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# Collective decision-making in white-faced capuchin monkeys

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In group-living animals, collective movements are a widespread phenomenon and occur through consensus decision. When one animal proposes a direction for group movement, the others decide to follow or not and hence take part in the decision-making process. This paper examines the temporal spread of individual responses after the departure of a first individual (the initiator) in a semi-free ranging group of white-faced capuchins (*Cebus capucinus*). We analysed 294 start attempts, 111 succeeding and 183 failing. Using a modelling approach, we have demonstrated that consensus decision-making for group movements is based on two complementary phenomena in this species: firstly, the joining together of group members thanks to a mimetic process; and secondly, a modulation of this phenomenon through the propensity of the initiator to give up (i.e. cancellation rate). This cancellation rate seems to be directly dependent upon the number of followers: the greater this number is, the lower the cancellation rate is seen to be. The coupling between joining and cancellation rates leads to a quorum: when three individuals join the initiator, the group collectively moves. If the initiator abandons the movement, this influences the joining behaviour of the other group members, which in return influences the initiator's behaviour. This study demonstrates the synergy between the initiator's behaviour and the self-organized mechanisms underlying group movements.

**Keywords:** cohesion; collective movements; quorum; mimetism; leadership; *Cebus capucinus*

## 1. INTRODUCTION

In group-living animals, the widespread phenomenon of collective movements is the keystone of many social activities with a highly adaptive, function-like response to predation or foraging (Alexander 1974). Collective movements involve many interconnected questions concerning whether the group should move or stop. Among other concerns, should they move together or in subgroups? Which direction should be chosen? The mechanisms underlying such decisions remain poorly understood. Two different explanations are often discussed, namely leadership and self-organized mechanisms (Krause & Ruxton 2002; Conradt & Roper 2005). However, the synergy between both mechanisms is rarely taken into account (Couzin *et al.* 2005; Biro *et al.* 2006; Sumpter 2006).

In the study of mechanisms underlying such collective decisions, a typical approach of leadership implies that specific high-ranking individuals are often key decision-makers for when and where the group should move (dwarf mongooses (*Helogale undulata rufula*): Holekamp *et al.* 2000; golden shiners (*Notemigonus crysoleucas*):

Leblond & Reeb 2006; mountain gorillas (*Gorilla gorilla berengei*): Schaller 1963; leaf monkeys: Stanford 1990; hanuman langurs (*Presbytis entellus*): Sugiyama 1976; brown lemurs (*Eulemur fulvus fulvus*): Kappeler 2000). This kind of process has been labelled 'personal leadership' by Leca *et al.* (2003). From their results on white-faced capuchins (*Cebus capucinus*), Leca *et al.* (2003) defined a 'distributed leadership', where any individual can initiate a movement and successfully be followed. In other words, dominance, age and gender do not consistently affect leadership in group movements. Moreover, these authors found that leadership was not limited to a single individual in white-faced capuchins. Indeed, any individual within this species could initiate a collective movement, and many group members regularly succeeded in recruiting at least three followers. Leadership implying turnover within the group for the role of initiator has also been reported in several species (hamadryas baboons (*Papio hamadryas*): Kummer 1968; white-faced capuchins: Leca *et al.* 2003; Tonkean macaques (*Macaca tonkeana*): Sueur & Petit 2008; Brown lemurs: Jacobs *et al.* 2008; cattle (*Bos taurus*): Reinhardt 1983, Dumont *et al.* 2005; Przewalski horses (*Equus ferus przewalskii*): Bourjade *et al.* 2009; plains zebras (*Equus burchellii*): Fischhoff *et al.* 2007; domestic geese (*Anser domesticus*): Ramseyer *et al.* 2009; bar-headed geese (*Anser indicus*): Lamprecht 1992).

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In collective movements, the decision to move is the result of a consensus between the initiator's proposal and the acceptance of group members to follow. In white-faced capuchins, when the first moving individual emitted glances, trills and/or walked slowly, the success of a start attempt was enhanced and led to a collective movement (Leca *et al.* 2003). Despite the positive contributions of these behaviours, it is important to note that an initiator could nevertheless succeed in leading a group movement without displaying any such behaviour (Leca *et al.* 2003). Conversely, it has been reported that an attempt with trill could also fail to trigger group movement (Boinski 1993; Boinski & Campbell 1995). Similar results have been reported for macaques (Sueur & Petit 2008). One might suggest that the decision could have been made before the first individual proposed to move, with the group having established a consensus via vocal or visual signals. In this case, the group would have already decided to leave, and any individual could thus lead the group (Kummer 1968; Visscher & Seeley 2007). Menzel & Beck (2000) suggested that the majority of studies focusing on collective movements were based on the use of signals; they noticed nonetheless that animals could reach a consensus based on very well-organized and coordinated actions, without displaying any obvious signal. In brown capuchins (*Cebus apella*), for instance, the alpha male appeared responsible for the great majority of travel decisions without displaying evident signals towards conspecifics (Janson 1990). In all these cases, one essential cue for movement appears to exert a major influence on the subsequent success of an attempt: the motion of the initiator itself.

It is equally important to consider the initiator's response to the behaviour of its followers. In golden lion tamarins (*Leontopithecus rosalia*), Menzel & Beck (2000) reported that the tendency to follow other animals, and to wait if not followed, showed a cohesive quality of group movement. Moreover, the authors noticed that animals that were not followed typically returned to the group within several minutes. Byrne *et al.* (1990) described in detail cases of this type in mountain baboons (*Papio ursinus*), where the initiator soon returned to the main group. Byrne and collaborators distinguished several situations where the first moving individual showed its decision to move long enough for other group members to follow it. After moving several metres, the initiator's waiting time could either be very short (when immediately joined by the group) or very long (if group members were slow to decide to follow). In several cases, the initiator gave up and returned to its departure point. Indeed, the initiator may end up alone if it keeps moving while the rest of the group stays still. The authors considered these different cases as an index of the specific roles and weight that particular individuals could have in travel decisions (Byrne *et al.* 1990). On the contrary, we consider that these different initiation outcomes may result from a unique process where the tendency of the first moving individual to give up could vary and thus modulate the collective movement.

In this study, we investigated the collective decision-making process of a semi-free ranging group of white-faced capuchins, free to switch between two locations. Previous studies have established that leadership is distributed throughout the whole group and that individuals can be successful leaders in the absence of explicit signals (Leca *et al.* 2003). The mechanisms

used, however, remain unknown. Here, we aimed to determine, firstly, whether mimetism is the underlying mechanism of joining group movements and, secondly, whether the likelihood of the initiator giving-up would modulate the outcome of initiations. If these reasonable assumptions hold, the temporal organization of the individual decisions (movement initiation and responses) should account for the collective decision-making for group departure. More precisely, we assume that if an initiator has not been joined by a certain quorum of followers, the collective departure would fail.

## 2. MATERIAL AND METHODS

### (a) *Subjects and environment*

The group of white-faced capuchins was established in 1989 at the Primate Centre of Strasbourg University, France. At the beginning of the study, the group contained 11 individuals of three separate lineages. Five males (aged 2, 6, 6, 7 and at least 20 years old, respectively) and five adult females (5, 5, 7 years old and two individuals at least 20 years old) were sampled. Ages were estimated for the three oldest individuals, as they were wild-born. The remaining group members were born in captivity. One six-month-old juvenile male still clung to the mother. Three births and one removal occurred during the 2-year study period. These five individuals were not included in the analyses.

The group was kept and observed in an outdoor enclosure. The 25 m<sup>2</sup> indoor compartment connected to the outdoor enclosure had a concrete floor and metal perches. However, the indoor enclosure was not open to the group during observation periods in order to maintain individuals in the outdoor enclosure. At all other times, the monkeys had free access to both enclosures. Commercial primate pellets and water were available *ad libitum* in the indoor enclosure. Fresh fruit and vegetables were provided once a week but not during observations.

The outdoor enclosure was a 5000 m<sup>2</sup> park with natural vegetation and uneven ground. The park was designed to provide the animals with a large number of spatial options for organizing and carrying out their activities. A preliminary activity scan showed that the park roughly consisted of three functional areas for the monkeys (Leca *et al.* 2003). Firstly, a small area located around the indoor compartment was mainly devoted to social activities or resting as a group (40 m<sup>2</sup>). Second, a large wooded area was dedicated to foraging activities as a group (3000 m<sup>2</sup>). These first two areas (social/resting or foraging) are denoted hereafter as goal areas. A third zone was transitional: the animals used it as a passage between the other two areas (450 m<sup>2</sup>).

Observations took place between 9.00 and 13.00 and between 14.00 and 18.00 from April 1999 to October 2000, except during the coldest months (December 1999–February 2000). Two experimenters collected data using tape recorders.

Our experiments were all carried out in full accordance with the ethical guidelines of our research institution and comply with the European legislation for animal welfare.

### (b) *Definitions*

#### (i) *Initiator*

Any individual moving away from the stationary group, and moving more than 10 m away in less than 40 s was deemed to be making an initiation (or start attempt) and was subsequently labelled the initiator (Leca *et al.* 2003; Jacobs *et al.* 2008; Sueur & Petit 2008). All occurrences of initiation

were sampled (*all occurrence sampling*; Altmann 1974), and the position of the initiator was continuously recorded over a 10 min period by an observer (*focal animal sampling*; Altmann 1974). The observer also noted the initiator's time of arrival at the goal area, when relevant. Note that initiations never occurred at the same time; the group was never faced with a choice between two competing initiators.

(ii) *Followers*

Group members could respond to an initiation by following the initiator. A follower was defined as an individual departing from the same area within 15 min of the initiation and following the same direction as the initiator (Leca *et al.* 2003). A second observer recorded the identity of followers as well as their departure latencies (time elapsed since initiation).

(iii) *Successful/failed initiation*

Group members could either respond to the initiation or remain in the same place. Therefore, initiation events could only yield two opposing outcomes: either (i) some or all individuals responded to the initiation and moved to the other location (*successful initiation*) or (ii) the initiator (and its few initial followers, if any) cancelled its movement and returned to its original location, merging back into the group of individuals that had not followed (*failed initiation*). In the latter case, the group reassembled and the next initiation took place from the same location.

(c) *Survival analysis*

Many results deal with the temporal occurrence of behavioural events. The time of each event was assessed according to its latency (time elapsed since the onset of stimulus). Hence, this latency represented the duration during which the focal animal had not yet exhibited locomotive behaviour.

This latency could thus be considered as the survival time of its current state (not moving). In this way, individual behaviours could be analysed as (coupled) continuous-time Markov processes. Following the same logic, we could also consider them to be driven by a rate of occurrence probability (denoting the probability per unit of time to exhibit the behaviour). Furthermore, this probability rate could be enhanced or reduced to reflect the influence of internal or external stimuli, meaning that behaviour may be influenced by circumstances. When behavioural transition can be well defined (Colgan 1977), survival analysis is the best statistical framework to quantify time-structured behaviours (Cox & Oakes 1984). This has been successfully applied in numerous ethological studies (Haccou & Meelis 1992; Losey *et al.* 2001), including collective self-organized behaviours (Theraulaz *et al.* 2002; Jeanson *et al.* 2005; Gautrais *et al.* 2007). Details on survival time analysis and its link to continuous-time Markov processes can be found in the 'electronic supplementary material' section.

### 3. RESULTS

(a) *Collective departures*

The dataset used in this study was the same as in Leca *et al.* (2003). We recorded 315 initiations over a period of 76 observation days (representing a total of 682 h). Of these, 294 (93.3%) initiations occurred while the group had been together within the initiator's departure area.

In order to withdraw effects of various group sizes, data analysis was performed on these 294 initiations, among

which 111 succeeded and 183 failed. The overall probability for an initiation to yield a success was hence of approximately 0.37 per initiation event. The collective movements of the group are ruled by the rate of successful initiations.

The temporal organization of the events showed that collective movements were relatively scarce in time: the time devoted by the group to its social or foraging activity was much greater than the time it required to travel from one goal area to the other (figure 1). Each movement event was therefore well defined and distinct from the preceding and following ones. Provided that concurrent responses to an external stimulus can be excluded, this temporal aggregation of movements suggests that an endogenous process synchronizes the responses within the group.

(b) *Time of day effects*

To assess the endogenous nature of this process, we first checked for temporal effects on the propensity to reach or to leave the foraging zone. The distribution of events during the daytime seemed to be fairly equal. Moreover, the probability that an initiation would elicit a success did not depend on the time of day (electronic supplementary material). Therefore, we conclude that collective movements do not tend to occur around particular times of day.

(c) *The endogenous model*

The spread of followers' responses over the 15–20 min period following the initiator's departure (figure 1) ruled out any possibility that this process could consist of a prior negotiation followed by the simultaneous departure of all members. This response time rather indicated that the decisions to imitate the departing initiator were stochastic and could be mutually influential.

The distribution of the number of followers divided by the outcome of the initiation was strongly bimodal, with a peak at one individual (the initiator) and 10 individuals (the whole group). Initiations with four to eight followers were rare. This bimodal distribution is the total sum of failed initiations distribution (with a maximum at one individual) and successful initiations (with a maximum at 10 individuals) (figure 2). Furthermore, in the few cases of successful initiations with submaximal group sizes (seven to nine individuals), the same three adult individuals failed to follow, regardless of the initiator's identity. They were one male and two low-ranking females, all identified as spatially peripheral group members. Their refusal to join the group can be attributed to specific rationale (H. Meunier 2007, unpublished data) that will not be dealt with in the present study. Accordingly, the process will be regarded hereafter as producing an all-or-nothing outcome: either the whole group departed to the other area or the initiation failed.

The stochastic nature of individual decisions and this bimodality suggested a simple dynamical model with two balancing factors: (i) a propensity to follow the initiator, which increased as more and more members followed; and (ii) a cancellation mechanism that would abort the departure if too few individuals followed over too long a period.

From our field observations, the cancellation mechanism could be attributed to a decision made by the initiator: when its departure did not trigger enough following responses in a short time, there was a high

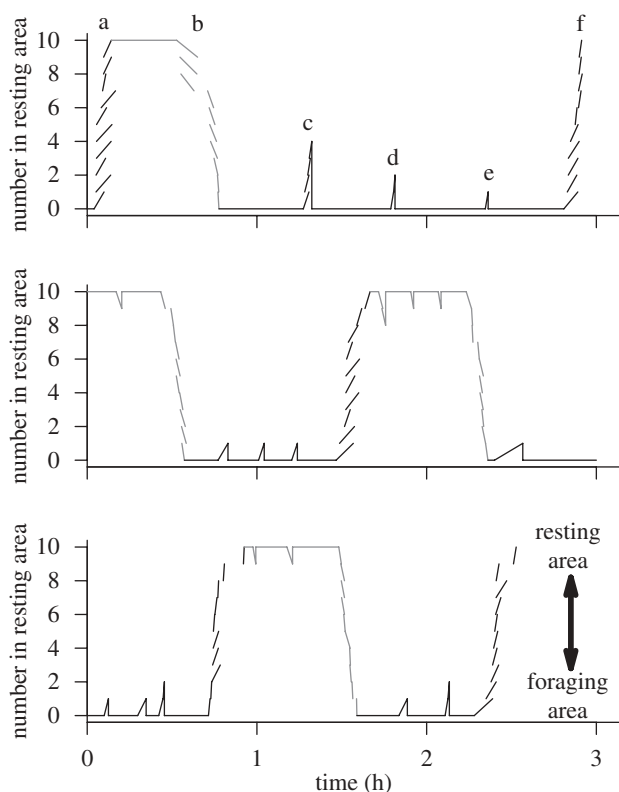


Figure 1. Typical examples of collective movement. The dynamics of the collective movement between the foraging area (bottom) and the resting area (top) is reported throughout the observation time (space–time diagram). Each segment represents an individual movement between both areas. The left end of a segment corresponds to its departure time, the right to its arrival time. For clarity, ordinates are conventionally set to the number of individuals remaining in the resting area. Hence, over time, upper segments correspond to movements towards the resting area (black), and lower segments to movements towards the foraging area (grey). Letters indicate typical scenarios during the collective movement. a, At the very beginning, the whole group is in the foraging area (bottom) and then move towards the resting area (top). b, The whole group travels back to the foraging area. Three successive failed initiations then occur with, respectively, two followers in c, one in d and none in e. f, The whole group travels back to the resting area.

probability that the initiator would cancel the movement and the initiation would thus fail. Inversely, the probability of cancellation practically disappeared as soon as a majority of individuals followed, eventually triggering the remaining individuals to follow and the whole group to move. This dynamical model could account for the occurrence of failed initiations, the all-or-nothing nature of initiation outcomes and the temporal spread of events. This model can be parameterized using the initiation rate, the following rates (which may depend on the number of individuals having already left) and the cancellation rates (which may also depend on the number of individuals having already left the group).

#### (i) Initiation rate

The initiation rate was quantified by the survival curve of initiation latencies (figure 3a). In order to put aside any potential effect of non-independence between successive failed initiations, this analysis was restricted to those

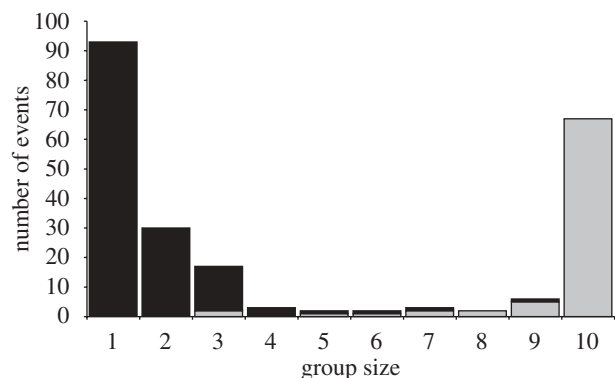


Figure 2. Distribution of group sizes. Distribution of the number of individuals involved in a movement (before potential giving-up) split by the outcome of the initiation (successful initiations when no giving-up occurred, failed initiations otherwise). The bimodal aspect is strongly correlated with the outcome of the initiation. (To prevent censoring effects owing to the stoppage of the survey, only the 225 unaffected initiations were analysed). Black bars, failed initiations; grey bars, successful initiations.

initiations immediately following the last gathering of the whole group in the area. The survival curve fitted a time constant exponential distribution of 1290 s (log likelihood ratio test:  $p = 0.66$ ), which indicated that the probability per time unit of observing an initiation was constant over time.

#### (ii) Following rates

Latency of the first follower was calculated to be the time elapsed from the initiator's departure to the first follower departure, if applicable. Its survival function also fitted an exponential distribution, but with a much shorter time constant of 96.3 s (log likelihood ratio test:  $p = 0.91$ , figure 3b). Note that these time constants referred to the event of observing the departure of any individual among those remaining. In the case of independent and similar behaviours, the time constant for each individual was simply the product of the collective time constant and the number of remaining individuals: in the present case, individual time constants would then be  $1290 \times 10 = 12\,900$  and  $96.3 \times 9 = 866.7$  s, respectively, for departing as an initiator and departing as a first follower.

The contrast between the two values confirmed the role of imitation: the mean probability rate for an individual to leave when the whole group was staying (initiation rate:  $1/12\,900 \approx 0.77 \times 10^{-4} \text{ s}^{-1}$ ) increased more than 10-fold once the initiator had departed ( $1/866.7 \approx 11.5 \times 10^{-4} \text{ s}^{-1}$ ). Moreover, the fitted time constants of following according to departure rank showed that they decreased (the rate of departure increased) as more and more followers had already departed (figure 3c). Interestingly, these time constants appeared to depend linearly on the ratio between the number of individuals still staying in the area and the number of individuals that had already departed.

$$\tau_r = \alpha + \beta \frac{N-r}{r}, \quad (3.1)$$

with  $\tau_r$  being the individual time constant for following during the  $(r+1)^{\text{th}}$  departure,  $r$  the number of

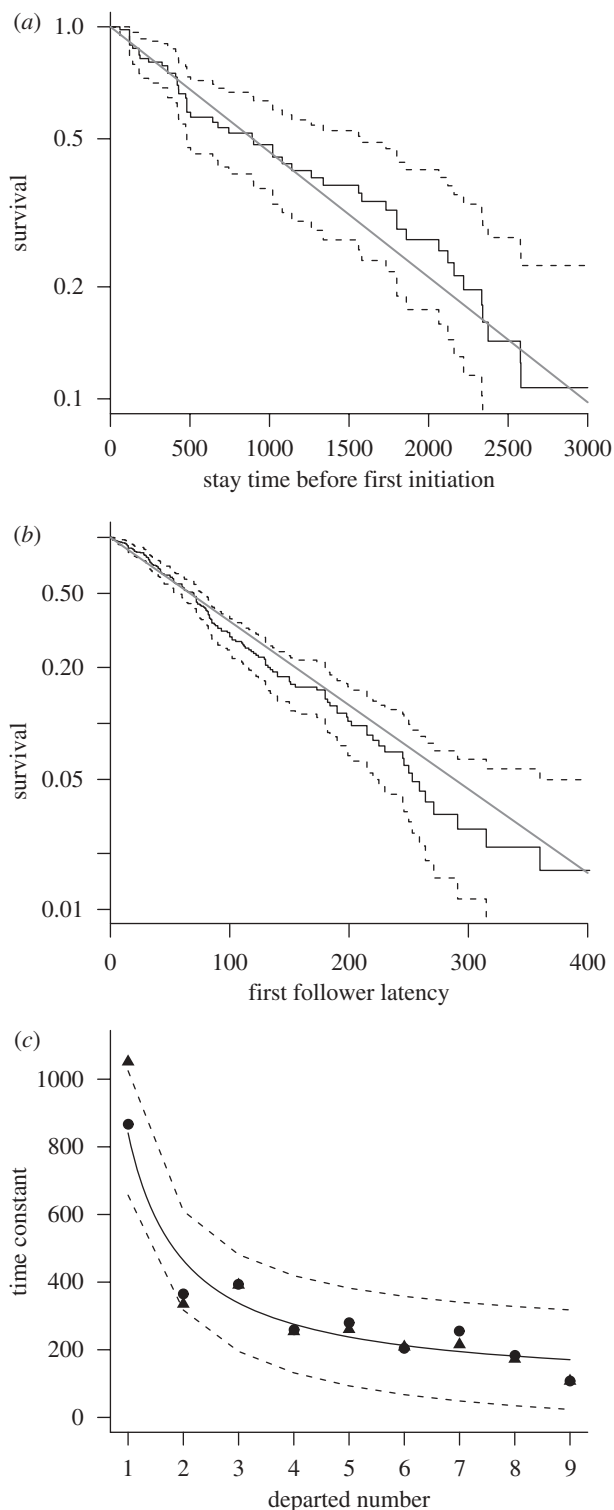


Figure 3. Dynamical analysis. (a) Survival function of duration in an area before an initiation (time constant = 1290 s). (b) Survival function of first follower latency (time constant = 96.3 s). Kaplan–Meier estimate and CI. The grey line is the exponential line of best fit. (c) Fitted time constants of following according to the number of individuals having already departed. Dots, every initiation considered; triangles, only initiations leading to a success; solid line, best fit; dotted lines, predictions of the best fit (see text for the fitted formula).

individuals having already departed,  $N$  the total number of individuals ( $N = 10$ ),  $\alpha = 162.3$  s,  $\beta = 75.4$  s (fit shown on figure 3c,  $R^2 = 0.94$ ,  $F$ -statistic  $p$ -value =  $1.46 \times 10^{-5}$ ). Hence, the responses to the initiation resulted in a positive feedback loop.

### (iii) Cancellation rates

If the process was unrestrained and unlimited in time, this process of imitation would result in all individuals following the initiator every time an initiation occurred. Obviously, this process broke down on some occasions, when the initiator cancelled the departure. The exact times at which cancellation occurred could not be measured experimentally, especially when the initiator had moved under the cover of vegetation. Hence, the cancellation rate was taken as a freely adjustable parameter of the model.

In this group, any individual could be an initiator and most of these initiators could induce a group movement (Leca *et al.* 2003). The cancellation rate may, at least on some occasions, depend on the number of individuals having already departed. The experimental distribution of group sizes (figure 2) was fitted as follows:

- (i) The initiation rate was evenly set among individuals to  $1/12\,900$  s $^{-1}$ .
- (ii) Likewise, the following rate was evenly set among still staying individuals and obeyed the linear dependence on the ratio  $(N - r)/r$  mentioned above (equation (3.1)).
- (iii) As a first step, we tested the simplest hypothesis of a constant cancellation rate ( $C = \alpha$ ). Indeed, this mechanism could yield our experimental distribution of group sizes (data not shown), but no rate value could lead to a quantitative agreement.

The cancellation rate  $C(r)$  was tested with a rule decreasing with  $r$ .

$$C(r) = \frac{\alpha}{1 + (r/\gamma)^\varepsilon}. \quad (3.2)$$

The experimental distribution of group sizes could be fitted by this procedure as accurately as desired (figure 4a,b). The best fitting was obtained with:  $\gamma = 2$ ,  $\varepsilon = 2.3$  and  $\alpha = 0.009$  s $^{-1}$  (figure 4c).

With this cancellation rate, the theoretical distributions of successful and failed initiations were in good agreement with experimental distributions (figure 4a) and therefore also between the theoretical and experimental distributions of the total number of initiations. Nonetheless, this demonstrated that this type of dynamic process actually accounted for the occurrence of failed initiations, the all-or-nothing outcomes and the temporal spread of events after each initiation event.

Our experimental data (distribution of group sizes, initiation and following rates) implied that the cancellation rate was modulated by the number of individuals having already departed because it showed a nonlinear decrease as the number of departed followers increased (figure 4c). Therefore, a threshold of more than three individuals appeared necessary to avoid giving-up and the subsequent failure of the collective movement. Indeed, the vast majority of initiations that attracted this number of participants succeeded, and the whole group consequently moved. This threshold or quorum resulted from the coupling of the joining and cancellation rate, both depending of the number of followers. Consensus decision-making was a stochastic process: each initiation had a probability of being successful, this probability being approximately that of reaching the quorum

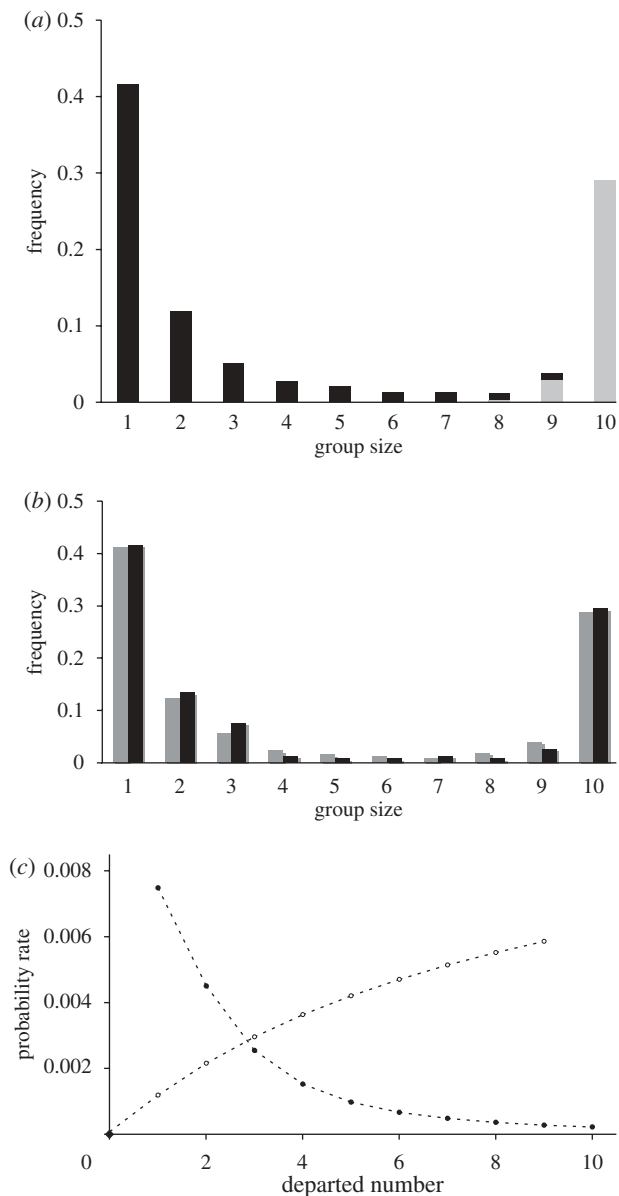


Figure 4. Anonymous model of the dynamic mechanism for the collective decision process. (a) Distribution of theoretical group sizes for failed and successful initiations (5000 simulations). Black bars, failed initiations; grey bars, successful initiations. (b) Distribution of group size with comparison of experimental data and model output (5000 simulations). Grey bars, model; black bars, experiment. (c) Model probability of following or cancellation as functions of the number of individuals already departed. The probability of cancellation (equation (3.2)) was dichotomously adjusted so as to obtain model results in (b). Filled diamonds, initiate; open circles, follow; filled circles, cancel.

(figure 5). Actually, a further investigation of the temporal relationship between the successful initiations proved the critical role of this modulation on cancellation rates in collective decisions.

#### (iv) Modulation by stay time

Even if the occurrences of successful initiations appeared unaffected by the time of day, the time course of events could still depend on an endogenous clock on a daily basis. For instance, the time already spent in the foraging area could have an effect on the probability of success for

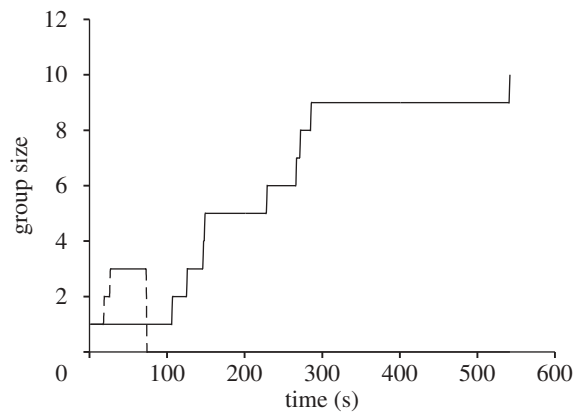


Figure 5. Number of participants over time for two collective movements. One movement succeeded and after around 10 min, all the individuals have moved. The second movement rapidly failed despite the fact that two individuals had quickly followed the initiator.

the next initiation. The survival analysis of these stay times showed that a longer stay time increased the probability of the group leaving the area (see electronic supplementary material, figure S2*a,b*). Among events characterizing dynamics, the cancellation rate seemed dependent on the stay time. On the other hand, the probability rate for an initiation to occur and to yield a success seemed independent of this stay time (see *modulation of the cancellation rate* in electronic supplementary material).

## 4. DISCUSSION

This paper explores the temporal organization of individual responses after stimulus onset (departure of a first individual). Using a modelling approach, we have demonstrated that consensus decision-making for group movements in our study group is based on two complementary phenomena: firstly, the joining together of group members thanks to a mimetic process, and secondly, a modulation of this phenomenon through the propensity of the initiator to give up if the number of followers is insufficient (i.e. cancellation rate). We considered the initiator's start attempt as well as the way group members followed and how they could subsequently act in response to the initiator's decision by their behaviour (staying or following). The initiator's giving-up will influence the joining behaviour of other group members, which will in return influence the initiator's behaviour. At the dynamics level, this leads to a threshold or quorum: the mimetism of individuals responding to the initiator reinforces the effect of followers on the probability of giving-up (the greater the number of followers, the lower the cancellation rate will be). To date, such feedback and the link between the two retroactions have only been reported in studies on collective decision-making in insects (Beekman *et al.* 2001). To our knowledge, the present study is the first of its kind in mammals.

The act of giving-up is difficult to measure but during observations, the initiator was seen to stop and sometimes return to the main group when not followed, or when followed by only one or two individuals. In the latter case, the followers returned to the group as well. Such behaviour has previously been described in golden lion

tamarins (Menzel & Beck 2000). The crucial role ascribed to giving-up implies that the initiator monitors how its conspecifics react to its initiation behaviour, as already shown in white-faced capuchins (Meunier *et al.* 2008) and macaques (Sueur & Petit *in press*). In macaques, positive feedback (the process by which group members follow) probably stops because the initiator decides to give up. No other reason could be invoked for individuals suddenly ceasing to follow, but there is a discrepancy between these two events.

We can assume that the initiator's giving-up is linked to either an internal state of motivation (Eibl-Eibesfeldt 1984) or the initiator's response threshold (Weidenmüller 2004; Maillieux *et al.* 2006). Motivation is a non-permanent situation that reflects either the tendency to continue a current behaviour (moving) or to switch to another behaviour (giving-up). In both cases, it is the probability of a change in state that is considered here. A high propensity to change behaviour could reflect either a low level of motivation or a high sensitivity to a threshold. The opposite could also be suggested. Different giving-up rates with different rates of following have been previously reported for this group of white-faced capuchins, whatever the identity of the initiator (Leca *et al.* 2003). 'Good' initiators (i.e. able to make many group members follow) exist and do not need to have an influential social status: the dominant animals are not the only ones followed, nor are the animals with many relatives (Leca *et al.* 2003). One of the conditions for being followed by the whole group (or by nearly all individuals) might be to wait longer after the previous initiation. Being able to wait a long time could depend on the internal motivation of the initiator or on its low response threshold, and may lead to different types of initiators (good or 'bad' initiators).

We found a refractory period during which no attempt could be transformed into success. More precisely, the cancellation rate of the initiator was modulated by the group's stay time. A start attempt was more likely to fail if it occurred too early after the preceding collective movement. The motivation or the threshold for reaction could be invoked for the initiator but also for other group members. These two parameters could be directly dependent on the time spent resting or foraging. For example, the quantity of ingested food could lead to a physiological state requiring consequent movement and the search for food. Thus, the initiator and the followers have a probability of movement that depends on each personal physiological condition or each energy-level reserve (Rands *et al.* 2008). The propensity of group members to follow could intervene in the success of a start attempt, although the initiator is unable to measure it.

Lastly, we need to understand why animals will make a start attempt even if there is a risk of failure. Some animals initiate group movements even though their probability of failing is higher than their probability of being followed. This behaviour occurs because leading a group could give an advantage to the initiator in two ways. The direction that the group will take is most often that proposed by the first moving animal. An individual may want to go to a particular place, but be reluctant to go there alone. In such a case, one possibility (which is not an active one for this individual) is that the direction chosen by the group is the same as its own choice (Conradt & Roper 2005). The other possibility is to make a start attempt to

pull the group in its preferred direction. Even if the chance of success is low, it is presumably worth trying in terms of potential benefits. Leading a group is costly in terms of energy and dangerous if other animals want to go somewhere else, but in the same way as aggressive interventions during conflicts, the immediate benefit for such an individual is the respect gained from other group members (Petit & Thierry 1994). Thus, another possible advantage gained from leading a group is that the initiator imposes itself on other group members not only during group movements but also during other daily interactions (King *et al.* 2008). Finally, while leading or following a group is often regarded as a foraging strategy, it may also affect individual opportunities for behavioural innovation (Leca *et al.* 2007).

From our results, we could propose a general scheme explaining the process of initiating and joining collective movements. In the field of collective decision-making during group movements, our approach adds a third alternative (that combines both extremes of the continuum) to the two classical views described hereafter. It is often described that one animal is a 'leader', which decides and controls group movement (for a review, see Conradt & List 2009). This situation seems rarely to occur in nature (Conradt & Roper 2005). Conversely, in other cases, all individuals have the same weight and no leader is identified as in self-organized systems (Deneubourg & Goss 1989; Conradt & Roper 2003; Couzin & Krause 2003). In this paper, we considered both the initiator that proposes a direction to move onwards and the other animals taking part in the decision-making process by following this first animal or not, as described in honeybees (*Apis mellifera*; Visscher & Seeley 2007). This study demonstrates the synergy between a specific individual—the initiator—and self-organized mechanisms underlying group movements. One of the main characteristics of our results is the U-shaped (or bimodal) distribution of the number of movements depending on the number of joiners; this distribution results from the addition of the failed initiation distribution (its maximum being with only the initiator) to that of the successful initiations (its maximum being with all the group). The dynamics leading to such distributions must exhibit a threshold. It may be owing to one of the behavioural responses governed itself by a quorum (for a discussion of quorum, see Sumpter & Pratt 2008). In the present case, the distribution (and the threshold) is a by-product of our dynamics governed by two positive feedbacks: the first governs the probability of joining, and the second the probability of giving-up. The dynamics, despite the rather continuous response of the individuals, leads to an all-or-nothing response at a collective level.

Many examples are reported in the literature where such positive feedback is involved, and not only in collective movement. From a very basic point of view, the number of individuals exhibiting a behaviour is governed by two probabilities similar to our probability of moving and of giving-up (Seeley & Visscher 2008). Our hypothesis is therefore that a U-shaped distribution of this type must be widespread in many species and in many activities. Little is known about the mechanisms underlying decision-making in vertebrate animal groups. However, Ward *et al.* (2008) recently showed that a quorum response to conspecifics can explain collective movement decision-making in sticklebacks (*Gasterosteus aculeatus*),



with or without a potential predation risk. In these experiments, a U-shaped distribution for group decision-making was also highlighted. It is surprising that no further examples have been reported in the literature if we exclude the case of hysteresis in social insects, which is associated to recruitment (Beekman *et al.* 2001).

Our model could in principle be tested on many species, with an adjustment of parameters according to each species or each specific situation. In the case of despotic species, for example (Conradt & Roper 2003), the decision would be imposed by a powerful animal that would never renounce as its status is high enough to be followed (King & Cowlshaw 2009). Conversely, initiators in less hierarchical species would need to convince other group members to follow them and would have a variable probability of giving-up. Such influence of dominance has been already proposed in a macaque model (Hemelrijk 1999). Moreover, if a single goal is available (a waterhole for example), any group member could start the movement and would probably never return to the main group, whereas much more negotiation would be necessary in the case of several simultaneous aims. To validate our assumption on generalization, we need to test this model in other social species.

Our experiments were all carried out in full accordance with the ethical guidelines of our research institution and comply with the European legislation for animal welfare.

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## REFERENCES

- Alexander, R. D. 1974 The evolution of social behavior. *Annu. Rev. Ecol. System.* **5**, 326–383. (doi:10.1146/annurev.es.05.110174.001545)
- Altmann, J. 1974 Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–265. (doi:10.1163/156853974X00534)
- Beekman, M., Sumpter, D. J. T. & Ratnieks, F. L. W. 2001 A phase transition between disordered and ordered foraging in pharaoh's ants. *Proc. Natl Acad. Sci. USA* **98**, 9703–9706. (doi:10.1073/pnas.161285298)
- Biro, D., Sumpter, D. J. T., 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)
- Boinski, S. 1993 Vocal coordination of group movement among white-faced capuchin monkeys, *Cebus capucinus*. *Am. J. Primatol.* **30**, 85–100. (doi:10.1002/ajp.1350300202)
- Boinski, S. & Campbell, A. F. 1995 Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour* **132**, 875–901. (doi:10.1163/156853995X00054)
- Bourjade, M., Thierry, B., Maumy, M. & Petit, O. 2009 Decision-making in Przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements. *Ethology* **115**, 321–330. (doi:10.1111/j.1439-0310.2009.01614.x)
- Byrne, R. W., Whiten, A. & Henzi, S. P. 1990 Social relationships of mountain baboons: leadership and affiliation in a non-female-bonded monkey. *Am. J. Primatol.* **20**, 313–329. (doi:10.1002/ajp.1350200409)
- Colgan, P. W. (ed.) 1977 *Quantitative ethology*. New York, NY: Wiley.
- Conradt, L. & List, C. 2009 Group decisions in humans and animals: a survey. *Phil. Trans. R. Soc. B* **364**, 719–742. (doi:10.1098/rstb.2008.0276)
- Conradt, L. & Roper, T. J. 2003 Group decision-making in animals. *Nature* **421**, 155–158. (doi:10.1038/nature01294)
- Conradt, L. & Roper, T. J. 2005 Consensus decision making in animals. *Trends Ecol. Evol.* **20**, 449–456. (doi:10.1016/j.tree.2005.05.008)
- Couzin, I. D. & Krause, J. 2003 Self-organization and collective behavior of vertebrates. *Adv. Study Behav.* **32**, 1–75. (doi:10.1016/S0065-3454(03)01001-5)
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)
- Cox, D. R. & Oakes, D. 1984 *Analysis of survival data*. London, UK: Chapman and Hall.
- Deneubourg, J. L. & Goss, S. 1989 Collective patterns and decision-making. *Ethol. Ecol. Evol.* **1**, 295–311.
- Dumont, B., Boissy, A., Achard, C., Sibbald, A. M. & Erhard, H. W. 2005 Consistency of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. *Appl. Anim. Behav. Sci.* **95**, 55–66. (doi:10.1016/j.applanim.2005.04.005)
- Eibl-Eibesfeldt, I. 1984 *Ethology: behavioural biology*, 3rd edn. Paris, France: Naturalia et Biologia.
- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M.-J. & Rubenstein, D. I. 2007 Social relationships and reproductive state influence leadership roles in movements of plains zebra *Equus burchellii*. *Anim. Behav.* **73**, 825–831. (doi:10.1016/j.anbehav.2006.10.012)
- Gautrais, J., Michelena, P., Sibbald, A., Bon, R. & Deneubourg, J. L. 2007 Allelomimetic synchronization in merino sheep. *Anim. Behav.* **74**, 1443–1454. (doi:10.1016/j.anbehav.2007.02.020)
- Haccou, P. & Meelis, E. 1992 *Statistical analysis of behavioural data: an approach based on time-structured models*. Oxford, UK: Oxford University Press.
- Hemelrijk, C. 1999 An individual-oriented model of the emergence of despotic and egalitarian societies. *Proc. R. Soc. Lond. B* **266**, 361–369. (doi:10.1098/rspb.1999.0646)
- Holekamp, K. E., Boydston, E. E. & Smale, L. 2000 Group travel in social carnivores. In *On the move* (eds S. Boinski & P. A. Garber), pp. 587–627. Chicago, IL: University of Chicago Press.
- Jacobs, A., Maumy, M. & Petit, O. 2008 The influence of social organisation on leadership in brown lemurs (*Eulemur fulvus fulvus*) in a controlled environment. *Behav. Process.* **79**, 111–113. (doi:10.1016/j.beproc.2008.05.004)
- Janson, C. 1990 Ecological differences of individual spatial choice in foraging groups of brown capuchin monkeys *Cebus apella*. *Anim. Behav.* **40**, 922–934. (doi:10.1016/S0003-3472(05)80994-7)
- Jeanson, R., Rivault, C., Deneubourg, J. L., Blanco, S., Fournier, R., Jost, C. & Theraulaz, G. 2005 Self-organized aggregation in cockroaches. *Anim. Behav.* **69**, 169–180. (doi:10.1016/j.anbehav.2004.02.009)
- Kappeler, P. M. 2000 Grouping and movement patterns in Malagasy primates. In *On the move* (eds S. Boinski & P. A. Garber), pp. 470–490. Chicago, IL: University of Chicago Press.
- King, A. J. & Cowlshaw, G. 2009 Leaders, followers and group decision-making. *Commun. Integr. Biol.* **2**, 147–150.
- King, A. J., Douglas, C. M. S., Isaac, N. J. B., Huchard, E. & Cowlshaw, G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)
- Krause, J. & Ruxton, G. 2002 *Living in groups*. London, UK: Oxford University Press.

- Kummer, H. 1968 *Social organisation of hamadryas baboons*. Chicago, IL: University of Chicago Press.
- Lamprecht, J. 1992 Variable leadership in bar-headed geese (*Anser indicus*): an analysis of pair and family departures. *Behaviour* **122**, 105–119. (doi:10.1163/156853992X00336)
- Leblond, C. & Reeb, S. 2006 Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour* **143**, 1263–1280. (doi:10.1163/156853906778691603)
- Leca, J. B., Gunst, N., Thierry, B. & Petit, O. 2003 Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Anim. Behav.* **66**, 1035–1044. (doi:10.1006/anbe.2003.2276)
- Leca, J. B., Gunst, N., Watanabe, K. & Huffman, M. A. 2007 A new case of fish-eating in Japanese macaques: implications for social constraints on the diffusion of feeding innovation. *Am. J. Primatol.* **69**, 821–828. (doi:10.1002/ajp.20401)
- Losey, G., Ross, D. & Higa, J. 2001 Estimating behavioral transition rates: problems and solutions. *Ethology* **107**, 89–110. (doi:10.1046/j.1439-0310.2001.00634.x)
- Mailleux, A. C., Detrain, C. & Deneubourg, J. L. 2006 Starvation drives a threshold triggering communication. *J. Exp. Biol.* **209**, 4224–4229. (doi:10.1242/jeb.02461)
- Menzel, C. R. & Beck, B. B. 2000 Homing and detour in golden lion tamarin social groups. In *On the move* (eds S. Boinski & P. A. Garber), pp. 299–326. Chicago, IL: University of Chicago Press.
- Meunier, H., Deneubourg, J. L. & Petit, O. 2008 How many for dinner: recruitment and monitoring by glances in capuchins. *Primates* **49**, 28–31. (doi:10.1007/s10329-007-0055-0)
- Petit, O. & Thierry, B. 1994 Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Anim. Behav.* **48**, 1427–1436. (doi:10.1006/anbe.1994.1378)
- Ramseyer, A., Petit, O. & Thierry, B. 2009 Decision-making in group departures of domestic domestic geese. *Behaviour* **146**, 351–371. (doi:10.1163/156853909X410955)
- Rands, S. A., Cowlishaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. 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)
- Reinhardt, V. 1983 Movement orders and leadership in a semi-wild cattle herd. *Behaviour* **83**, 251–264. (doi:10.1163/156853983X00183)
- Schaller, G. B. 1963 *The mountain gorilla: ecology and behavior*. Chicago, IL: University of Chicago Press.
- Seeley, T. D. & Visscher, P. K. 2008 Sensory coding of nest-site value in honeybee swarms. *J. Exp. Biol.* **211**, 3691–3697. (doi:10.1242/jeb.021071)
- Stanford, C. B. 1990 Colobine socioecology and female-bonded models of primate social structure. *Kroeber Anthropol. Soc. Pap.* **71–72**, 21–28.
- Sueur, C. & Petit, O. 2008 Shared or unshared consensus decision in macaques? *Behav. Proc.* **78**, 84–92. (doi:10.1016/j.beproc.2008.01.004)
- Sueur, C. & Petit, O. In press. Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. *Anim. Cogn.* (doi:10.1007/S10071-009-0261-9)
- Sugiyama, Y. 1976 Characteristics of the ecology of the Himalayan langurs. *J. Hum. Evol.* **5**, 249–277. (doi:10.1016/0047-2484(76)90029-4)
- Sumpter, D. J. T. 2006 The principles of collective animal behaviour. *Phil. Trans. R. Soc. B* **361**, 5–22. (doi:10.1098/rstb.2005.1733)
- Sumpter, D. J. T. & Pratt, S. C. 2009 Quorum responses and consensus decision-making. *Phil. Trans. R. Soc. B* **364**, 743–753. (doi:10.1098/rstb.2008.0204)
- Theraulaz, G. *et al.* 2002 Spatial patterns in ant colonies. *Proc. Natl Acad. Sci. USA* **99**, 9645–9649. (doi:10.1073/pnas.152302199)
- Visscher, P. & Seeley, T. 2007 Coordinating a group departure: who produces the piping signals on honeybee swarms? *Behav. Ecol. Sociobiol.* **61**, 1615–1621. (doi:10.1007/s00265-007-0393-3)
- Ward, A. J. W., Sumpter, D. J. T., Couzin, L. D., Hart, P. J. B. & Krause, J. 2008 Quorum decision-making facilitates information transfer in fish shoals. *Proc. Natl Acad. Sci. USA* **105**, 6948–6953. (doi:10.1073/pnas.0710344105)
- Weidenmüller, A. 2004 The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self-reinforcement in fanning response. *Behav. Ecol.* **15**, 120–128. (doi:10.1093/beheco/arg101)