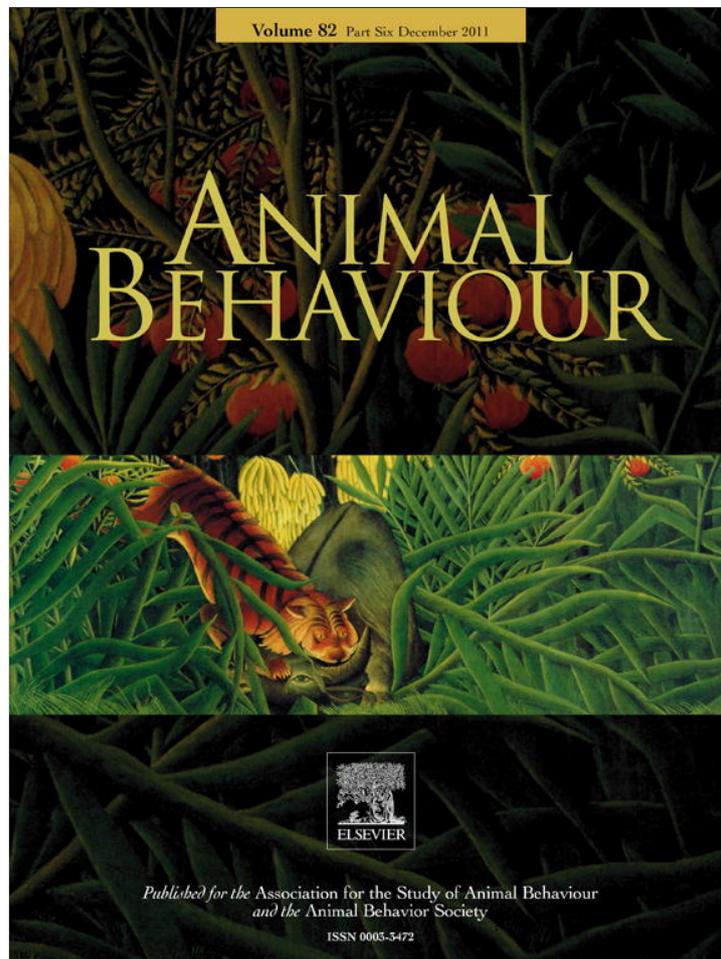


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A rule-of-thumb based on social affiliation explains collective movements in desert baboons

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Animals living in groups will profit most from sociality if they coordinate the timing and nature of their activities. Self-organizing mechanisms can underlie coordination in large animal groups such as insect colonies or fish schools, but to what degree these mechanisms operate in socially complex species that live in small stable groups is not well known. We therefore examined the collective departure of wild chacma baboons, *Papio ursinus*, from their sleeping sites. First, in line with previous observations, the departure process appeared to be coordinated through the cue of individuals 'moving off', with no role for specific vocal or visual signalling. Second, we employed network analyses to explore how inter-individual relationships influenced departure patterns, and found that a local rule, to follow the movements of those baboons with whom they shared a close social affiliation, determined when the baboon group departed. Finally, using an agent-based model, we were able to simulate mathematically the observed patterns of collective movements based upon the emergent rule that we identified. Our study adds weight to the idea that social complexity does not necessitate cognitive complexity in the decision-making process, consistent with heuristic decision-making perspectives studied by cognitive psychologists and researchers studying self-organization in biological systems.

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Animals living in groups will profit most from sociality if they coordinate the timing and nature of their activities. This requires that group members organize their movements and collectively 'agree' on the coordination of important events such as where and when to travel, commonly referred to as a 'consensus decision' (Conradt & Roper 2005). Failure to reach a consensus may result in group fission and individuals forfeiting many of the advantages gained from being in that group (Krause & Ruxton 2002).

Self-organization, whereby properties at the group level arise as a consequence of multiple local interaction rules between individuals, is a process that is known to underlie coordinated behaviour

and collective decisions of large groups of individuals that share similar goals, for example insect colonies, fish schools and bird flocks (Couzin & Krause 2003). In contrast, in smaller heterogeneous groups in which all individuals can interact with one another and there are strong conflicts of interest (e.g. most social carnivores and primates), coordinated behaviour might rather be mediated by one-to-all interactions, that is, global rules. This distinction concerning the scale of information transfer has been referred to as local versus global communication (Conradt & Roper 2005). In the latter case, visual and vocal signals are often implicated (Boinski & Garber 2000; Conradt & Roper 2003) since they can allow individuals to 'declare' their motivation to perform a particular activity (Kummer 1995; Prins 1996), reflecting an individual's internal physiological state, or 'mood' (Heinroth 1911), which in turn varies with social and ecological contexts (Boinski & Garber 2000; King & Sueur 2011). However, there is increasing evidence that small heterogeneous groups may also be coordinated by local interaction rules. Recent studies on captive primates have found that mechanisms for coordination can be self-organized (Meunier et al. 2006; Petit et al. 2009), albeit with interindividual relationships mediating local interaction rules (Sueur et al. 2009). This suggests that local 'rules-of-

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thumb' or 'heuristics' (Hutchinson & Gigerenzer 2005) may in fact play an important role in the collective movements of small groups too, although it remains possible that these previously reported patterns were influenced by their captive setting, where conflicts of interests are minimized by careful management practices.

We investigated whether local interaction rules may be sufficient to coordinate collective movements in wild social groups typified by conflicts of interest. We used the collective movements of baboons, *Papio ursinus*, away from their sleeping sites for this analysis, since such departures have already been well documented in baboons (Byrne et al. 1990; Kummer 1995; Stueckle & Zinner 2008) and other primates (Sueur & Petit 2008a, 2010; Sueur et al. 2009). We began by assessing the evidence for global rules in group departures. Since, in other primates, vocalizations or 'stereotyped' movements have been found to increase before departure, potentially indicating a group's readiness to leave and/or the 'intention' of the first moving individual, we tested whether baboon groups were more likely to depart (1) when the total number, or rate, of grunt vocalizations was higher prior to a departure initiation (Boinski 1993; Stewart & Harcourt 1994), and (2) when the individual moving first showed stereotyped behaviours, that is, backward glances and/or pauses while moving away from the group (Kummer 1995; Sueur & Petit 2010).

Since the specific visual or vocal behaviours that we observed did not appear to be acting as signals mediating departure, the remainder of our analysis focused on the role of movement cues acting as local rules to coordinate group departures. Specifically, we tested whether the properties of the dyadic relationship between two individuals might affect the likelihood that one would respond to the movement cue, that is, 'moving off', of the other, and how this affected the likelihood of the whole group moving from their sleeping site. We began by testing three hypotheses: that the likelihood of individual i following individual j was related to dyadic patterns of dominance rank, social affiliation (indexed by grooming interactions and spatial associations) and kinship in the dyad (Sueur & Petit 2008a; King et al. 2009a; Nagy et al. 2010). To confirm our findings, we then used an agent-based model to predict the emergent patterns of following, and compared five variants of the agent-based model predictions with our natural observations (Sueur et al. 2010, 2011). Finally, to aid in the interpretation of our results, we also investigated whether particular individual characteristics, namely sex, age and dominance rank, were more likely to be associated with initiations ('moving off') in the first place (Boinski & Garber 2000; King et al. 2009a).

METHODS

Study Site and Subjects

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S 15°45'W), on a habituated and individually recognizable group of chacma baboons ($N = 32$), between June and December 2005 and 2006. Observations of collective departures were undertaken from before sunrise until the group's departure from its sleeping cliff, while social interaction data were collected throughout the day. Data were collected on all adults in the group, comprising 15 core group members (four males, 11 females) and two peripheral males; infants and juveniles were never observed to move away from their sleeping site without adults.

Behaviour Prior to Departures

We observed 43 group departures of the whole troop at eight different sleeping sites during the 2005 field season. Observations were made from the base of sleeping sites (typically at a distance of 25 m from the group) and began at sunrise when individuals were huddled together in small groups along the sleeping cliff edge. Data

were collected on 'grunt' vocalizations and departure initiations (successful and unsuccessful), including pauses during departures, using continuous sampling. In the first case, since observations were made from the base of the cliff, individual grunts were distinguishable but the identity of the caller could not always be ascertained, so we analysed here only total grunt frequencies at the group level. In the second case, an individual departure by an adult, termed an 'initiation', was defined as a movement that took an individual at least 10 m beyond the periphery of the group when no departing movement had taken place in the preceding 10 min. The frequency of 'pauses', where an individual momentarily stops and looks back to the group when moving away from the core group, was also recorded. All departing movements within 10 min of an initiation were termed follows. Where an initiation elicited follows, and the whole troop moved away from the sleeping site within a 10 min period towards local foraging patches, this initiation was considered successful, and a collective departure had occurred. Initiations that did not result in all individuals following within a 10 min period, and thus did not result in the group leaving the sleeping site, were considered 'failed initiations'. These criteria were adopted following preliminary observations, and are analogous to those used by previous studies on baboons (Stueckle & Zinner 2008), white-faced capuchins, *Cebus capucinus* (Petit et al. 2009), and macaques, *Macaca tonkeana* and *Macaca mulatta* (Sueur & Petit 2008a, b; Sueur et al. 2009). Because baboons were habituated to observation, it is extremely unlikely that either failed or successful initiations could be attributed to observer presence: lone individuals of all ages would move past and totally ignore observers at distances of a few metres. Overall, 197 initiations were observed across 43 days, with 4.58 ± 0.50 initiations per day. The individual orders of movements for collective departures were then calculated. The first departing individual was ranked 1, the first follower ranked 2, and the rank of the j th follower was $j + 1$. Where two individuals joined a movement at approximately the same time it was always possible to identify who moved first, so two individuals never had the same rank on a given movement.

Age and Relatedness between Individuals

Age data and genetic material were collected under anaesthetic. Each troop was captured using cages (one for each individual) baited with maize. Cages were set at dusk to capture the baboons at dawn the following morning. A wildlife vet anaesthetized individuals using 100 mg/ml of tiletamine–zolazepam (Zolatil Virbac Australia Ltd., NSW, Australia) at a dose rate of 5 mg/kg administered intramuscularly by darting. Each baboon was under anaesthesia for about 45 min (infants were not anaesthetized) and kept under continuous observation in the shade (using sheets or natural shade) from capture to release. Dental data were collected to estimate age: tooth eruption schedules were used to assign age up to the eruption of the molars and beyond this point age was estimated on the basis of molar wear (for further detail see Huchard et al. 2009). On this basis, our study subjects had an age range of 6–19 years. One female was not captured (LF09) but was clearly older than any other female, and thus estimated to be the oldest female in the group. Genetic relatedness between group members was estimated using DNA from ear biopsies (approximately 0.25 cm²) collected under anaesthetic (except LF09, for whom the DNA came from a faecal sample). DNA extraction, amplification, and sequencing at 16 microsatellite markers were conducted for the purposes of calculating pairwise genetic relatedness (Huchard et al. 2010a). Baboons were then released together the following morning, when fully awake. Our capture and processing protocols were assessed and approved by the Ethics Committee of the Zoological Society of London, and approved by the Ministry of Environment and Tourism in Namibia (Research/Collecting Permit 1039/2006).

Social Interactions between Individuals

Data describing social interactions, that is, aggressive behaviour, grooming interactions and spatial associations, were collected throughout the 2005 and 2006 field seasons. Since our patterns of social interaction showed a high consistency between years (the dominance ranks were identical, and the grooming and spatial data were both highly correlated: Pearson correlations: $P < 0.001$ in both cases), these data were combined across years to maximize their resolution. Dominance interactions that included all agonistic and approach–avoid interactions were collected ad libitum. These interactions produced a linear dominance hierarchy which was determined with Landau's linearity index, correcting for unknown relationships (2005: $N = 640$ interactions: $h' = 0.67$, $P < 0.01$; 2006: $N = 957$: $h' = 0.59$, $P < 0.001$), implemented in Matman (De Vries 1998). Grooming interactions ($N = 1727$) were also collected ad libitum. Spatial associations were recorded during 1 h focal watches ($N = 359$) on all core adults during 102 full-day dawn-to-dusk follows (mean \pm SE: watches per adult = 30 ± 2 ; watches per day = 3.5 ± 0.15). During focal watches the nearest neighbour of the focal individual (regardless of distance) was recorded continuously in real time, providing the total proportion of time that the focal individual, i , spent with all other adults as nearest neighbours.

Network Analyses

Network analyses take association or interaction data presented in a standard actor–recipient matrix, and create abstractions of group structure (rather than literal depictions), which can allow researchers to quantify, among other things, the 'roles' individuals have in a group context (Brent et al. 2011). Here, we used this approach to test whether the likelihood of two individuals following one another from the sleeping site was related to dyadic patterns of dominance rank, spatial association, social affiliation and/or kinship. We also quantified whether individuals that are important (have numerous and strong connections) in dominance, affiliative or kin networks are also important in a network created from departure data.

To do this, we first constructed a matrix of departures composed of the relative frequency of following for each dyad during successful departures (i.e. where all adults and their offspring joined the movement). For each dyad, say i and j , we calculated (the total number of events where i followed j) + (the total number of events where j followed i) / (the total number of departures). We were able to sum events where i followed j and j followed i since following behaviour within dyads (and thus within the matrix) was symmetrical (Dietz-R = 0.53, $P = 0.001$).

We then took our 'leader–follower matrix' and compared it to matrices of grooming, spatial association, dominance and kinship data. In the case of grooming interactions, we took the frequency of grooming for each possible dyad ij and divided this by the mean frequency of grooming for all dyads in the group (grooming behaviour was undirected and therefore the matrix was symmetric). This gave a distribution of scores for which 1.0 was the average and for which higher values represented dyads with stronger bonds than expected and lower values those that had weaker bonds (King et al. 2008, 2009b). Our spatial matrix was populated with data expressed as the proportion of observation time that the focal individual, i , spent with all other adults as nearest neighbours, the dominance matrix contained relative difference in rank between individuals, and the kinship matrix was based on the triadic coefficient of relatedness, calculated using Coancestry software (Huchard et al. 2010b; Wang 2011).

Matrices were represented as graphs (sociograms) drawn using Netdraw in Ucinet 6.0 (Borgatti et al. 2002), and eigenvector centrality coefficients were calculated for each individual in

SOCPROG version 2.4 (Whitehead 2009). Eigenvector centrality coefficients represent a measure of the 'centrality' of individuals in the network, and range from 0 (least central) to 1 (most central). Individuals that have large coefficients are either highly connected themselves (e.g. often groom, or are often spatial neighbours with many other individuals) or are connected to other network members that are highly connected themselves (Sueur et al. 2011). The coefficient also takes into account the strength of the links between individuals (e.g. the frequency of grooming or the time spent as neighbours), which makes it a particularly useful quantitative index for determining an individual's centrality within weighted networks (Freeman 1979; Girvan & Newman 2002), such as a leader–follower network (Sueur & Petit 2008a) or grooming network (Kanngiesser et al. 2011).

Agent-based Model

To confirm the findings of our network analyses, we then used an agent-based model to predict the emergent patterns of following, comparing five variants of the model predictions with our natural observations. The basic model structure we used is based on rules of mimetism/cohesion (using a Markov chain process) and has been described in several studies on collective phenomena (Ame et al. 2006; Gautrais et al. 2007; Sueur et al. 2009, 2010; Jacobs et al. 2011). In this model, the probability of an individual joining a collective movement depends not only on the number but also the strength of relationships it has with those individuals that have already departed.

To build the model based on our field system, we used the identities and relationships among the baboons described by the empirical data, and calculated two basic parameters of the model: (1) the time until first initiation and (2) the probability of an individual departing (first individual or subsequent followers). The time until the first initiation was calculated as the latency of the first departing individual, $\Delta T_{0,1}$, by scoring the time elapsed between the end of the previous unsuccessful collective movement (or sunrise for the first departure of the day) and a new initiation. We then scored the departure latency of each follower, that is, the departure latency of the follower, $\Delta T_{j-1,j}$, corresponding to the time elapsed between the departure of follower $j - 1$ and the departure of the joiner j (Sueur et al. 2009, 2010).

The time to the first initiation ($\Delta T_{0,1}$) corresponded to an exponential distribution (curve estimation test: $F_{1,29} = 3723$, $R^2 = 0.97$, $P < 0.001$; $y = 0.8724e^{-0.00117x}$; Fig. 1a), and the probability of the first departure, $\Psi_{0,1}$, was the exponent of this exponential distribution, equalling 0.00117 (Sueur et al. 2009, 2010). Thus, the first departure probability per individual λ_i equalled $(\Psi_{0,1} \times F_i)/N$, where F_i is the relative frequency of initiations for each individual and N is the number of group members.

The departure probabilities of all followers conformed to an exponential law, was constant per time unit and equalled 0.019 (curve estimation test: $F_{1,6} = 642$, $R^2 = 0.98$, $P < 0.001$; $y = 0.4265e^{-0.019x}$; Fig. 1b). Using this equation we then calculated the mean departure probability of followers, and found that this followed a parabolic curve (curve estimation test: $F_{1,15} = 642$, $R^2 = 0.99$; $P < 0.001$; $y = -0.0142x^2 + 0.0728x + 1.2446$). This relationship between departure probability and departure order shows that the probability of an individual departing increases with the number of individuals already departed, and this increase in probability can be translated to a mimetic coefficient, C (Sueur et al. 2009, 2010). Here, $C = 0.0142$, similar to the coefficient found for macaques and capuchins (Petit et al. 2009; Sueur et al. 2009). Further details on how we calculated C can be found in Appendix 1.

We then used our data on dominance rank, social affiliation (indexed by grooming interactions and spatial associations) and

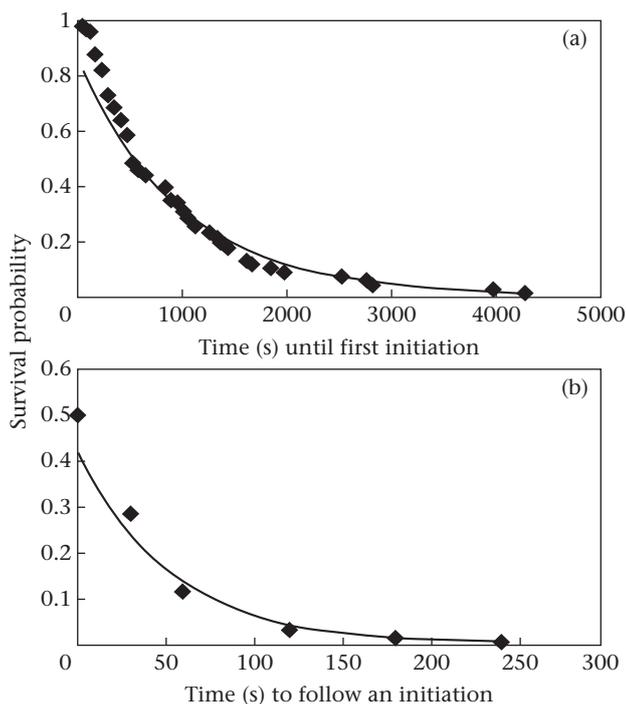


Figure 1. (a) Time before the first initiation expressed as a probability of all initiations; (b) the same analysis of follower–departure latencies, i.e. time taken to follow an initiation. For both graphs, diamonds represent the observed data and the line represents the exponential curve best fitting with the observed data: (a) $y = 0.8724e^{-0.00117x}$, (b) $y = 0.4265e^{-0.019x}$. The survival probability represents the inverse cumulative distribution of departures (a) of initiator and (b) of follower. For instance in (a) at $t = 0$, $y = 1$, an initiator had departed in 0% of the observation data; at $t = 5000$, $y = 0$, an initiator had departed in 100% of the observation data.

kinship across dyads to model the probability of an individual, i , becoming a follower j in a series of agent-based simulations as:

$$\Psi_i = \lambda_i + C \left(\sum_{k=1}^N M(i, k) \right) \quad (1)$$

Where λ_i is the individual (i.e. intrinsic) probability of departing and C is the mimetic coefficient ($C = 0.0142$), that is, the likelihood of a departing individual being followed. $M(i, k)$ is the property of the dyad, namely the dominance rank difference, the strength of social affiliation (grooming interactions and spatial associations) or the genetic relatedness between the resting (not moving) individual i and the already departed individual k . $M(i, k) = 0$ if k is resting. According to equation 1, the stronger the relationship a resting agent holds with moving agents, the greater the probability of the resting agent joining. Consequently, the stronger the relationship a moving agent has with resting agents, the greater the probability of the moving agent being followed. For further comparison, we also generated a null model where $M(i, k)$ was derived from a theoretical weighted network (an Erdos–Renyi random network generated with Ucinet 6.0).

The agent-based model was implemented in Netlogo 3.1.4 (<http://ccl.northwestern.edu/netlogo/3.1.4/>). At each time step (1 min) in the model, a number between 0 and 1 was randomly attributed to each resting agent (i.e. at the sleeping site). When this number was smaller than the theoretical departure probability Ψ_i of each agent (equation 1), the individual left the sleeping site; if this number was higher than the theoretical departure probability, the agent did not move. Data on the identity of individual agents, their departure order and their times of departure were recorded by the model for each simulated collective movement. We ran 1000 simulations for each variation of the model

and recorded the departure order of all agents during successful initiations (i.e. where all agents joined a departing agent within 10 min of the initiation).

Statistical Tests

To assess whether the behaviours that we observed during departures could act as one-to-all cues or signals during group departures, we ran a generalized linear mixed model (GLMM) in MLwiN (Rasbash et al. 2009). The GLMM response was binary: did a collective departure occur, yes or no? This allowed us to consider each initiation that each baboon made ($N = 197$ across all individuals), and test whether a series of fixed effects, both categorical and continuous, affected the outcome. We provided tests of those effects that we could quantitatively measure and for which we had clear predictions. The significance of the effects was tested using the Wald statistic, evaluated against the chi-square distribution. Our two fixed categorical effects were the occurrence of pausing by the departing individual (yes, no) and the occurrence of looking back to the group by the departing individual (yes, no). Our two continuous fixed effects were the (group) mean rate of grunting per min and the cumulative number of grunts by all individuals in the 5 min before the initiation. Where other factors could have influenced the patterns we observed, we tried to control for as many of these as we could. We controlled for the position of the departing individual before initiation (categorical: central, peripheral), since this may improve the perception of both movement cues and auditory signals (Boinski & Campbell 1995; Boinski & Garber 2000), and three nested random effects were also included: ‘initiation number’, ‘observation day’ and ‘sleeping site location’. Including these random effects accounts for potential nonindependence of initiations within observation days and the (unmeasured) variability in sleeping site characteristics; these characteristics are difficult to quantify and test (e.g. topography, predation risk), but may have influenced the success of any given initiation. However, only initiation number within a day explained any variance in the model as a random effect, suggesting that such characteristics have little effect on initiation success (but may still play a role in sleeping site selection and arrival/departure times in general).

Spearman rank correlation tests were conducted in SPSS 10.0 (SPSS Inc., Chicago, IL, U.S.A.) to compare the observed orders (empirical data) and simulated orders (agent-based model predictions) of individuals at departure, as well as correlations between the number of initiations (total, successful) and individual traits (age, dominance rank). Mann–Whitney U tests were used to test for differences in the number of initiations (total, successful) between sexes. We used a Dietz–R test for the correlations of matrices (setting the number of permutations to 10 000 for matrices correlations), and used a partial correlation Dietz–R test when we wanted to explore the relationship between two variables while holding a third variable constant. The Dietz–R test is the nonparametric variant of the Mantel test and is based on a Spearman rank correlation test. Because the peripheral males associated with the group (GM02, GM03) were not always present ($N = 10$, $N = 8$ initiation attempts, respectively, i.e. present on <20% of days), the social interactions data concerning these males were limited and consequently omitted from all network analyses (above).

RESULTS

Role of Global Rules in Successful Initiations

Despite the coordinated departure of the group from its sleeping cliff each morning, on average 28 min after sunrise ($SE = 4$ min,

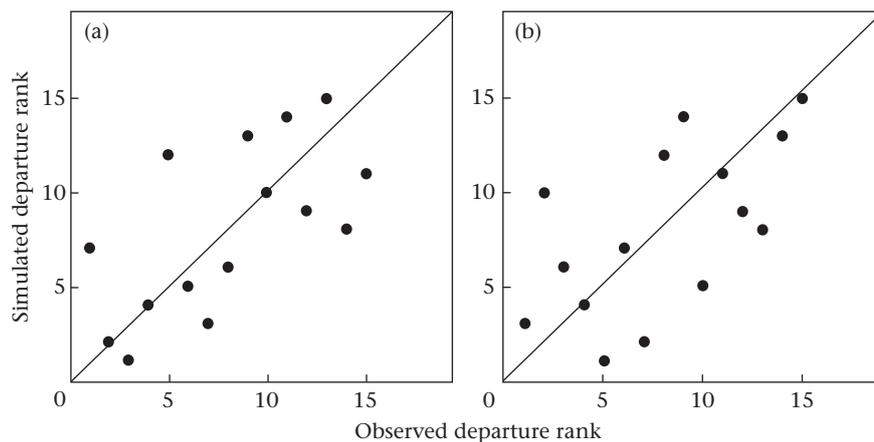


Figure 3. The relationship between the mean rank of observed departures and the mean rank of simulated departures from our agent-based model weighted by (a) grooming interactions and (b) spatial associations. The lines indicate a theoretical perfect correlation between the two data sets.

$P = 0.40$; dominance: $r_s = -0.41$, $N = 15$, $P = 0.13$). However, on an individual basis, the alpha male (HM23) did make more successful initiations than any other group member (binomial test: $P < 0.001$). No comparable pattern was seen with the beta male who was also the oldest male (HM08), the alpha (HF11) or beta females (LF01), or the oldest female (LF09) in the group (binomial tests: $P > 0.05$ in each case).

DISCUSSION

Our findings support the hypothesis that social animals living in small groups are able to coordinate collective movements through adopting local rules-of-thumb. We have shown that the departures of wild baboons from their sleeping cliffs appear to be coordinated by individuals setting an example by ‘moving off’, in line with previous research on chacma baboons in another population (Stueckle & Zinner 2008). However, we further show that the pattern of following an initiator is not random, but follows a clearly defined rule, such that collective departures appear to be mediated through individuals copying the behaviour of those with whom they are socially affiliated, via grooming interactions and spatial associations.

Our results suggest that a ‘follow-a-friend’ rule, where friendships (social affiliations) are indexed by grooming interactions and spatial associations, satisfactorily explains both the outcome and process of baboon collective departures from sleeping sites. When individuals with high centrality in the grooming or spatial network

initiate a departure, many individuals tend to follow, and the group collectively moves away from its sleeping site. In contrast, when individuals that are peripheral to these networks initiate a departure, they are rarely followed, and the group does not depart. The relative importance of grooming interactions and spatial associations was difficult to disentangle, reflecting the fact they are highly correlated in primate societies (indeed, they are often used together in a composite index of social affiliation: Silk et al. 2006a, b; Clark 2011). Nevertheless, where a distinction was possible (through partial correlations) the results indicated that spatial association was of primary importance. One interpretation of this finding might be that the influence of grooming was an artefact of its relationship to spatial association, and that the ‘follow-a-friend’ rule could be reduced to one of ‘copy my neighbour’s actions’, directly akin to those predicted for a variety of flocking animal models (Couzin & Krause 2003; Couzin & King 2010), and described in shoaling fish (Katz et al. 2011). However, this would be a misleading simplification, since spatial associations are more likely to be an emergent property of grooming interactions, and social relationships more generally, rather than vice versa. A more accurate interpretation would be that individuals do follow ‘friends’, but preferentially those friends that are in closest proximity. The benefits of following friends in complex societies are likely to be manifold. In chacma baboons, for example, close social bonds between females increase the longevity of females and the survival of their offspring (Silk et al. 2009, 2010). Previous studies in this population further indicate that lactating

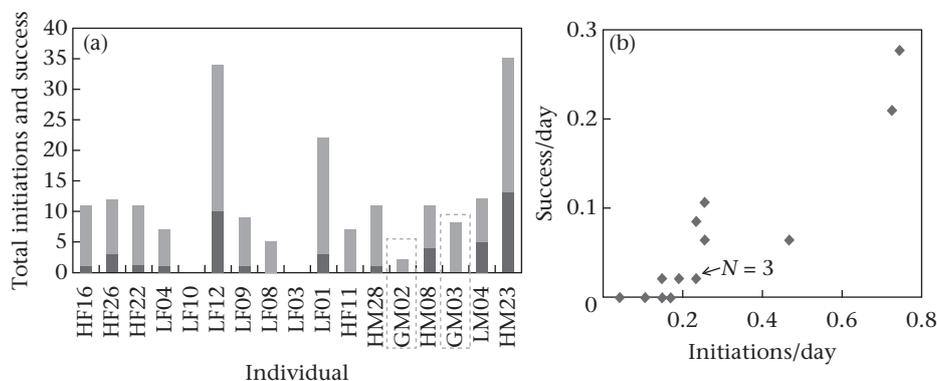


Figure 4. (a) The total number of initiations by individuals (light grey) and the number of initiations that were successful (dark grey). Individual are listed by ID code and ordered by dominance rank from left (low) to right (high; the six highest-ranking animals are males, the remainder females). Individuals GM02 and GM03 are highlighted as peripheral males. (b) The relationship between the number of initiations/day and the number of successful initiations/day. Note that three individuals (HF16, HF22, HM28) scored equally on both measures, and two individuals never made an initiation (LF10, LF03), so only 13 points are visible.

females associate with male friends for the protection of infants from infanticidal attacks (Huchard et al. 2010b), and that foraging females are more likely to scrounge from close grooming partners (King et al. 2009b).

The apparent lack of importance of vocal signals to the success of collective departures is at odds with previous investigations, since there are many examples of other social vertebrates using travel coordination signals (Boinski & Garber 2000). This is somewhat surprising, not least because 'movement' grunts in this species (*P. ursinus*) have previously been identified and shown to be associated with group movements (Owren et al. 1997; Rendall et al. 1999). Moreover, at Mt Assirik, Senegal, Guinea baboons, *Papio papio*, use single and double-phase barks to coordinate foraging over large, densely vegetated areas (Byrne 1982). Such behaviour, however, is not seen at the present site, where groups are much smaller and the environment more open. Indeed, our observations of groups in other activities throughout the day do not suggest any qualitatively different patterns in the coordination of collective movement to those we have described at the sleeping site. One possibility is that such movement grunts do not occur in this population (recent research at this site found it difficult to identify such grunts acoustically, despite being able to distinguish grunts associated with infant handling, foraging and social interaction: Meise et al. 2011). In line with this, another study of collective movement in another chacma baboon population similarly failed to find an effect of such grunts (Stueckle & Zinner 2008). This would suggest that either (1) the movement grunts identified in previous reports were unique to that study population (in the Okavango Delta, Botswana: Owren et al. 1997; Rendall et al. 1999) or (2) the tests conducted in this study and by Stueckle & Zinner (2008) were inadequate to detect the role of movement grunts. The latter is certainly a possibility, given that neither study was able to examine the individual patterns of grunt performance (our study looked solely at the frequency or total cumulative number of all grunts at the group level, while Stueckle & Zinner similarly recorded the presence or absence of grunts at the group level). However, the fact that patterns of social affiliation are so strongly associated with patterns of departure, and the agent-based model provides such a good prediction of departure order on the basis of social affiliation alone, suggests that if such vocalizations do independently contribute to the coordination of group departures it is only likely to be in a supporting role.

We similarly found no role of visual signals. In a classic and much-cited study, Kummer (1995) reported that hamadryas baboons, *Papio hamadryas*, coordinated group departures from their sleeping cliff through a process of 'notification', which involved initiating animals pausing to recruit followers. We found the contrary: backward glances did not influence the success of initiations, and pauses during initiations significantly reduced the likelihood of a collective movement occurring. We interpret the latter as an indication of hesitancy owing to a lack of followers and/or lower motivation to leave the group (Gautrais 2010). Stueckle & Zinner (2008) similarly failed to find an effect of visual signals on group departures in chacma baboons. The differences between the species are instructive, since they may reflect the constraints imposed by the different social systems involved: hamadryas baboon groups are composed of discrete (unaffiliated) one-male units which would not be able to coordinate collective departure through a 'follow-a-friend' rule, unlike more integrated groups typical of other baboons where a rule-of-thumb based on affiliative relationships could conceivably evolve.

We also considered three possible traits that might be associated with an individual's initiation attempts and their success: age, on the basis that older individuals have better knowledge of the home range (Radford 2004); sex, on the basis that males are

less vulnerable to predators (Cowlshaw 1994) and should thus be more willing to lead the group (Rhine & Tilson 1987); and dominance rank, on the basis that subordinate animals direct more visual attention towards dominant animals than vice versa (Pannozzo et al. 2007), and therefore initiations by dominant animals may have been more likely to be followed. We found that neither the total number of initiations nor the number of successful initiations made by an individual was influenced by its age, sex or rank. In the absence of such effects, the most likely explanation for individual variation in initiation attempts may be food rewards (i.e. individual motivation to feed). Under most circumstances, this will simply translate as hunger, such that as individuals grow hungrier they are more likely to attempt to initiate departures to begin foraging (Rands et al. 2003). The number of successful initiations will therefore depend on how quickly an individual grows hungry, together with its ability to attract followers. Thus, it is only when those individuals with high centrality in the grooming or spatial network have grown sufficiently hungry to initiate a departure that the rest of the group collectively acts and moves away from its sleeping site. This interpretation is supported by our result that at an individual level the alpha male, whose eigenvector centrality coefficients were the highest of all individuals in both the grooming and spatial networks, made more successful initiations than expected by chance alone. This conclusion is also consistent with the finding that, when food rewards are experimentally increased for the alpha male, he is able to act as a leader, and drive the movement patterns and foraging choices of the entire troop (King et al. 2008).

Finally, our findings are also consistent with research on baboon progression orders, which observed alpha males positioned at the leading edge/front of movement progressions and subordinate adult males and low-ranked females at the rear/periphery (Rhine 1975; Collins 1984). This pattern was interpreted to be a consequence of minimizing predation according to individual risk, but would also result if those baboons with more numerous and stronger connections to conspecifics were more often followed (King & Cowlshaw 2009; King et al. 2009a). Such 'embedded leadership', in which leader-follower dynamics are embedded in networks of interindividual relationships (King & Sueur 2011), may therefore explain why those individuals with the strongest social ties to other group members, such as dominant individuals (Sarova et al. 2010), elder females in matrilineal societies (McComb et al. 2011) and central 'broker individuals' that link network subcomponents in species with high fission-fusion dynamics (Lusseau & Conradt 2009), more often function as leaders across a variety of animal societies. A follow-a-friend rule during collective movements might also enhance the accumulation (McComb et al. 2011) and transmission of information among group members (Lusseau & Conradt 2009), increasing the accuracy of group-level decisions (Lusseau & Conradt 2009; Lewis et al. 2011; McComb et al. 2011), if individuals are more likely to gather information from their friends than other group members.

In sum, our finding, that local individual rules are adequate to generate complex collective behaviour at the group level, mirrors both the ideas of self-organization in biological systems (Sumpter 2006; Sumpter et al. 2008) and the heuristic decision-making perspective taken by some cognitive psychologists (Gigerenzer et al. 1999). This is not to say that baboons following what appear to be cognitively simple heuristics have 'simple' minds, and one must carefully consider the evolved capacities required to implement the rule we have identified (Stevens 2008; Stevens & King, in press). Here, individual baboons still have to recognize and monitor the behaviours of those around them, and this can involve a variety of mechanisms, simple or complex. Nevertheless, our study

demonstrates that social complexity does not necessitate cognitive complexity in the decision-making process itself (Barrett et al. 2007).

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Appendix 1

Calculation of the mimetic coefficient

The individual departure probability Ψ_j appeared as:

$$\Psi_j = \lambda n + (Cj)^p \quad \text{A1}$$

The departure latency of the joiner j was:

$$\Delta T_{j-1,j} = \frac{1}{(\lambda + C(j-1))(n - (j-1))} \quad \text{A2}$$

or

$$\begin{aligned} \frac{1}{\Delta T_{j-1,j}} &= (\lambda + C(j-1))(n - (j-1)) \\ &= (\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2 \end{aligned} \quad \text{A3}$$

As the inverse distribution of departure latencies of joiners fitted a parabolic curve (see main text), the departure probability equation was:

$$\frac{1}{\Delta T_{j-1,j}} = -0.0142j^2 + 0.0728j + 1.2446 \quad \text{A4}$$

then

$$(\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2 = 1.2446 + 0.0728j - 0.0142j^2$$

So $(\lambda - C)(n+1) = 1.2446$, $(2C + Cn - \lambda) = 0.0728$ and $C = 0.0142$.

For simulations, we therefore took a mimetic coefficient equalling 0.0142, which is very close to the inverse of the mean departure latency of followers (=0.019).