Harcourt JL, Ang TZ, Sweetman G, Johnstone RA, Manica A. 2009. Social feedback and the emergence of leaders and followers. *Current Biology* **19**:248–252.

Hemelrijk CK. 2000. Towards the integration of social dominance and spatial structure. *Animal Behaviour* **59**:1035–1048. doi:10.1006/anbe.2000.1400

Herbert-Read JE, Krause S, Morrell LJ, Schaerf TM, Krause J, Ward AJW. 2013. The role of individuality in collective group movement. *Proceedings of the Royal Society B* **280**:20122564. doi:10.1098/rspb.2012.2564

Herbert-Read JE, Wade ASI, Ramnarine IW, Ioannou CC. 2019. Collective decision-making appears more egalitarian in populations where group fission costs are higher. *Biol Lett* **15**:20190556. doi:10.1098/rsbl.2019.0556

Houston AI, McNamara JM. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* **24**:205–219.

Houston AI, McNamara JM, Hutchinson JMC. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B* **341**:375–397.

Hoyle ZE, Miller RA, Rands SA. 2021. Behavioural synchrony between fallow deer *Dama dama* is related to spatial proximity. *BMC Ecol Evo* **21**:79. doi:10.1186/s12862-021-01814-9

Huth A, Wissel C. 1992. The simulation of the movement of fish shoals. *Journal of Theoretical Biology* **156**:365–385.

Ioannou CC. 2017. Swarm intelligence in fish? The difficulty of demonstrating distributed and self-organised collective intelligence in (some) animal groups. *Behav Process* **141**:141–151. doi:10.1016/j.beproc.2016.10.005

Ioannou CC, Dall SRX. 2016. Individuals that are consistent in risk-taking benefit during collective foraging. *Scientific Reports* **6**:33991. doi:10.1038/srep33991

Ioannou CC, Rocque F, Herbert-Read JE, Duffield C, Firth JA. 2019. Predators attacking virtual prey reveal the costs and benefits of leadership. *Proc Natl Acad Sci USA* **116**:8925–8930. doi:10.1073/pnas.1816323116

Ioannou CC, Singh M, Couzin ID. 2015. Potential leaders trade off goal-oriented and socially oriented behavior in mobile animal groups. *American Naturalist* **186**:284–293. doi:10.1086/681988

James R, Bennett PG, Krause J. 2004. Geometry for mutualistic and selfish herds: the limited domain of danger. *Journal of Theoretical Biology* **228**:107–113. doi:10.1016/j.jtbi.2003.12.005

Jennings DJ, Carllin CM, Hayden TJ, Gammell MP. 2010. Investment in fighting in relation to body condition, age and dominance rank in the male fallow deer, *Dama dama*. *Animal Behaviour* **79**:1293–1300. doi:10.1016/j.anbehav.2010.02.031

Killen SS, Cortese D, Cotgrove L, Jolles JW, Munson A, Ioannou CC. 2021. The potential for physiological performance curves to shape environmental effects on social behavior. *Front Physiol* **12**:754719.

Killen SS, Marras S, Steffensen JF, McKenzie DJ. 2012. Aerobic capacity influences the spatial position of individuals within fish schools. *Proceedings of the Royal Society B* **279**:357–364. doi:10.1098/rspb.2011.1006

Kimbell HS, Morrell LJ. 2015. 'Selfish herds' of guppies follow complex rules, but not when information is limited. *Proceedings of the Royal Society B* **282**:20151558. doi:10.1098/rspb.2015.1558

King AJ, Cowlishaw G. 2009. Leaders, followers, and group decision-making. *Commun Integr Biol* **2**:147–150.

Koski SE, Burkart JM. 2015. Common marmosets show social plasticity and group-level similarity in personality. *Sci Rep* **5**:8878. doi:10.1038/srep08878

Krause J. 1993. The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): a field study. *Oecologia* **93**:356–359.

Krause J, Reeves P, Hoare D. 1998. Positioning behaviour in roach shoals: the role of body length and nutritional state. *Behaviour* **135**:1031–1039.

Lachlan RF, Crooks L, Laland KN. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour* **56**:181–190.

Laubu C, Dechaume-Moncharmont F-X, Motreuil S, Schweitzer C. 2016. Mismatched partners that achieve postpairing behavioral similarity improve their reproductive success. *Sci Adv* **2**:e1501013. doi:10.1126/sciadv.1501013

Lecheval V, Jiang L, Tichit P, Sire C, Hemelrijk CK, Theraulaz G. 2018. Social conformity and propagation of information in collective U-turns of fish schools. *Proc R Soc B* **285**:20180251. doi:10.1098/rspb.2018.0251

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640. doi:10.1139/z90-092

MacGregor HEA, Herbert-Read JE, Ioannou CC. 2020. Information can explain the dynamics of group order in animal collective behaviour. *Nat Commun* **11**:2737. doi:10.1038/s41467-020-16578-x

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C. 2011. Leadership in elephants: the adaptive value of age. *Proc R Soc B* **278**:3270–3276. doi:10.1098/rspb.2011.0168

McDonald ND, Rands SA, Hill F, Elder C, Ioannou CC. 2016. Consensus and experience trump leadership, suppressing individual personality during social foraging. *Science Advances* **2**:e1600892. doi:10.1126/sciadv.1600892

Morrell LJ, Greenwood L, Ruxton GD. 2015. Consequences of variation in predator attack for the evolution of the selfish herd. *Evolutionary Ecology* **29**:107–121. doi:10.1007/s10682-014-9743-6

Morrell LJ, James R. 2008. Mechanisms for aggregation in animals: rule success depends on ecological variables. *Behavioral Ecology* **19**:193–201. doi:10.1093/beheco/arm122

Morton TL, Haefner JW, Nugala V, Decimo RD, Mendes L. 1994. The selfish herd revisited: do simple movement rules reduce relative predation risk? *Journal of Theoretical Biology* **167**:73–79. doi:10.1006/jtbi.1994.1051

Nakayama S, Johnstone RA, Manica A. 2012. Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish. *PLoS One* **7**:e43747. doi:10.1371/journal.pone.0043747

Niemelä PT, Dingemanse NJ. 2018. Meta-analysis reveals weak associations between intrinsic state and personality. *Proc R Soc B* **285**:20172823. doi:10.1098/rspb.2017.2823

Pettit B, Ákos Z, Vicsek T, Biro D. 2015. Speed determines leadership and leadership determines learning during pigeon flocking. *Curr Biol* **25**:3132–3137. doi:10.1016/j.cub.2015.10.044

R Development Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rands SA. 2017. Leaving safety to visit a feeding site: is it optimal to hesitate while exposed? *Royal Society Open Science* **4**:160910. doi:10.1098/rsos.160910

Rands SA. 2011a. Approximating optimal behavioural strategies down to rules-of-thumb: energy reserve changes in pairs of social foragers. *PLoS One* **6**:e22104. doi:10.1371/journal.pone.0022104

Rands SA. 2011b. The effects of dominance on leadership and energetic gain: a dynamic game between pairs of social foragers. *PLoS Comput Biol* **7**:e1002252. doi:10.1371/journal.pcbi.1002252

Rands SA. 2010. Self-improvement for team-players: the effects of individual effort on aggregated group information. *PLoS One* **5**:e11705. doi:10.1371/journal.pone.0011705

Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA. 2008. The emergence of leaders and followers in foraging pairs when the qualities of individuals differ. *BMC Evol Biol* **8**:51. doi:10.1186/1471-2148-8-51

Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA. 2003. The spontaneous emergence of leaders and followers in a foraging pair. *Nature* **423**:432–434. doi:10.1038/nature01630

Rands SA, Muir H, Terry NL. 2014. Red deer synchronise their activity with close neighbours. *PeerJ* **2**:e344. doi:10.7717/peerj.344

Rands SA, Pettifor RA, Rowcliffe JM, Cowlishaw G. 2006. Social foraging and dominance relationships: the effects of socially mediated interference. *Behav Ecol Sociobiol* **60**:572–581. doi:10.1007/s00265-006-0202-4

Rands SA, Pettifor RA, Rowcliffe JM, Cowlishaw G. 2004. State-dependent foraging rules for social animals in selfish herds. *Proc R Soc B* **271**:2613–2620. doi:10.1098/rspb.2004.2906

Reebs SG. 2001. Influence of body size on leadership in shoals of golden shiners, *Notemigonus crysoleucas*. *Behaviour* **138**:797–809. doi:10.1163/156853901753172656

Reebs SG. 2000. Can a minority of informed leaders determine the movements of a fish shoal? *Animal Behaviour* **59**:403–409. doi:10.1006/anbe.1999.1314

Reluga TC, Viscido SV. 2005. Simulated evolution of selfish herd behavior. *Journal of Theoretical Biology* **234**:213–225.

Romey WL. 1995. Position preferences within groups: do whirligigs select positions which balance feeding opportunities with predator avoidance? *Behavioral Ecology and Sociobiology* **37**:195–200.

Šárová R, Špinka M, Stěhulová I, Ceacero F, Šimečková M, Kotrba R. 2013. Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Animal Behaviour* **86**:1315–1323. doi:10.1016/j.anbehav.2013.10.002

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**:372–378. doi:10.1016/j.tree.2004.04.009

Sumpter DJT. 2010. Collective animal behavior. Princeton: Princeton University Press.

Tang J-Y, Fu S-J. 2020. The relationship between personality and the collective motion of schooling fish. *J Ethol* **38**:333–341. doi:10.1007/s10164-020-00655-1

Vanthournout B, Greve M, Bruun A, Bechsgaard J, Overgaard J, Bilde T. 2016. Benefits of group living include increased feeding efficiency and lower mass loss during dessication in the social and inbreeding spider *Stegodyphus dumicola*. *Front Physiol* **7**:18. doi:10.3389/fphys.2016.00018

Viscido SV, Miller M, Wethey DS. 2002. The dilemma of the selfish herd: the search for a realistic movement rule. *Journal of Theoretical Biology* **217**:183–194.

Watts I, Nagy M, Holbrook RI, Biro D, Burt de Perera T. 2017. Validating two-dimensional leadership models on three-dimensionally structured fish schools. *R Soc Open Sci* **4**:160804. doi:10.1098/rsos.160804

Webster MM, Ward AJW. 2011. Personality and social context. *Biol Rev* **86**:759–773. doi:https://doi.org/10.1111/j.1469-185X.2010.00169.x

Wickham H. 2009. *ggplot2*: elegant graphics for data analysis. New York: Springer-Verlag.

Wilensky U. 2003. Statistical mechanics for secondary school: the GasLab multi-agent modeling toolkit. *International Journal of Computers for Mathematical Learning* **8**:1–41.

Wilensky U. 1999. *NetLogo* [online: http://ccl.northwestern.edu/netlogo/]. Evanston: Center for Connected Learning and Computer-based Modeling, Northwestern University.

Wood AJ, Ackland GJ. 2007. Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. *Proceedings of the Royal Society B* **274**:1637–1642. doi:10.1098/rspb.2007.0306

Figure 1. The effects of the outward probability adjustment parameter $\omega_{difference}$ on timing of measures of group behaviour, comparing the three social interaction rules with simulations where all individuals behaved non-socially. Within each panel, $\omega_{difference}$ is systematically increased from 0.0001 (dark green) to 0.0020 (yellow), with the colour gradient representing equally-sized increments of 0.0001 between these values, and other parameters are set as described in the 'model exploration' methods. Each panel plots the results of a social rule against the non-social values, and the non-social results are therefore identical in the panels for the three different social rules, and are replicated here to allow comparison between social and non-social behaviour. The black diagonal line on each panel represents the scenario where social and non-social individuals are behaving identically; if points fall below this line, the measured behaviour is happening faster with the social rule; if points fall above the line, the non-social rule causes the behaviour to happen faster. The panels show ***a***) – ***c***) the mean time until the end of a simulation, indicated by the last individual moving to the foraging site that is d_{food} units away from the refuge; ***d***) – ***f***) the mean time an individual spends travelling between the threshold distance close to the refuge and the foraging site; ***g***) – ***i***) the mean time that an individual first passes beyond the threshold distance away from the refuge; ***j***) – ***l***) the mean latency shown by other group members to pass the threshold distance once the first individual has left; ***m***) – ***o***) the mean time at which the first individual arrives at the foraging site beyond d_{food}; ***p***) – ***r***) the mean latency shown by other group members to arrive at the foraging site once the first individual has arrived. All datapoints show the mean value (± SD) for 10,000 independent group simulations.

Figure 2. *F* values describing the ratio of within- and between-parameter-set variance for the mean simulation value of the six behavioural measures that were recorded, when the parameter being systematically altered was: ***a***) probability adjustment parameter, $\omega_{difference}$; ***b***) baseline time-dependent probability of moving outward, $p_{baseline}$; ***c***) distance to the foraging site, d_{food}; or ***d***) group size, *n*. The shape and colour of the points indicates the social interaction rule that was followed within a simulation set.

Figure 3. Illustrative examples of mean rescaled individual behaviour, when comparing non-social and the three social behaviours. Individuals are labelled 1-10, where 1 is the individual with the baseline levels of all parameters, and incremental increases in the label represent the incremental increase by $\omega_{difference}$ as described in the methods. This means that when all individuals within a simulation are behaving independently (non-socially), individual 1 is the least likely to start moving towards the feeding site (the shyest), and individual 10 is the most likely (the boldest). Panels **a**-**d** show rescaled travel times, where 0 is the travel time of the

individual who reaches the feeding site in the shortest time, and 1 is for the individual who takes the longest; **e**-**h** show rescaled leave times (at which an individual first crosses a threshold 10 units away from the start point), and **i**-**l** show rescaled arrival times at the feeding site. **a**, **e** and **i** show the behavioural metrics for individuals behaving non-socially (independently) within a simulation; **b**, **f** and **j** show the metrics for individuals using the central social rule; **c**, **g** and **k** show the metrics for individuals using the nearest neighbour rule; and **d**, **h** and **l** show the metrics for individuals using the majority rule. All boxplots show the median and interquartile values of the mean rescaled behavioural metric, and the tails show 1.5 × interquartile range, with points representing outliers. Data shown for dataset where $\omega_{difference}$ has been systematically altered in order to explore variation in response to this parameter (200 replicates each for $\omega_{difference}$ = (0.0001, 0.0002, … 0.0020), pooling all of these simulations together for each of the figures), with $p_{baseline}$ = 0.001, d_{food} = 100 units and n = 10.

Figure 4. Mean rescaled differences in behavioural metrics between the non-social rule and each of the social interaction rules for each individual. Positive values mean that individuals switch the observed behaviour to later in the hierarchical group order when behaving socially, and negative values mean they switch to earlier in the group order when behaving socially. This means a value of 1 represents the case where the individual is always first to finish/leave/arrive when behaving non-socially, and always the last to finish/leave arrive when behaving socially, a value of -1 represents the case where the individual is always last to finish/leave/arrive when non-social and always first to finish/leave/arrive when social, and a value of 0 represents the case where the individual does not change the ordering of its behaviour between social and non-social behaviours (*e.g.* the third individual to arrive when performing a non-social behaviour is also the third individual to arrive when performing a social behaviour). **a**, **b** and **c** show the difference in travel time; **d**, **e** and **f** show the difference in leave time; and **g**, **h** and **i** show the difference in arrival time. **a**, **d** and **g** give the values when comparing the central and non-social rules; **b**, **e** and **h**, the nearest neighbour and non-social rules; and **c**, **f** and **i**, the majority and non-social rules. See the legend of figure 3 for a description of the boxplot ranges and the parameter set used for generating the figure.

	Non-Social		Central		Nearest Neighbour		Majority	
	Parameter *F*	**Individual *F***	**Parameter *F***	**Individual *F***	**Parameter *F***	**Individual *F***	**Parameter *F***	**Individual *F***
$\omega_{difference}$								
travel time	4797	157054	15	291	51	4876	48	318
leave time	911	133875	2	2526	23	8487	6	2956
arrival time	8021	200045	41	1966	10	19566	59	3753
$p_{baseline}$								
travel time	583	97981	3	2311	16	9679	6	7808
leave time	251	30072	<1	447	8	1903	1	316
arrival time	1706	157742	6	11168	22	10625	13	34995
d_{food}								
travel time	141	77372	18	1156	22	6406	44	3253
leave time	1	37140	1	446	1	1757	2	313
arrival time	157	326247	34	4843	30	8211	52	11270

Table 1. *F* values describing the contributions of both the model parameter being varied and the 'boldness' of the individual within a simulation, according to the behavioural metric measured and the parameter being varied. Higher values in the 'Individual *F*' mean that it is easier to identify a specific individual by measuring its behaviour alone.

Supplementary Materials

Figure S1. The effects of the baseline time-dependent probability of moving outward $p_{baseline}$ on timing of measures of group behaviour, comparing the three social rules to simulations where all individuals behaved non-socially. Within each panel, $p_{baseline}$ is systematically altered increased from 0.0001 (dark green) to 0.0020 (yellow), with the colour gradient representing equally-sized increments of 0.0001 between these values, and other parameters are set as described in the 'model exploration' methods. See legend for figure 1 for more detail.

Figure S2. The effects of the distance of the foraging site d_{food} on timing of measures of group performance, comparing the three social rules with simulations where all individuals behaved non-socially. Within each panel, d_{food} is systematically altered between 20 (dark green) and 200 distance units (yellow), with the colour gradient representing equally-sized increments of 10 units between these values, and other parameters are set as described in the 'model exploration' methods. See legend for figure 1 for more detail.

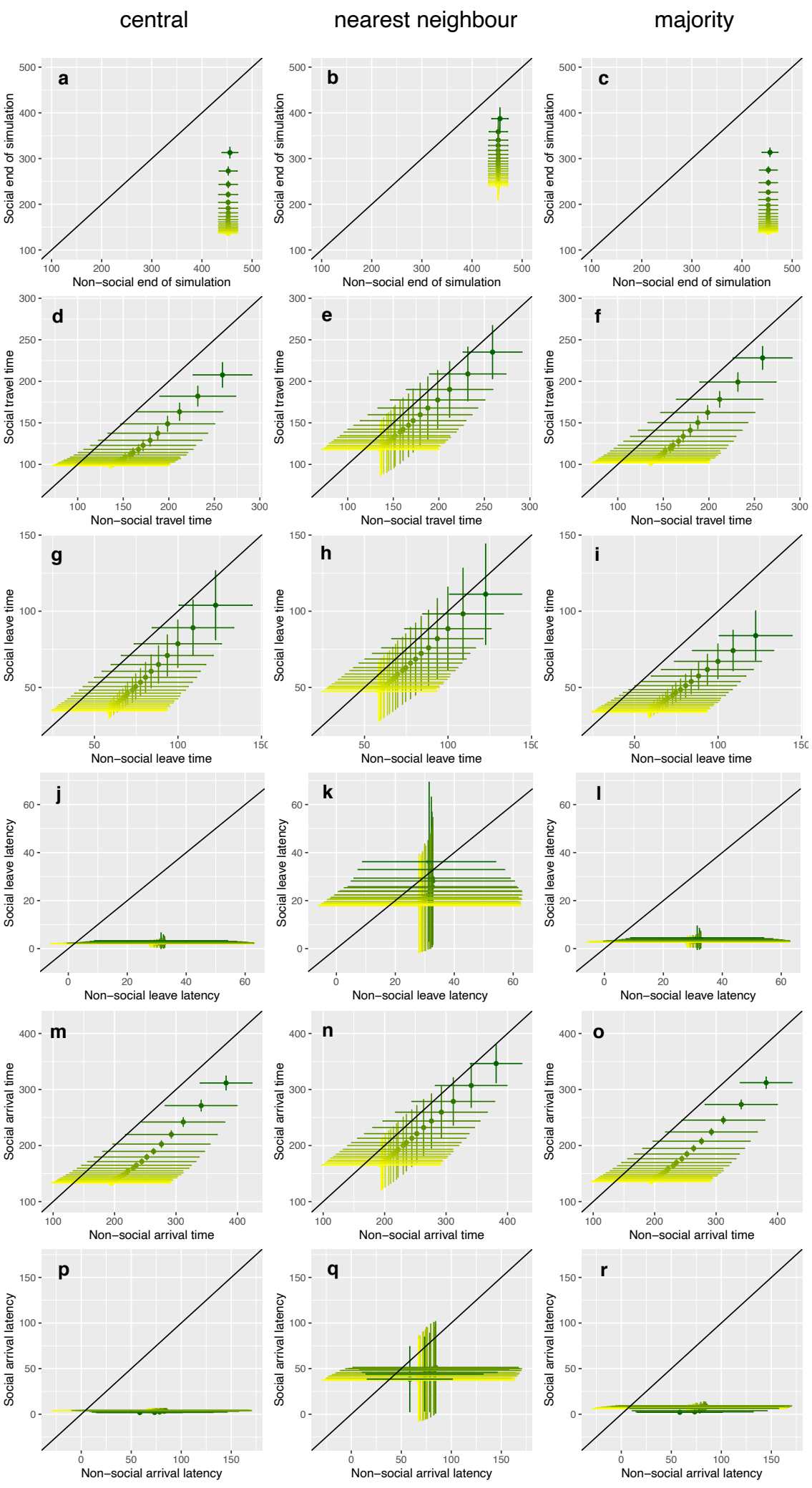
Figure S3. The effects of the group size n on timing of measures of group performance, comparing the three social rules with simulations where all individuals behaved non-socially. Within each panel, n is systematically altered between 5 (dark green) and 50 individuals (yellow), with the colour gradient representing equally-sized increments of 5 individuals between these values, and other parameters are set as described in the 'model exploration' methods. See legend for figure 1 for more detail.

Figure S4. The effects of the outward probability adjustment parameter $\omega_{difference}$ on group performance when the social interaction rule is varied. The panels show summaries of the difference in the behavioural metrics (the labels at the left of the figure describe each statistic) when comparing the six possible pairs of social behaviour (indicated by the labels at the top of the figure), noting that the differences were calculated by comparing the behavioural metrics for simulations of groups experiencing the same starting conditions but following different behavioural rules. Boxplots represent the median and quartile values for each simulation, with whiskers representing the minimum of the maximum value and 1.5 $\times$ interquartile range, with points representing outliers beyond this range.

Figure S5. The effects of the baseline outward movement probability $p_{baseline}$ on group performance when conducting different social behaviours. See the legend to figure S4 for details.

Figure S6. The effects of the distance to the foraging site d_{food} on group performance when conducting different social behaviours. See the legend to figure S4 for details.

Figure S7. The effects of group size n on group performance when conducting different social behaviours. See the legend to figure S4 for details.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nearest neighbour
majority
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b
c
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Non−social end of simulation
d
e
f
Social travel time
Non−social travel time
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h
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Social leave time
Non−social leave time
j
k
l
Social leave latency
Non−social leave latency
m
n
o
Social arrival time
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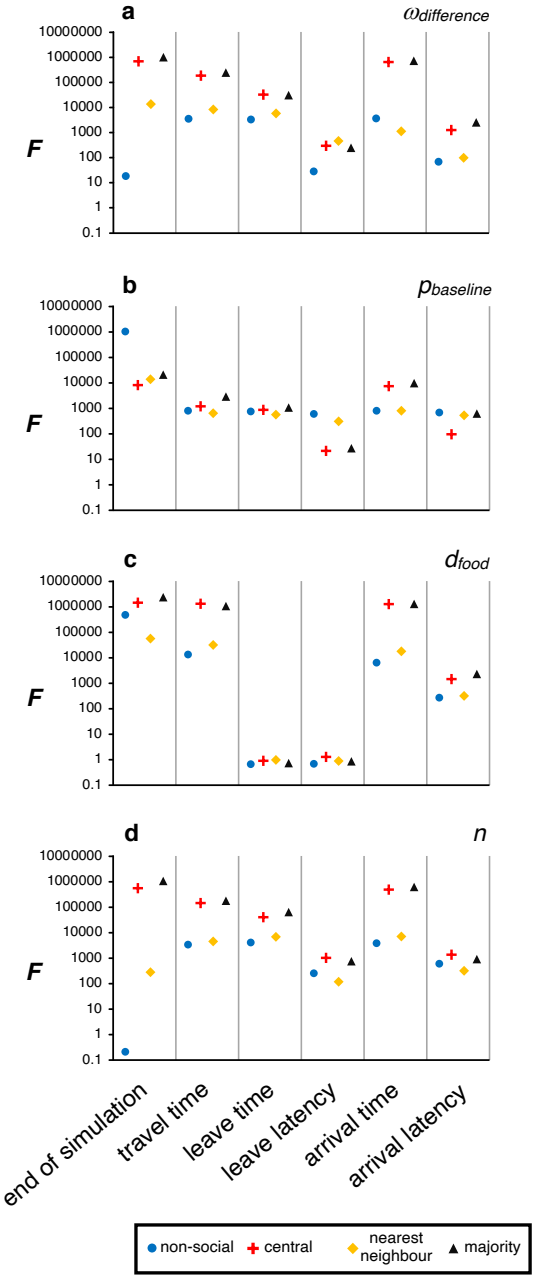
p
q
r
Social arrival latency
Non−social arrival latency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100000
10000
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travel time
leave time
leave latency
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arrival latency
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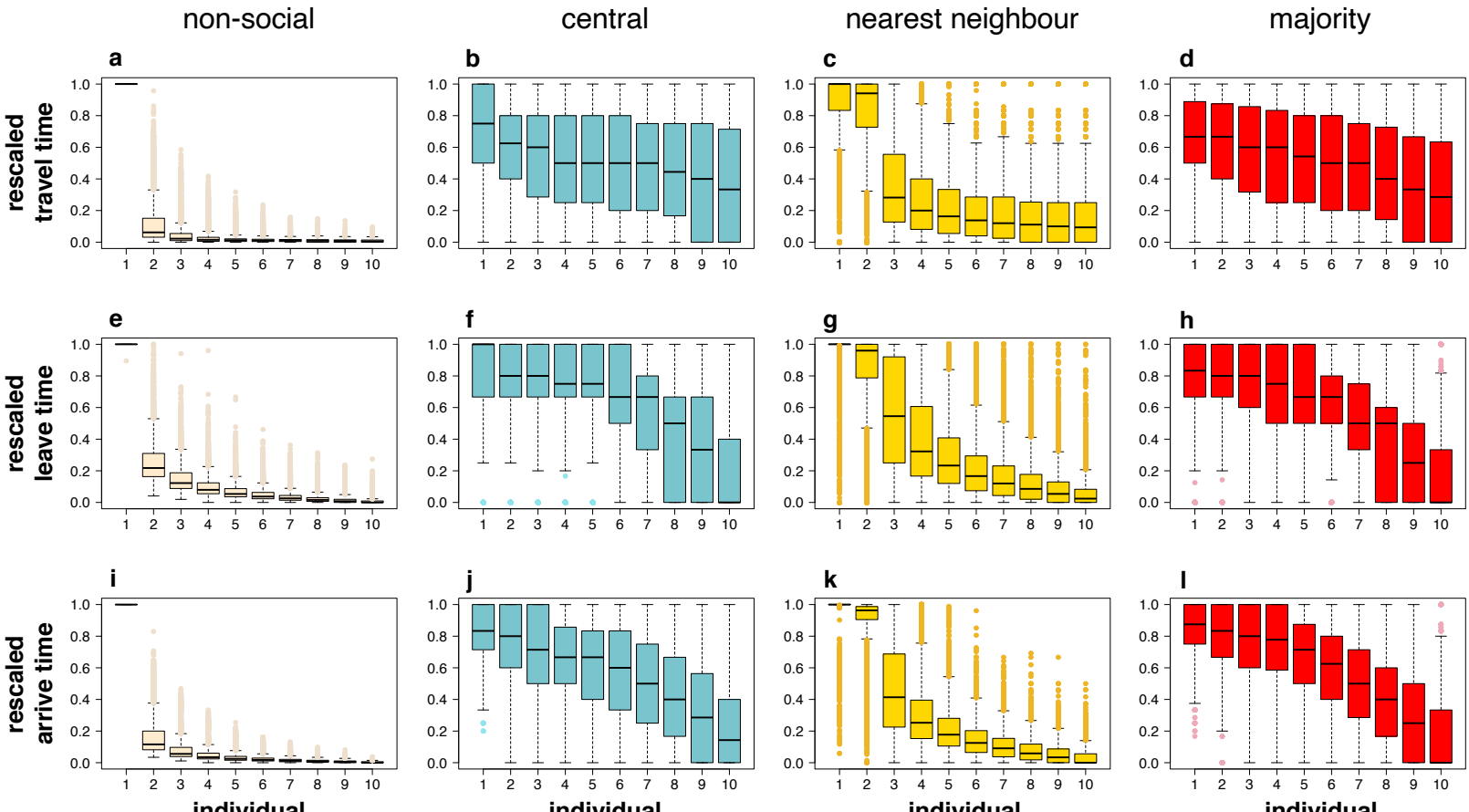
majority


non-social
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nearest neighbour
majority
a
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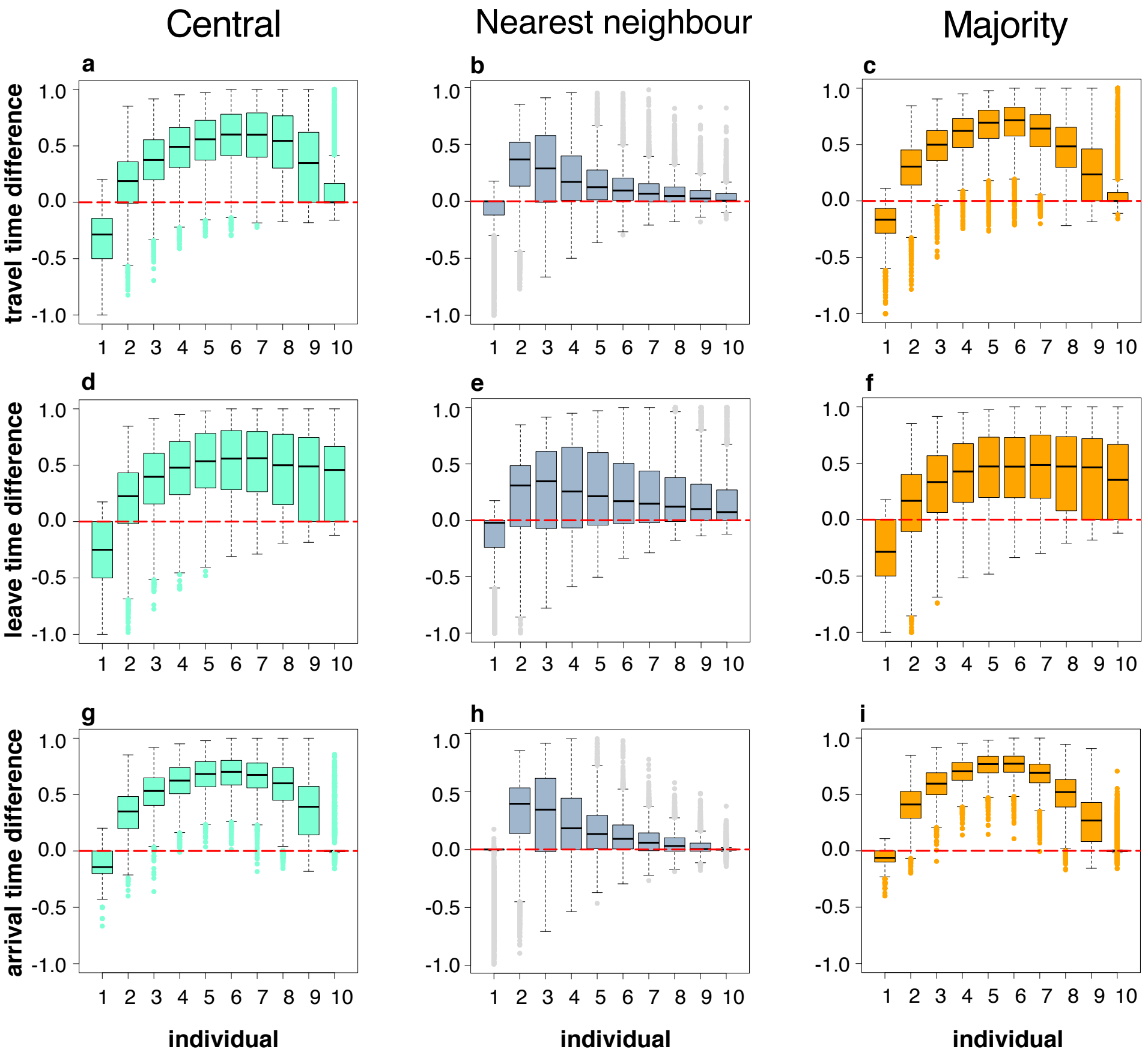
rescaled travel time
rescaled leave time
rescaled arrive time
individual
individual
individual
individual


Central
Nearest neighbour
Majority
a
b
c
d
e
f
g
h
i
travel time difference
leave time difference
arrival time difference
1.0
0.5
0.0
-0.5
-1.0
1 2 3 4 5 6 7 8 9 10
individual