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Leadership, consensus decision making and collective behaviour in humans

John R. G. Dyer[1,*], Anders Johansson[2], Dirk Helbing[2], Iain D. Couzin[3] and Jens Krause[1]

[1]*Institute of Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK*
[2]*Department of Humanities, Social and Political Sciences, ETH Zurich, UNO D 11, Universitätstrasse 41, 8092 Zurich, Switzerland*
[3]*Department of Ecology and Evolutionary Biology, Princeton University, 106a Guyot Hall, Princeton University, Princeton, NJ 08544-1003, USA*

This paper reviews the literature on leadership in vertebrate groups, including recent work on human groups, before presenting the results of three new experiments looking at leadership and decision making in small and large human groups. In experiment 1, we find that both group size and the presence of uninformed individuals can affect the speed with which small human groups (eight people) decide between two opposing directional preferences and the likelihood of the group splitting. In experiment 2, we show that the spatial positioning of informed individuals within small human groups (10 people) can affect the speed and accuracy of group motion. We find that having a mixture of leaders positioned in the centre and on the edge of a group increases the speed and accuracy with which the group reaches their target. In experiment 3, we use large human crowds (100 and 200 people) to demonstrate that the trends observed from earlier work using small human groups can be applied to larger crowds. We find that only a small minority of informed individuals is needed to guide a large uninformed group. These studies build upon important theoretical and empirical work on leadership and decision making in animal groups.

Keywords: leadership; consensus decision making; collective behaviour; human group

1. INTRODUCTION

This paper will begin by reviewing the literature on leadership in vertebrate groups, including recent empirical work on human groups. We will then present the results of three new human crowd experiments that build upon the work of Dyer *et al.* (2008).

Consensus decisions are defined by Conradt & Roper (2005) as 'when the members of a group choose between two or more mutually exclusive actions with the aim of reaching a consensus'. They are very important for both animal and human groups as they allow groups to remain together despite individual differences in preference and consequently help prevent individuals from losing the benefits associated with being part of a large group (Conradt & Roper 2009; Sumpter & Pratt 2009). Decision making almost always involves some form of leadership. Here, we define leadership as 'the initiation of new directions of locomotion by one or more individuals, which are then readily followed by other group members' (Krause *et al.* 2000). Leadership may either be designated or emerge spontaneously due to individuals possessing qualities or experience in certain situations, or because they are of a personality type that is generally more inclined to lead. In the words of William Shakespeare in *Twelfth Night:* 'some men are born great, some men achieve greatness and some have greatness thrust upon them'.

Evidence of leadership behaviour has been found in a number of vertebrate species across a range of taxa, including ungulates (Leicester sheep, *Ovis aries*; Squires & Daws 1975; sable antelope, *Hippotragus niger*: Stine *et al.* 1982; Charolais heifers, *Bos taurus*; Dumont *et al.* 2005; zebras, *Equus burchellii*: Fischhoff *et al.* 2007), primates (gorillas, *Gorilla gorilla beringei*: Fossey 1972; chimpanzees *Pan troglodytes*: Wilson 1980), canids (bush dogs *Speothos venaticus*: Macdonald 1996; wolves *Canis lupus*: Peterson *et al.* 2002), birds (bar headed geese *Anser indicus*: Lamprecht 1992; zebra finches *Taeniopygia guttata*: Beauchamp 2000; homing pigeons *Columba livia domestica*: Biro *et al.* 2006) and fishes (roach *Rutilus rutilus*: Bumann *et al.* 1997; golden shiners *Notemigonus crysoleucas*: Reebs 2000, 2001). In some species, it has been shown that groups tend to be led by dominant individuals (gorillas *G. g. beringei*: Fossey 1972; Leicester sheep, Squires & Daws 1975; chimpanzees *P. troglodytes*: Wilson 1980; sable antelope *H. niger*: Stine *et al.* 1982; bush dogs *S. venaticus*: Macdonald 1996; wolves *C. lupus*: Peterson *et al.* 2002). In other species, it has been demonstrated that leadership can be more variable and that there is no correlation with dominance (bar-headed geese *A. indicus*: Lamprecht 1992; zebra finches *T. guttata*: Beauchamp 2000; white-faced capuchins *Cebus capucinus*: Leca *et al.* 2003).

* Author for correspondence (bgyjdd@leeds.ac.uk).

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Research on fish shoals has provided insight into leadership in the absence of dominance hierarchies and complex signalling between individuals. Reader *et al.* (2003) demonstrated that four demonstrator guppies, *Poecilia reticulata*, could guide four uninformed conspecifics through a hole to escape an oncoming trawl net. Similarly, Reebs (2000, 2001) found that a small minority of informed fish (golden shiners *N. crysoleucas*) could guide uninformed conspecifics from a preferred area of a tank, to a less preferred brightly lit area where food was expected. Reebs (2001) also found an influence of body size on leadership with large knowledgeable fish being readily followed by small uninformed fish whereas small knowledgeable fish were less readily followed by larger individuals. Krause *et al.* (1998) found that front positions tended to be occupied by larger fish and food-deprived fish. Bumann *et al.* (1997) showed that individuals in front positions in shoals of roach *R. rutilus* led the group, finding that just a single individual in a front position could have a strong influence on an entire shoal of 16 fish.

Couzin *et al.* (2005) used a simple individual-based model to look at the mechanisms of leadership and decision making in moving animal groups, in the absence of complex signalling and in situations where it is not possible for individuals to establish which other individuals, if any, have information. First, they ask how small numbers of individuals with information on a migration route or the location of resources can influence the rest of the group; and second, how groups can overcome conflicts in individual preferences in order to achieve consensus. These questions are particularly relevant to an understanding of the mechanisms of leadership and decision making in large animal groups, such as insect swarms or fish schools, where individuals may not have the capacity for individual recognition and where crowding may limit the range over which individuals can see each other. The model is a simple individual-based model in which individuals attempt to maintain personal space by avoiding other individuals within a certain region. If no neighbours are detected within this region then the individual will become attracted towards and aligned with neighbours within a local interaction range in order to maintain cohesion with neighbours. The model assumes that all individuals move at the same speed and are identical except that a certain proportion is given a directional preference (unit vector) representing, for example, the direction to a known resource, whereas all other individuals have no preferred direction of travel. Couzin *et al.* (2005) predicted that a small proportion of informed individuals (approx. 5% of group members) can accurately guide an uninformed group and that for any given group size the accuracy of group motion increases as the proportion of informed individuals is increased. Furthermore, they predict that where there are conflicts in the preferences of informed individuals and the number of individuals with each preference is unequal, the group will always go with the majority of informed individuals. When the number with each preference is equal, the group averages over the preferences if the differences are small (less than 120°). However, when individual differences are large (more than 120°) then the group decides in favour of one set of informed individuals. This prediction has received empirical support from work on pairs of homing pigeons, *C. l. domestica* (Biro *et al.* 2006).

Dyer *et al.* (2008) tested some of the predictions of the Couzin *et al.* (2005) model using small human groups. Similar to the model of Couzin *et al.*, individuals had no information about which other individuals had information, and participants were not allowed to talk or gesture in order to minimize information exchange through active signalling. All individuals were instructed that they must remain together as a group. The groups started in the centre of a circular arena, and instead of a preferred direction of travel informed individuals were instructed to reach a target (a number between 1 and 16) on the edge of the 10 m circle. This enabled Dyer *et al.* to measure not only the accuracy of group motion but also the time taken to reach their intended target. Using mixed sex groups of eight people, they found that just one informed individual (12.5% of the group informed) could guide the group with great accuracy. They found the effect on time to be less immediate with two informed individuals (25% of the group informed) being required to bring about a significant decrease in the time taken to reach the circle periphery. Interestingly, Dyer *et al.* (2008) found no evidence of a trade-off between the speed and accuracy of decision making as has been found from previous work on humans (Edwards 1965; Vitevitch 2002), ants (Franks *et al.* 2002, 2003, 2009), monkeys (Roitman & Shadlen 2002) and bees (Chittka *et al.* 2003). Dyer *et al.* (2008) also tested scenarios where a conflict (different numbers of informed individuals were instructed to reach targets 180° apart) was introduced in the preferences of informed individuals, finding that the direction of group motion was almost always decided by the majority. These results provide good initial empirical support for the predictions of Couzin *et al.* (2005) but leave a number of questions unanswered: first, it is not clear what the role is of uninformed individuals in reaching consensus decisions. Second, how the spatial positioning of informed individuals affects the speed and accuracy with which they guide uninformed group members to a target. Third, whether the results found by Dyer *et al.* (2008) using small groups are also applicable to large groups (‘crowds’).

To answer these questions, we present the results of three experiments using human groups that build upon the work of Dyer *et al.* (2008). Whenever we refer to groups in this paper we use the flexible definition of Forsyth (1999) who defines a group as ‘two or more interdependent individuals who influence each other through social interaction’. This definition does not imply permanence, structure or psychological meaning for members. When referring to crowds, we simply mean large groups of 100 individuals and over.

2. MATERIAL AND METHODS

(a) *Experiment 1: the importance of uninformed individuals in reaching consensus*

This experiment took place between February and March 2006 at the University of Leeds (England) and the University

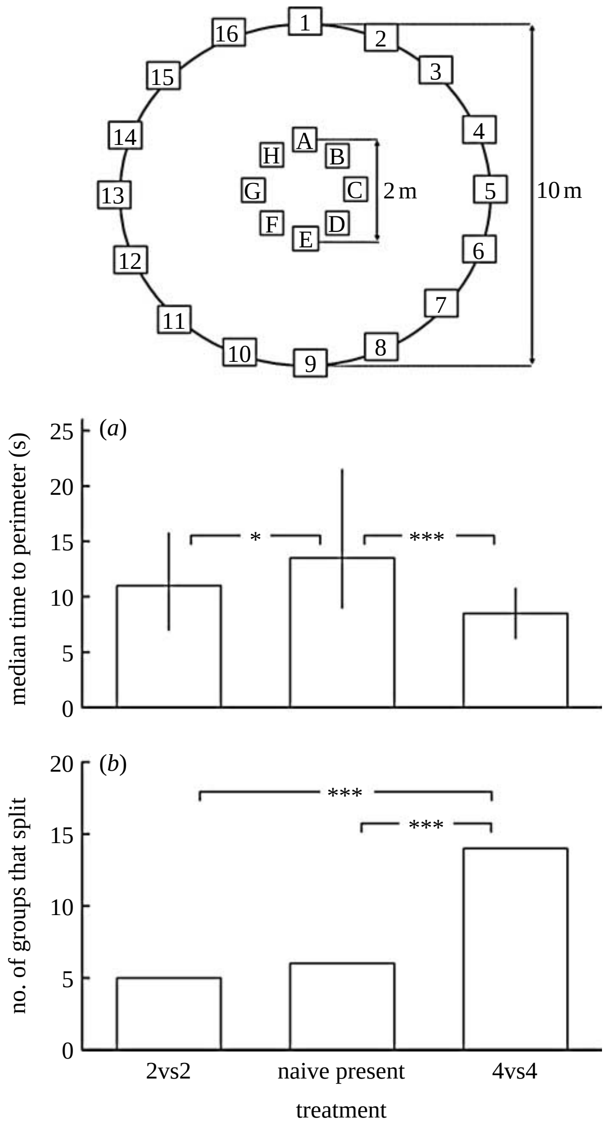

Figure 1. Experiment 1. (*a*) Median (± quartiles) time taken to reach the periphery of the circle by groups tested in the three different experimental treatments. (*b*) Number of groups that split up at least once during their trial in each of the three different experimental treatments. Treatment differences are indicated by FDR corrected pairwise comparisons. ***0.001, **0.01 and *0.05. (Inset) Overhead view of the arena used in experiment 1. Letters represent starting positions for participants and numbers were used to orientate them and as targets.

of Wales at Bangor. Participants were undergraduate students. In total, 22 mixed-sex groups of eight individuals were used for testing. All experiments were carried out double-blind in that both the participants and the individuals who measured the response variables were not aware of the purpose of the experiment.

A circular arena with a 10 m diameter was marked on the floor and cards labelled 1–16 were spaced equally around its perimeter. A circle with a diameter of 2 m was marked out in the centre of the first circle with the letters A–H spaced equally around its perimeter (figure 1 (inset)). Individuals were asked to stand on a letter (A–H) on the inner circle to ensure that all starting positions were equal and equidistant from the outer periphery. To avoid any bias due to initial direction of locomotion, the initial orientation of each individual in a trial was randomized by instructing them to face a number from the outer circle chosen at random without replacement.

Each group was given the following standard set of instructions: 'when we tell you to begin you should start walking at a normal speed and do not stop before being told to do so. You can walk anywhere inside or outside the circle but you have to stay within an arm's length of another individual and you should not talk or gesture to each other.' Both walking speed and the distance they should keep from each other were demonstrated to them before the experiment. These instructions attempted to make the participants as comparable as possible to the agents in the Couzin *et al.* (2005) model in which they move at the same standard speed, they can move anywhere and are attracted to each other within a certain zone. The instruction not to talk and gesture attempted to minimize active information transfer between individuals. We found (J. Krause & J. R. G. Dyer 2005, personal observation) that in real-life situations the conditions apply remarkably often because strangers getting off planes, interacting in pedestrian zones, entering or leaving buildings regularly do interact without talking to each other and without obvious gestures. In fact, this seems to be the norm in many countries.

In addition to these standard instructions, participants were each handed a slip of paper with an additional individual behavioural rule to follow. They were instructed to read and memorize the information, then hide the slip to ensure that no other member of the group could see it. The slips of paper gave one of two different behavioural rules, one for uninformed individuals and one for informed individuals. Behavioural rule 1 gave instructions to simply 'stay with the group', resulting in uninformed individuals. Behavioural rule 2 gave instructions to 'Go to number X, without leaving the group' creating informed individuals (X represents a randomly chosen number on the outer circle between 1 and 16). This rule creates a scenario that is similar to the model of Couzin *et al.* (2005) in which although individuals have a preferred direction, they are still attracted to other individuals and so must balance social attraction against individual directional preference.

Each group was tested in three different treatments. In each treatment, the informed individuals were given one of two separate targets, 180° apart. In the first treatment (the '2 versus 2' treatment), two individuals were each given a target and no uninformed individuals were present (group size = 4). In the second treatment (the 'uninformed present' treatment), two individuals were each given a target and four uninformed individuals were also present (group size = 8). In the third treatment (the '4 versus 4' treatment), four individuals were each given a target and no uninformed individuals were present (group size = 8). These three different treatments allowed us to look at the effect of the presence and the absence of uninformed individuals both when group size remains constant (by comparing the 4 versus 4 with the uninformed present treatment) and when number of informed individuals remains constant (by comparing the 2 versus 2 with the uninformed present treatment).

Four informed individuals were randomly assigned and were used as the informed individuals in both the 2 versus 2 and the uninformed present treatments. Treatment order was systematically rotated to minimize its effect on the results. This meant that on some occasions (e.g. if the 2 versus 2 or the uninformed present treatments followed the 4 versus 4 treatment) some individuals who were informed in a previous trial would then be uninformed in a subsequent trial. Previously informed individuals have been shown by Dyer *et al.* (2008) not to affect the results of subsequent trials, but we also test for their effects here. During the 2 versus 2 trials, the four individuals who were not assigned as informed individuals and therefore not involved in the trial were taken to the side of the arena. This may have given them a chance to observe the trial, which could potentially have given them clues as to the nature of the experiment. Consequently, we tested for any potential effects of observing a previous trial by comparing the performance of groups in each of the other treatments separately, on occasions when they preceded and followed the 2 versus 2 treatment. There was no significant difference in time taken to reach the circle periphery when comparing groups within the uninformed present and 4 versus 4 treatments on occasions where these treatments preceded and succeeded the 2 versus 2 treatment (uninormed present treatment: Mann–Whitney *U*-test: $z=-1.284$, $n=11$, 11, $p=0.210$; 4 versus 4 treatment: Mann–Whitney *U*-test: $z=-1.320$, $n=11$, 11, $p=0.197$). This suggests that there was no effect on subsequent trials of the four individuals watching the 2 versus 2 treatment from the side.

After we signalled the start of a trial, it lasted until any member of the group came within 50 cm of the perimeter of the circle. This was judged by two observers on either side of the arena who were blind to the purpose of the experiment. The observers recorded the time taken by the group to come within 50 cm of the periphery and the target which they finished closest to or the two targets if they finished in between the two targets.

(b) *Experiment 2: spatial position of informed individuals*

This experiment took place between January 2006 and March 2007 at the University of Leeds (England) and the University of Wales at Bangor. Participants were undergraduate students. In total, 15 mixed-sex groups of ten individuals were used for testing. All experiments were carried out double-blind in that both the participants and the individuals who measured the response variables were not aware of the purpose of the experiment.

A circular arena was marked out in the same way as in experiment 1 except that this time the letters I and J were also placed in the centre of the inner circle of letters (figure 2 (inset)). Individuals were asked to stand on a letter (A–J) on the inner circle. The rest of the protocol was exactly the same as in experiment 1 except that this time each group of 10 was tested in four different treatments that differed only in the starting positions of the two informed individuals with the same target direction (see figure 2 and inset). In the first treatment ('mixed treatment'), one of the informed individuals started in a core position (position J) and one started on the periphery (position E). In the second treatment ('close treatment'), the two informed individuals started close together both on the periphery (positions C and D). In the third treatment ('far treatment'), the two informed individuals started far apart at opposite sides of the periphery of the group (positions B and F). In the final treatment ('2 core treatment'), both leaders started in core positions within the group (positions I and J). Treatment orders were systematically rotated to minimize any order effects. The two informed individuals were randomly assigned for the first treatment and these same individuals were the informed individuals in each of the other treatments.

(c) *Experiment 3: leadership and decision making in large human crowds*

This experiment will yield mainly anecdotal evidence as it is based on a small sample size consisting of, in part, a single group of 200 people, and in other parts, an additional group of 100 people. The experiments took place on 4 March 2007

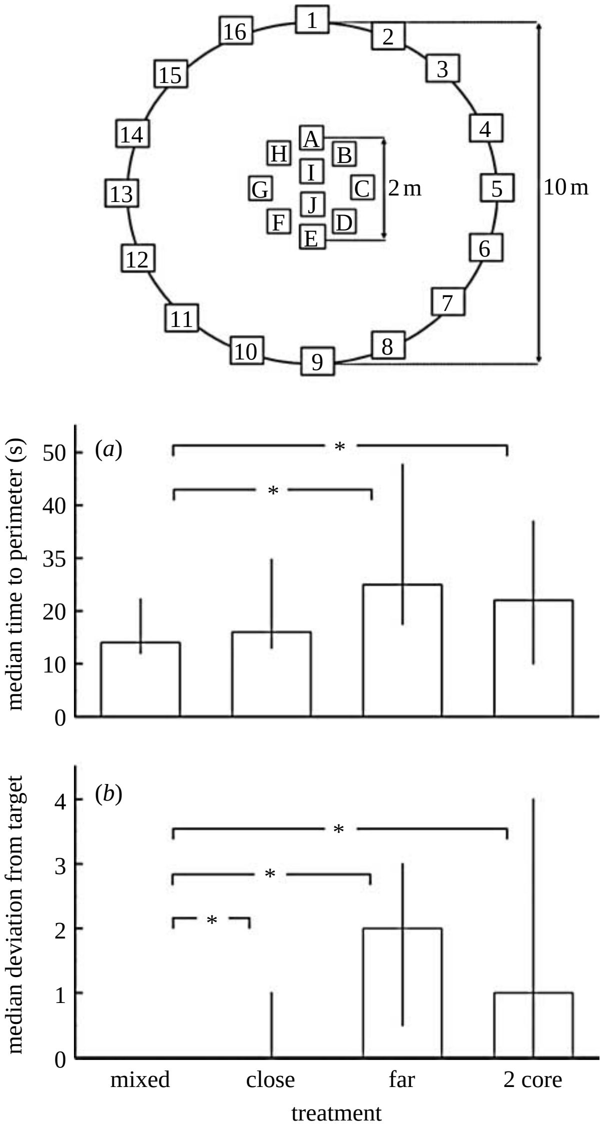

Figure 2. Experiment 2. (*a*) Median ($\pm$ quartiles) time taken to reach the periphery of the circle by groups tested in the four different experimental treatments. (*b*) Median ($\pm$ quartiles) deviation of groups from their target under the four different experimental treatments (filled circles represent leaders' starting positions and empty circles represent uninformed individuals' starting positions). Treatment differences are indicated by FDR corrected pairwise comparisons. ***0.001, **0.01 and *0.05. (Inset) Overhead view of the arena used in experiment 2. Letters represent starting positions for participants and numbers were used to orientate them and as targets.

in Cologne (Germany) and 5 May 2007 in Freiburg (Germany). Participants were volunteers between the age of 18 and 70 of both sexes who had answered TV or radio advertisements asking for participants for a swarm experiment (no further information on the nature of the experiment was given until the experiment was finished).

A circular arena with a 50 m diameter was marked on the floor, and large mounted wooden boards raised approximately 2 m above the ground and printed with the numbers 1–12 were spaced equally round its perimeter (as a clock face). Two more circles were marked out in the centre of the first circle with diameters of 12 and 32 m (figure 3). The smallest circle in the centre (12 m in diameter) represented the starting area for the group of participants with the middle circle (32 m in diameter) acting as a guide for us to observe

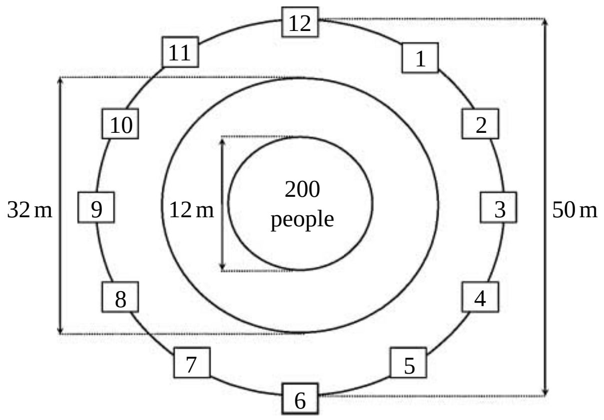

Figure 3. Overhead view of the arena used in experiment 3. The numbers were used to orientate individuals and as targets.

the distance moved by the group. Controls were run with no circles on the floor, which confirmed that the same collective behaviours were found in the presence or the absence of these floor markings.

Each participant was given one of 10 different coloured caps (20 individuals with each colour). This was done in order to facilitate the organization of such large numbers of people and also to later identify informed individuals in the video recordings. Each individual was handed a slip of paper, which they were instructed not to open before being told to do so. On the left-hand side of each slip of paper was an instruction that read 'before we say 'GO' you should face number X' (with X representing one of the 12 numbers on the outer circle). On the right-hand side was a behavioural rule for them to follow. Uninformed individuals were told to 'Stay with the group'. Informed individuals (leaders) were told to 'Go to 9 o'clock, but do not leave the group'.

The participants were then read the same set of standardized instructions as in experiments 1 and 2, and normal walking speed and staying together as a group were demonstrated to them. The participants of each hat colour group in turn were then asked to spread themselves out in the smallest circle in the centre, starting with the hat colour that contained the informed individuals. This ensured that whatever colour hats the informed individuals were wearing they were spread out among the group.

A single group of 200 people was tested in five different treatments. In the first treatment (20 leader treatment), 20 individuals received the rule for informed individuals. In the second treatment (five leader treatment), five individuals received the rule for informed individuals. In the third treatment (10 leader treatment), 10 individuals received the rule for informed individuals. In the fourth treatment (control treatment), all individuals received the rule for uninformed individuals. In the fifth treatment (20 versus 10 conflict treatment), we introduced conflict so that 20 individuals were instructed to go to one target and 10 were instructed to go to a target opposite (180° away) from this. After each treatment, all individuals wearing the colour of hat worn by the informed individuals were removed from the group and replaced by 20 more participants wearing the same coloured hats. This was done in order that no individuals who were previously informed would be uninformed individuals in a subsequent trial. The uninformed treatment and the 10 leader treatment were repeated with a different group of 100 participants.

(d) *Statistical analyses*

All statistical analyses were carried out using R v. 2.5.1. All data failed to meet the preconditions required for parametric testing even after transformation. Therefore, generalized linear mixed models (GLMMs) were used to analyse the effects of the different treatments and the order the groups experienced the treatments, and their potential two-way interaction on the response variables of time to circle periphery and the likelihood of a group splitting in experiment 1, and time to circle periphery and deviation from intended target in experiment 2. Group ID was entered as the random factor in each model due to the repeated-measures design of the study (each group was tested in each treatment). In all cases, time and deviation data were overdispersed and quasi-Poisson error distributions were found to be the best fit to the data. In the case of the splitting data, a binomial error distribution was used. In no cases were the response variables affected by treatment order and so this variable was removed from the model and further analysis. Where a significant effect of treatment was found from a GLMM, pairwise comparisons were made between the treatments by correcting the alpha level using an FDR correction (see Benjamini & Hochberg 1995). All p-values from pairwise tests throughout the paper were ranked and the lowest p-value was compared with an alpha level of 0.00278 (0.05/no. of pairwise comparisons). The next lowest p-value was then compared with 0.05/(no. of comparisons − 1) and so on until the highest p value is compared with 0.05.

3. RESULTS

(a) *Experiment 1: the importance of uninformed individuals in reaching consensus*

(i) *Time to periphery*

The time taken to reach the periphery differed significantly between treatments (GLMM PQL: $F_{2,42} = 12.417$, $p < 0.0001$). Groups with uninformed individuals took significantly longer to reach the periphery than groups in the 2 versus 2 or 4 versus 4 treatments, but there was no significant difference between groups in the 2 versus 2 and 4 versus 4 treatments (figure 1*a*).

(ii) *Deviation from target*

Deviation was measured as how many targets away from the closest intended target of the informed individuals the group finished (e.g. if one set of informed individuals were given target 1 and the others were given target 9 and the group finished at target 7, then the deviation is 2). Most groups were highly accurate, finishing at their targets and therefore scoring no deviation (19/22 groups in the 2 versus 2 treatment, 20/22 groups in the uninformed treatment and 21/22 groups in the 4 versus 4 treatment). Consequently, there was no significant difference between the treatments in deviation from target (GLMM PQL: $F_{2,42} = 0.0583$, $p = 0.944$).

(iii) *Group splits*

The likelihood of a group splitting was significantly affected by treatment (GLMM PQL: $F_{2,42} = 15.604$, $p < 0.0001$). Groups were significantly more likely to split in the 4 versus 4 treatment than in either the uninformed or 2 versus 2 treatment, but there was no difference between the uninformed and 2 versus 2 treatments (figure 1*b*). Where group splits were

Table 1. Proportion of informed individuals needed to guide an uninformed group.

group size	proportion of individuals that are informed (%)	group split?	time until first subgroup/unsplit group reaches the target (s)	proportion of uniformed individuals that reach target in first subgroup/unsplit group (%)
200	2.50	yes	222	5
200	5	yes	250	89
200	10	no	75	100
100	10	no	103	100

observed, we recorded the size of the separate groups. In the 2 versus 2 treatment, all five group splits (100%) were into two separate groups of two individuals. In the uninformed present treatment, five out of seven group splits (71%) were into one group of six and another group of two individuals. In the 4 versus 4 treatment, 9 out of 13 splits (69%) were into two separate groups of four individuals.

(b) *Experiment 2: spatial position of informed individuals*

(i) *Time to periphery*

The time taken to reach the periphery differed significantly between treatments (GLMM PQL: $F_{3,42}=3.712$, $p=0.0186$). Groups with one informed individual starting in the core and one on the group periphery reached the perimeter in significantly less time than groups with two core leaders and groups with two leaders on opposite sides of the edge. There were no other significant differences between treatments in time to periphery (figure 2*a*).

(ii) *Deviation from target*

Deviation from target differed significantly between treatments (GLMM PQL: $F_{3,42}=3.798$, $p=0.0170$). Groups with informed individuals in core and peripheral positions deviated from their targets significantly less than groups in all other treatments. There were no other significant differences between the treatments (figure 2*b*).

(c) *Experiment 3: consensus decision making in large human crowds: proportion of leaders*

The results presented in this section are largely anecdotal as they are based on a small sample size (one group of 200 people and for some treatments a further group of 100 people) due to the logistical difficulties in testing such large groups of people.

At least 5 per cent of group members had to be informed in order to lead the group with reasonable effectiveness (90% of the group) to the target (table 1). If 10 per cent of the members were informed, the whole group reached the target without a split (see appendix 1 in the electronic supplementary material).

(i) *Conflict: 20 versus 10 informed*

Within 60 s, approximately half of the group were together at the target of the 20 informed individuals, while the other half were still fairly close to the centre of the arena joined to the other group by a bridge of people being exchanged between the groups. The group then proceeded to become increasingly stretched out across the arena between the targets of the different informed individuals. After approximately 110 s the 10 informed individuals had also reached their target and managed to take at least 40 per cent of the group with them. A bridge of people remained between the two targets with a constant oscillation of people between the two targets (see appendix 2 in the electronic supplementary material). The experiment was terminated after the oscillation had continued for a further 4 min.

(ii) *Controls: no informed individuals*

When there were no informed individuals, the group formed a torus with multiple lanes of people moving in opposite directions (see appendix 3 in the electronic supplementary material). The torus formed after approximately 30 s and ranged between 14 and 17 m in diameter (figure 4*a*). The torus was not stationary and moved position within the arena (figure 4*b*). The same collective behaviour also occurred with a group size of 100 people without informed individuals.

4. DISCUSSION

Experiment 1 demonstrates the importance of uninformed individuals in the process of reaching consensus movement decisions. Interestingly, when we compare the 2 versus 2 treatment with the 4 versus 4 treatment we find that increasing group size *per se* does not increase the time taken to reach the periphery. Only the presence of uninformed individuals is associated with an increase in this time. Our results for the number of groups that split show that groups in the 4 versus 4 treatment split significantly more frequently than those in the 2 versus 2 and the uninformed present treatments. This suggests that by increasing group size we also increase the likelihood of group fragmentation, but only if the additional group members are informed individuals (significantly more groups split in the 4 versus 4 than the 2 versus 2 treatment). When the additional group members were uninformed, groups were no more likely to split (no significant difference between the 2 versus 2 and the uninformed present treatments). It is likely that the increased splitting in the 4 versus 4 treatment occurs due to a ‘strength in numbers’ effect, whereby the two sets of informed individuals can split and still feel that they have stayed with the group. This is backed up by the fact that 9 out of 13 (69%) of group splits in the 4 versus 4 treatment were into two separate groups of four individuals.

To our knowledge, few empirical studies on vertebrate groups outside the social science literature on human groups have looked at decision making in conflict situations. Dyer *et al.* (2008) have found support for the model of Couzin *et al.* (2005) showing

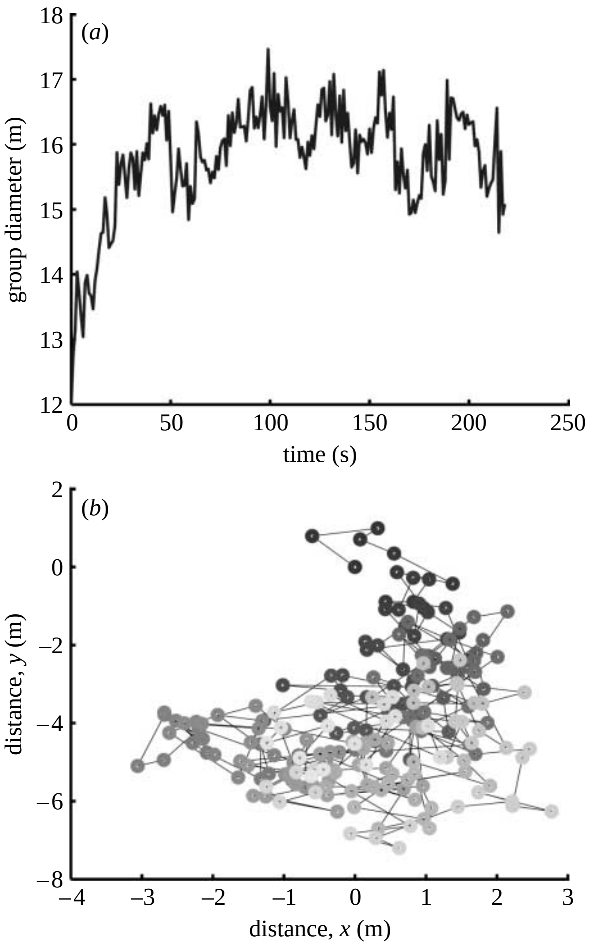

Figure 4. Experiment 3: no informed individuals. (*a*) Time evolution of the central point (average position) of the group. At time $t=0$, the marker is black and the marker becomes increasingly light for later times. (*b*) Diameter of the group, as a function of the time. Calculated as the mean distance to the centre for all individuals, multiplied by $\pi/2$.

that where differences in preference are large and where there is an imbalance in the number of individuals with each directional preference, human groups tend to choose the direction preferred by the majority. However, in contrast to some recent studies (e.g. Ward *et al.* 2008; Franks *et al.* 2009; Sumpter & Pratt 2009), Dyer (2008) did not find evidence that consensus decisions followed a quorum decision rule. Kerth *et al.* (2006) found that Bechstein's bats, *Myotis bechsteinii*, can make group roost decisions that follow a majority rule. They also found that the temporary splitting of groups could allow individuals to avoid following majority decisions that did not favour them. Biro *et al.* (2006) provided further support for Couzin *et al.* (2005); finding that when differences between the directional preferences of two homing pigeons were small, they would average over these preferences, but when differences were large, one of the birds would become leader. Here, we look more specifically at the role of uninformed individuals and demonstrate that both the presence of uninformed individuals and group size can affect the speed with which a group decides between two opposing directional preferences and the likelihood of group fission. There are also several further studies (briefly reviewed in Conradt & Roper 2003; table 1) on buffalo, red deer, gorillas, baboons, howler monkeys, capuchins, elephants and swans, which suggest that conflicts about timings and movement directions are resolved by majority decisions. However, these are largely anecdotal.

In experiment 2, we find that the spatial starting position of informed individuals affects both the speed and the accuracy with which they can guide an uninformed group to a target. We find that having one informed individual starting in the centre and one starting on the periphery of the group is the most effective way of guiding the group quickly and accurately to a target. Our results are in line with the model of Aube & Shield (2004), which predicted that having leaders positioned in a mix of places (centre, peripheral and distant) meant that more people could be saved in a shorter time from a simulated evacuation scenario. Although there are obviously clear differences between our study and real evacuation situations where there could be widespread panic and more erratic behaviour, our results may offer some insight into considerations on the best places to position officials/marshals in order to evacuate people most efficiently.

It is likely that the mixed treatment is most effective due to the benefits of having the two different types of leader. The leader on the periphery is likely to be more mobile and unconstrained and can move freely around the outside of the group and quickly find and align with the target, while the other leader in the core position, although being initially more constrained and surrounded by people, may be able to influence more uninformed individuals through his/her movements towards the target. Beckman *et al.* (2006) found evidence that informed scout bees guide largely uninformed swarms to a new nest site by flying through the swarm indicating the direction of travel. Leca *et al.* (2003) found that white-faced capuchin monkeys starting from core positions were more likely to initiate group movements than those on the edge of a group. Our results suggest possible navigational benefits to animal groups from informed individuals being spread out through the group. For example, in migrating groups of birds, we may expect more accurate navigation of the route if the experienced older individuals, who have already completed the migration in past years, are spread out through the flock. Unfortunately, very little work has been carried out on the extent to which younger individuals use the experience of older individuals in bird flocks or on the relative positioning of adult and juvenile birds (Alerstam 1990; Berthold 1993; Maransky & Bildstein 2001). One such study by Maransky & Bildstein (2001) found that in mixed-age flocks of broad-winged hawks, *Buteo platypterus*, adults were more likely (but not always) the lead bird and were more likely to be (but were not always) in the lead half of the flock.

In experiment 3, we found anecdotal evidence that the results of Dyer *et al.* (2008) on small human crowds (eight individuals) can be scaled up to large human crowds (100 or 200 individuals). First, we showed that a small informed minority (5%) could effectively guide a large uninformed group to a target. This is in close agreement with theoretical results by Couzin *et al.* (2005). Second, when there was a conflict in the information given to different informed individuals, the majority of the group initially went towards the target of the majority. However, the arena was not large enough to decide whether the group would have reached the majority preferred target cohesively, or split. Third, when no directional information was given to any members of the group, we observed the formation of a torus as seen with smaller groups (Dyer *et al.* 2008). Our work indicates that this collective behaviour arises when people are in continuous motion without any strong directional cues. This potentially sheds interesting light on torus formation in animal groups where the behaviour is frequently found in pelagic fish species such as barracuda, *Sphyraena barracuda* and jack, *Trachurus symmetricus*, and has also been described for wrinkle-lipped bats, *Chaerephon plicata* (Siemers & Nill 2001).

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