

An Agent-Based Model of Group Decision Making in Baboons

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Abstract

We present an agent-based model of the key activities of a troop of chacma baboons (*Papio hamadryas ursinus*) based on data collected at De Hoop Nature Reserve in South Africa. The construction of the model identified some key elements that were missing from the field data that would need to be collected in subsequent fieldwork. We analyse the predictions of the model in terms of how well it is able to duplicate the observed activity patterns of the animals and the relationship between the parameters that control the agent's decision procedure and the model's predictions. At the current stage of model development we are able to show that, across a wide range of decision parameter values, the baboons are able to achieve their energetic and social time requirements. The simulation results show that decisions concerning movement (group action selection) have the greatest influence on the outcomes. Group decision making is a fertile field for future research, and agent-based modelling offers considerable scope for understanding group action selection.

1 INTRODUCTION

Group living is a common strategy among mammals and is key to understanding the success of the primate order in general and early humans in particular. For animals that forage or move in social groups, decisions about when and where to move often depend upon social interactions between group members (Krause & Ruxton 2002; Couzin *et al.* 2005). Little is actually known, however, about how groups of animals arrive at such collective decisions (Conradt & Roper 2003). We focus on the problem of

action selection in groups, i.e., where an individual's action choice is constrained by the choices of other members of the group.

We present an agent-based model of the key activities of a troop of chacma baboons (*Papio hamadryas ursinus*) based on data collected at De Hoop Nature Reserve in South Africa. Baboons (*Papio* sp.) are one of the most widely studied primate species and are ideal for studies of primate ecology since they often live in open, terrestrial habitats, and can be observed closely for long periods of time (Richard 1985). This means that there are a wealth of data available documenting most aspects of their behaviour in great detail. Many of these studies have managed to quantify the activity patterns of individuals both in terms of durations and also the costs and benefits of the activity. *Papio* sp. are found across most of sub-Saharan Africa (Jolly 2001), at a range of altitudes, with attendant large changes in average rainfall and temperature. Thus they can be said to inhabit a wide variety of habitats and ecotypes, and studies have shown that their diet and foraging varies in response to environmental determinants (Hill & Dunbar 2002).

Our model extends that presented in (Sellers, Hill, & Logan 2007). The model consists of two components: an environment model and a baboon model. The environment model is based on the 200m \times 200m map grid used for field data recording, and consists of 660 cells within an area 5.4km by 8.4km. Each cell contains a mixture of the 6 primary habitat types found at De Hoop, and each habitat type is characterised by a maximum food availability, food intake rate when foraging and travel-foraging, and replenishment rate for each month of the study period. The baboons are modelled as agents with physical parameters based on well-known baboon physiology. For ecological purposes, it has been shown that baboon activity can be well characterised by four behavioural categories: drinking, foraging, socialising and resting (Dunbar 1992). At each timestep each agent selects, based on its physiological state, one of four possible actions (drinking, foraging, socialising or resting) and whether it would prefer to move to a different habitat cell to allow it to perform its preferred action more effectively. As different agents may wish to move in different directions (or not to move at all), the agents utilise a voting-based mechanism to make consensus decisions whether to move and the direction of group travel. Such consensus decisions may result in a consensus cost for some agents, if they are not able to perform their preferred action as a result of a group decision to move in a particular direction.

While the agents in the Sellers *et al.* model were able to achieve their goals under a wide range of conditions, the model was less successful in predicting energy budgets and habitat utilisation. Sellers *et al.* (2007) speculated that the model's poor fit to the data may be due in part to the agents foraging too easily. Agents uniformly deplete 200m \times 200m cells without incurring additional search costs. In reality, local resource depletion occurs on a much finer scale with more rapidly diminishing foraging returns, and this is not captured in the model. In an attempt to address these issues, we have incorporated a simple model of diminishing foraging returns into the environment model. In our revised model, the rate of energetic return available to an agent in a given habitat cell declines at a rate which is proportional to the food remaining in the cell. This has the effect of making it progressively more difficult to obtain food at a given location, making it more likely that an agent will choose to forage in another cell at the next timestep. This new model allows us to test one of the hypotheses resulting from the

original model, and to determine the sensitivity of the model of group decision making to changes in the agents' environment. We analyse the predictions of the revised model in terms of how well it is able to duplicate the observed activity patterns of the animals and the relationship between the parameters that control the agents' decision procedure and the model's predictions.

The remainder of the paper is organised as follows. In section 2 we review recent theoretical work on decision making in animal groups. In section 3 we review the relevant agent-based modelling literature and motivate our modelling approach. In section 4 we briefly summarise the field data on which our model is based and in section 5 we outline our agent-based model and the decision procedure which the agents use to choose their activities, and explain how the model differs from that presented in (Sellers *et al.* 2007). In section 6 we present the results of a Monte-Carlo sensitivity analysis of the predictions of the model in terms of how well it is able to duplicate the observed activity patterns of the animals, and the relationship between the parameters that control the agent's decision procedure and the model's predictions. In section 7 we discuss the results and outline directions for future work.

2 DECISION MAKING IN ANIMAL GROUPS

Animal groups must routinely arrive at collective decisions, such as when and where to feed and the location of nesting sites. Many group decisions will be crucial to the individual fitness of the group members, yet may also involve a conflict of interest between individuals since not all animals will have the same preference for an activity or travel destination. Consensus must nevertheless be reached or the group will split and members will forfeit many of the advantages of group living. The existence of collective decision-making in animals that do not communicate verbally is a field of considerable current theoretical interest.

Conradt and Roper (2005) distinguish two conceptually different types of group decisions: *combined decisions* and *consensus decisions*. Combined decisions refer to situations where animals decide individually, but in a manner that is dependent on other group members. These decisions often affect the group as a whole, such as decisions to leave or join groups in fission-fusion species (Deneubourg *et al.* 2002) or the allocation of tasks in eusocial insects (Beshers & Fewell 2001). Consensus decisions, on the other hand, are made by spatially cohesive groups and concern issues such as movement direction (Couzin *et al.* 2005), travel destination (Stewart & Harcourt 1994) and activity timing (Conradt & Roper 2003). Consensus decisions thus require mechanisms (such as voting) for groups to arrive at agreements. Although group decision making is an issue of fundamental importance in evolutionary biology, little is known about how animal groups arrive at such consensus decisions (Conradt & Roper 2003).

Two mechanisms which represent the extremes of how groups can reach collective decisions are despotism and democracy (Conradt & Roper 2003). Although democracy seems improbable for the majority of animal species given the perceived implicit cognitive requirements, empirical examples of 'voting' behaviours have been documented across a range of animal taxa (honey bees (*Apis mellifera*): (Seeley & Buhrman 1999); whooper swans (*Cygnus cygnus*): (Black 1988); African buffalo (*Syncerus caffer*):

(Prins 1996); capuchins (*Cebus capucinus*): (Leca *et al.* 2003); gorilla (*Gorilla gorilla*): (Stewart & Harcourt 1994)). Furthermore, models of group decision-making have shown democratic decisions to be more beneficial than despotic decisions across a wide range of conditions (Conradt & Roper 2003). Indeed, ‘majority rules’ appears to be a robust and highly adaptive form of decision-making in groups (Hastie & Kameda 2005). Nevertheless, there is also theoretical support for the emergence of effective leadership in certain contexts (Rands *et al.* 2003; Couzin *et al.* 2005). Group decision-making is thus a field of considerable current theoretical interest (Simons 2004; List 2004; Conradt & Roper 2005) that provides significant scope for further work. Agent-based modelling offers a valuable technique for exploring how animal groups arrive at consensus decisions.

3 AGENT-BASED MODELLING

In this section we briefly review previous work on agent-based modelling of non-human primates and motivate our modelling approach.

Individual-based ecological models have been growing in importance over the last 20 years and it has been predicted that this reductionist approach will provide valuable insight into system wide properties (Lomnicki 1992). Early work in Artificial Intelligence has shown that complex group behaviours such as flocking and following can be produced using simple rules applied to individuals (Reynolds 1987). Agent-based modelling is an extension of this approach where each individual retains information about its current and past states, and its behaviour is controlled by an internal decision process. An agent in this context is a software system that perceives its environment and acts in that environment in pursuit of its goals. Agents integrate a range of (often relatively shallow) competences, e.g., goals and reactive behaviour, emotional state, memory and inference. In agent-based modelling, the agents are situated in a simulated environment, and are equipped with sensors with differing ranges and directional properties (e.g., smell, hearing, vision) and the ability to perform a range of actions which change the state of the environment or the perceptible characteristics of the agent. The environment may contain passive objects (e.g., topography) and active objects and processes which change spontaneously during the course of the simulation (e.g., weather) and/or in response to the actions of the agents (e.g., food bearing plants).

Agents are commonly described using anthropomorphic terms such as *beliefs* (what the agent believes the state of the environment and other agents to be), *desires* (those states of the environment it is designed to bring about) and *intentions* (the state(s) of the environment it is currently engaged in bringing about)—indeed the the so-called *Belief–Desire–Intention*, or BDI, model of agency (Rao & Georgeff 1991) is perhaps the dominant paradigm in agent theory, (see, e.g., Georgeff *et al.* 1999). In some cases the agent’s beliefs and desires are explicitly represented within the software state of the agent. However not all agents represent beliefs and goals explicitly, even though they act in a goal-directed manner. For example, the behaviour of an agent may be controlled by a collection of decision rules or reactive behaviours which simply respond to the agent’s current environment. In such cases it can still be useful to view the agent as an *intentional system*, that is we ascribe to it the beliefs and goals it *ought* to have, given

what we know of its environment, sensors and (putative) desires (Dennett 1987, 1996). For example, an agent which has an ‘avoid obstacles’ behaviour, can be said to have a goal of “avoiding collisions” even though this goal is not explicitly represented in the agent. This approach, which Dennett calls “adopting the intentional stance”, allows us to ascribe propositional attitudes to agents which do not explicitly represent beliefs and goals, and is licensed on the grounds that viewing an agent as an intentional system is more likely to yield useful insights than would a description couched in terms of the low level details of the the agent’s implementation.

The outcomes determined by an agent-based model depend on the set of desires and goals within each individual agent, its current internal state (which may include an internal world model) and the sensory information it receives. This reliance on individual choice makes agent-based modelling especially useful when dealing with animals which live in groups, since it is likely that the optimal strategy for an individual depends on the strategies adopted by others in the group (Milinski & Parker 1991). Moreover, while the factors influencing the decisions made by an individual may vary as the environment changes, the decision process itself is likely to be conserved, and an agent with a robust decision procedure will demonstrate reasonable behaviour under a wide range of conditions. Such models can therefore be used to explore the potential effects of situational changes: climate, food distribution and body size can all be altered and the effects on the agents’ behaviour can be observed. If we are confident that the decision procedure is robust, then we can use the behaviour of the agents to predict the behaviour of real populations.

There are a number of different types of ‘agent-based’ model, and different terms are used in the literature for essentially the same kind of model. In some cases, e.g., population ecology models, the emphasis is on tracking the properties of individuals and/or of the population as a whole, with little or no interaction between the individual agents or between the agents and their environment. For example Robbins and Robbins (2004) have developed a model to simulate the growth rate, age structure and social system of mountain gorillas in the Virunga Volcanoes region. The model uses a one year time step and is based on the probabilities of life history events (birth rates, mortality rates, dispersal patterns etc.) as determined by census data from habituated research groups of gorillas. The gorillas do not interact with an environment model (or each other) and the only decisions the gorillas make as individuals is whether to move to a new group.

In other cases, the agents do interact with each other and/or their environment. In these models, individuals base their decisions on their beliefs about the state of the environment and/or the state of other agents, and their actions (changing position, eating food) change the environment perceived by other agents, which may in turn change their state and influence the decisions they make. This focus on interaction through the medium of the environment means that these models are often *spatially explicit*, i.e., the individuals are associated with a location in geometrical space. Such spatially explicit agent systems are sometimes called *situated* in the agent literature, e.g., (Ferber 1999)

Situated models allow consideration of social and spatial interactions between individuals. As a result, they have become a popular technique for modelling interactions in humans and non-human primates. Much of the work on agent-based modelling of

non-human primates has been done by Charlotte Hemelrijk and her colleagues. They have developed an agent-based model which has been used to investigate dominance interactions in primates, e.g., chimpanzees and macaques (Hemelrijk 1999a, 1999b, 2000, 2002; Hemelrijk *et al.* 2003; Hemelrijk & Wantia 2005; Hemelrijk *et al.* 2005). For example, Hemelrijk (2002) presents a model of primate social behaviour in which agents have two tendencies: to group and to perform dominance interactions, and shows how increased levels of aggression can induce female dominance over males. (See Bryson & Lehmann in this issue for an analysis of the Hemelrijk (2002) results.) Bryson and Flack (2002) have used an agent-based model to investigate primate social interactions. The agents are represented as 2D rectangles in a walled enclosure which alternate between two behaviours: grooming neighbours and wandering (feeding in relative isolation). The model investigated the effect of a 'tolerance behaviour' on the amount of time spent grooming. These models explicitly take into account the spatial position and orientation of individuals: in the Hemelrijk model, cohesiveness is determined by the 'SearchAngle', the angle by which an agent will rotate to locate other agents when there are none in sight; in the Bryson and Flack model, grooming requires being adjacent to and properly aligned with another agent.

Although agent-based models are increasingly finding acceptance, such computer simulations are not without their critics. John Maynard-Smith has famously described these approaches as "fact-free science" (Maynard-Smith 1995). To overcome such objections and to enable us to use this technique as a tool for exploring primate behavioural ecology, the models produced must be tested by using them to predict behaviours in a given population and comparing the predictions with field observations. For example the predictions of the model developed by Robbins and Robbins (2004) are directly comparable with future population data from this region, and Hemelrijk *et al.* (2003) have proposed model-guided studies of female dominance in real animals.

Existing agent-based models have tended to focus on interactions between the agents and their environment, or pairwise interactions (e.g., dominance interactions) between individuals and emergent properties arising from such interactions. There has been relatively little work to date on agent-based modelling of decision making in animal groups. However work on social insects in particular allows good experimental testing of the role of individuals in group decisions such as the classic work on honeybees (Seeley *et al.* 1991) as well as more recent agent based modelling approaches using ants (Pratt *et al.* 2005). While there is an extensive literature on agent-based models of human behaviour in a wide range of domains including resource exploitation, economics, and politics (see, for example, the article by Laver and Schilperoord in this issue), this work has not been applied (and in many cases would be difficult to apply) to group decision making in animals. In Artificial Intelligence there is a substantial literature on joint actions, (see, e.g., Grosz & Sidner 1990; Cohen & Levesque 1991; Tambe 1997). However this work has tended to view actions by individuals within a group as directed towards the achievement of a joint intention, with each agent committing to performing a (possibly different) action from a shared or team plan, rather than the selection of an action which is performed by all agents but which only serves the interests of a subset. It seems unlikely that non-human primates have explicit joint intentions, or the shared plans and models of teamwork necessary to achieve them.

In the remainder of this paper we present a model of group action selection in

baboons. Each baboon is modelled as an agent which chooses actions and interacts with its environment (and indirectly with other agents) based on its individual state. A key feature of the model is that an agent's choice of which action to perform is constrained by a group level decision whether the group as a whole will move at the next timestep, which in turn is determined by the actions proposed by the other agents. To the best of our knowledge this integration of individual and group level action selection (where all the members of the group participate in the selection and execution of a common action) has not been addressed in previous work.

4 FIELD DATA

The model is based on data from a study of chacma baboons (*Papio hamadryas ursinus*) at De Hoop Nature Reserve, a coastal reserve in Western Cape Province, South Africa. The baboons ranged in an area surrounding the De Hoop Vlei, a large landlocked body of brackish water lined by cliffs along its eastern edge and fed by several freshwater springs. Due to its southerly latitude, De Hoop is a highly seasonal environment with significant annual variation in rainfall, temperature and day length that has important implications for the behavioural ecology of this population (Hill *et al.* 2003, 2004; Hill 2005). Vegetation is dominated by coastal fynbos, a unique and diverse vegetation type comprising Proteaceae, Ericaceae, Restionaceae and geophyte species. Six distinct habitat types were classified on the basis of vegetation structure within the home range of the baboons (Hill 2006a) (Table 1; see Hill (1999) for detailed descriptions and further information on the ecology of the reserve).

Habitat Type	Proportion of Range (%)	Food Availability	Predation Risk
Acacia Woodland	15.8	High	High
Burnt Acacia Woodland	1.2	Low	Intermediate
Burnt Fynbos	27.6	Low	Intermediate
Climax Fynbos	25.7	Low	High
Grassland	11.0	Intermediate	Low
Vlei	18.7	High	Low

Table 1: Home range composition, vegetation food availability and predation risk of the major habitat types at De Hoop.

The data presented here are for a 7-month period (June to December 1997) from a single troop of chacma baboons that ranged in size from 40 to 44 individuals over the course of the study. Data were collected by means of instantaneous scan samples (Altmann 1974) at 30-minute intervals, with 2-4 adult males and 12 adult females sampled for a minimum of five full days each month. At each sample point, information was recorded on the identity, habitat type and activity state (feeding, moving, socialising or resting) of all visible individuals. Each scan lasted a maximum of 5 minutes. A more detailed description of the data collection methods is given in Hill (1999), with further information on patterns of habitat use in Hill and Weingrill (2006).

5 THE MODEL

Based on the field data, we developed and implemented an agent-based model of baboon behaviour and used this to simulate a troop of 50 baboons over a seven month period (June–December). The model determined the activity chosen by each baboon at each timestep and the resulting energy balance, time between drinking, time spent socialising and time spent resting.

The simulation model consists of two components: the environment model and the baboon model. The environment model is based on the $200\text{m} \times 200\text{m}$ map grid used for field data recording, and consists of 660 cells within an area 5.4km by 8.4km. Each cell contains a mixture of the 6 primary habitat types found at De Hoop (Acacia Woodland, Burnt Acacia Woodland, Climax Fynbos, Burnt Fynbos, Grassland and Vlei) and may also include one or more ‘special features’: water sources, sleeping sites, and refuges (primarily cliffs). When more than one habitat type occurs in a cell, it is assumed that they are present in equal proportions. Each habitat type is characterised by a maximum food availability, food intake rate when foraging and travel-foraging, and replenishment rate for each month of the study period. The energy value of the food available was estimated at 13.98kJg^{-1} (Stacey 1986) for all habitat types. The habitat types and distributions are illustrated in the graphical output of the simulator, shown in Figure 1.

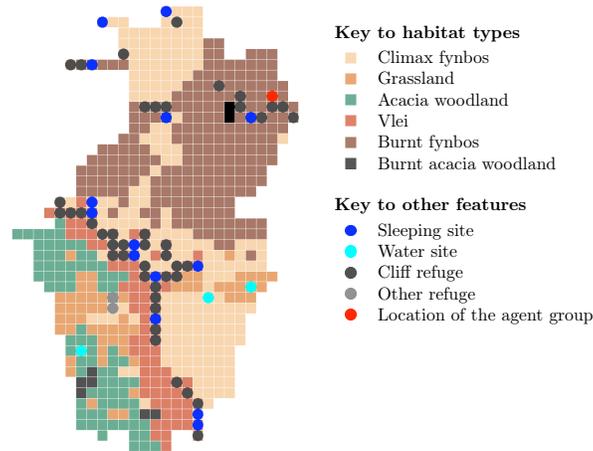


Figure 1: Graphical output from the simulator showing the habitat types and distributions.

The second component of the simulation is the baboon model. Each baboon is modelled as an agent with physical parameters based on well-known baboon physiology. In addition, each agent maintains an individual score for water, energy and social time which function as ‘drives’ in biasing the agent’s choice of preferred activity. At each timestep an agent can perform one of four actions corresponding to the activities recorded for the baboons at De Hoop: foraging, moving (travel foraging), socialising or resting. In addition, an agent can perform an instantaneous drinking action

which can be combined with any of the other four actions (assuming the agent is in a cell which contains a water source). Foraging, moving, socialising and resting actions have an associated energy cost which decreases the agent’s energy score. Energy costs were calculated using the formulae given in (Tucker 1970) for an average adult female baboon with a body mass of 16.1 kg (with the heavier males offset by the lighter infants and juveniles) and assuming that the baboons moved relatively slowly (0.5 ms^{-1}) since they customarily foraged whilst moving. Thus foraging requires 36.71 W; moving (travel foraging) 50.59 W; socialising 64.04 W; and resting 34.63 W. These values are not directly based on the field data from De Hoop so must be viewed as approximate. The agents rest at night, and the energy this requires is also subtracted from their energy score. In addition to its energy cost, each action also updates the energy, water and social time scores. Thus foraging increases the agent’s energy score depending on the type of food consumed (i.e., the habitat type(s) of the current cell).

In (Sellers *et al.* 2007) it is evident that the agents spend considerably less time foraging than their natural counterparts yet still achieve their energetic requirements. The authors speculated that this disparity was a consequence of the relatively coarse granularity of the environmental model, and specifically the constant rate at which resources are depleted by the agents. In an attempt to address these issues, we have extended the model presented in (Sellers *et al.* 2007) to incorporate a model of diminishing foraging returns. The diminishing returns model assumes that the food in a cell is uniformly distributed and uniformly depleted by the agents. Under these assumptions the rate of energetic return in each cell at time t , r_t , is equal to the product of the maximum possible rate of return r_{max} and the ratio of the remaining energetic resource e_t to maximum available energetic resource e_{max} in the cell. That is:

$$r_t = r_{max} \times \frac{e_t}{e_{max}}$$

The model, which relies solely on information present in the simulation, exhibits the intuitive behaviour that as resource within each cell becomes increasingly sparse the agents must spend proportionately more time foraging to obtain the same energetic return, i.e., once resource available in a cell has halved, twice as much time must be spent foraging to obtain the same energetic return.

The agents also forage while moving, which increases the agent’s energy score at a lower, travel-foraging, rate. Drinking adds one to the agent’s water score. Socialising increases the agent’s social time score by the length of the timestep. Not drinking causes the agent’s water score to decrease by the reciprocal of the timestep, and any action other than socialising causes the social score to decrease by the length of the timestep.

The baboon model simulates the activities of each baboon during daylight hours at a 5 minute timestep. At the beginning of each timestep the agents execute a two stage decision procedure which determines the action performed by each agent at this timestep. In the first phase, each agent chooses a preferred action and whether it would prefer to move to allow it to perform the action more effectively. In the second phase, a group decision is taken to determine whether the agents actually move to another cell. This may force some agents to choose an alternative, less preferred, action, as explained below.

In the first phase of the decision procedure, each agent’s preferred action is determined by a combination of individual constraints and the agent’s goals. The agents have a single individual constraint: they must return to a sleeping site to rest each night. In addition they have 3 goals: to maintain their energy balance (i.e., to eat sufficient food to make up for the energy expended each day), to drink (i.e., visit a grid cell constraining a water source) at least once every 2 days, and to spend 2 hours a day in social activity. The requirement that the agents must return to a sleeping site each night constrains the choice of the preferred action (and ultimately the preferred cell) so that the agent can always reach a sleeping site in the time remaining before nightfall. If the individual constraint does not force the agent to move at this timestep, the agent’s preferred action is determined using a weighted random function with weights proportional to the current desire to forage, drink and socialise. Desires are linear functions of the corresponding scores with gradients proportional to relative importance values for each action: W_F (the relative importance of foraging), W_D (the relative importance of drinking), and W_S (the relative importance of socialising). These desire functions fall to zero when the target amount has been reached and when they are all zero the agent will opt to rest. By aiming to keep all desires at zero, the agents will eat enough food to balance their energy expenditure, drink on average once per day, and socialise on average 2 hours per day.

The agent then determines whether it could perform its preferred action more effectively in another cell. The agent will *vote to move* if the best grid cell within a search radius, S , is more than an action-specific threshold better than the current cell for its preferred action. (If the search radius is greater than the maximum distance the baboon can travel and still reach the closest sleeping site by dusk, only cells within the maximum travel distance are considered.) In the case of foraging the threshold is denoted by T_F , and depends on the food availability, in the case of socialising and resting the thresholds (denoted by T_S , T_R) are a measure of predation risk. For example, if the agent would prefer to forage, it will vote to move if the best cell within the search radius has more than T_F times as much food as the current cell. It is assumed that the agent has perfect information about food availability and predation risk for all cells within the search radius of its current position, and that the agent knows where the nearest water source is, irrespective of search radius.

In the second phase, the votes for all the agents are counted, and a *group decision* is taken on whether *all* the agents will move. If the number of agents which voted to move is higher than a user specified threshold, V , then the whole group moves in the most commonly preferred direction (i.e., each agent performs a move action in the specified direction at this timestep). If fewer than V agents opt to move, then the agents which voted to move choose their most preferred action for the current cell at this timestep. This is because the group decision not to move may invalidate an individual’s initial choice of preferred action: for example, it is impossible to drink if there is no water in the current cell, or if the current cell’s predation risk is greater than T_K then the agent will not want to socialise or rest.

The interaction between individual and group level decisions is summarised in Table 2. Note that the adoption of the group-level decision by all agents may involve an element of coercion for some agents. If the group decision is not to move, then all the agents which didn’t vote to move get to perform their preferred action and those that

Group decides to move	Individual votes to move	
	yes	no
yes	travel-forage in the most preferred direction	
no	choose best available action for the current cell	perform preferred action in the current cell

Table 2: Interaction between individual and group level decisions.

did vote to move are forced to choose another action to execute in the current cell. This could be the same action as their first choice (but in this case they are forced to perform it in the current cell which is at least T_X worse than their preferred cell for this action). In other cases it may be impossible or too risky to perform their preferred action in the current cell and they must choose another action. If, on the other hand, more than V agents voted to move, then those that preferred to stay in the current cell are coerced to move (travel-forage) in the most commonly preferred direction. Moreover, since the group decision is to move in the most preferred direction, it is possible that some of the agents which voted to move will ultimately not be able to perform their preferred action in their preferred cell. For example, an agent which wants to move west to a water source may be forced to move east towards a cell which is better for foraging or resting/socialising.

The agents then spend the next 5 minutes either moving in the chosen direction or performing their chosen action, and their scores in terms of energy, water and social time are adjusted accordingly. If the agent’s preferred action is to forage, socialise or rest, the agent will opportunistically drink if it finds itself in a grid cell containing a water source.

Critically, the actions of the agents also affect the environment, which in turn affects the action chosen by the agents at the next timestep. For example, foraging and travel-foraging causes the food available in the grid cell containing a baboon to be depleted at the appropriate food intake rate for each habitat type occurring in the cell. While food consumed is replaced at the replenishment rate for the current simulation month for each of the habitat type(s) occurring in the grid cell, this is lower than the corresponding food intake rate. Foraging therefore reduces the availability of food at the next timestep (relative to other cells within the agents’ perceptual range), making it more likely that an agent will choose to forage in another cell (or perform some other action) at the next timestep.

For the revised version of the model presented here the original simulation was reimplemented using the MASON multiagent simulation toolkit (Luke *et al.* 2005). To verify that the reimplementation was identical to that in (Sellers *et al.* 2007) we performed a replication and validation study. The original and reimplemented simulation (without diminishing returns) were run on the same input data and using an identical stream of random numbers (Will & Hegselmann 2008). This approach accounts for the stochastic elements within the model, and allows direct comparison of the internal state of both simulations. The re-implementation was shown to exhibit numerical identity

(Axtell *et al.* 1996) when compared to the original simulation (Zappala 2008).

The replication revealed a small number of minor defects in the original implementation relating to choice of direction and group action selection under extremely rare conditions. These defects were corrected and the revised and original models were statistically compared for distributional equivalence (Axtell *et al.* 1996) using a two-tailed t-test for matched pairs ($n = 1001$, $p < 0.05$). 1001 sets of parameter values were randomly chosen from the original Monte Carlo parameter ranges used in (Sellers *et al.* 2007) and the corresponding outputs analysed for each simulation. While there are statistically significant differences between the results of the original and revised models, the changes in the mean time spent in each activity and in each habitat type were relatively small ($< 20\%$), and the change in the mean success rate with respect to V (a key finding of Sellers *et al.* (2007)) was less than 5% (Zappala 2008). We take this as an indication that these defects did not materially affect the original findings of Sellers *et al.* The replication also gives us greater confidence that the results presented in (Sellers *et al.* 2007) were not due to artefacts of the original implementation.

6 SENSITIVITY ANALYSIS

We do not currently have values for the parameters used in the agents' decision procedure. Some we may be able to estimate empirically with more detailed field observations, but others are essentially unknowable. To overcome this we choose plausible ranges for each decision parameter and performed a Monte-Carlo sensitivity analysis (Campiono *et al.* 2000) where the simulation was repeated a large number of times and the values of the parameters randomly sampled from the appropriate ranges for each run. This allows us both to estimate the importance of a particular parameter on the outcome and to calculate the range of possible outcomes. Sensitivity analysis was chosen as our primary interests in this initial study were to see whether the range of possible outcomes predicted by the model were able to bracket those observed in the field and to highlight gaps in the field data, rather than to trying to find the parameter values that produced the best fit to the field data (although this will be a goal of future work). The parameter ranges used in the analysis are shown in Table 3.

Parameter	Min	Max
V vote to move threshold	0.1	0.9
S search radius	200	2200
W_F relative importance of foraging	1	10
W_S relative importance of social activity	1	10
W_D relative importance of drinking	1	10
T_F move to forage threshold	1	3
T_S move to socialise threshold	1	3
T_R move to rest threshold	1	3
T_K predation risk threshold	0	0.25

Table 3: Key parameters in the decision procedures showing the ranges used in the Monte-Carlo sensitivity analysis.

We analysed the predictions of the model in terms of how well it was able to duplicate the observed activity patterns in the baboon field data. The model was run 100,000 times sampling the parameters from Table 3 each time. Table 4 shows the success of the agents in achieving their goals for both the reimplemented (constant returns) model and the new diminishing returns model. We consider the agents successful if they achieve their energetic requirements (maintaining an energy intake of approximately 3500kJ depending on the activity pattern), water requirements (an interval between drinking of less than 2 days) and social requirements (a target of 2 hours of social activity). We consider a run successful if all these requirements are achieved simultaneously by all agents for the entire duration of the simulation.

	Constant Returns		Diminishing Returns	
	Success	Failure	Success	Failure
Water	69.6	30.4	66.0	34.0
Energy	79.4	20.6	77.3	22.7
Social	92.9	7.1	92.7	7.3
Total	69.4	30.6	65.9	34.1

Table 4: Percentage of simulations in which the agents successfully achieved their goals for the reimplemented constant returns model and the new diminishing returns model.

It is clear from Table 4 that the correction of the original constant returns model (Sellers *et al.* 2007) has resulted in an increase in the success of agents in achieving their goals. Nevertheless, the agents still fail to achieve their goals in over 30% of simulations and, as with the original simulation, this is primarily due to not meeting their water requirements. As with the original simulation, therefore, certain combinations of input criteria lead to significant levels of failure. Similar patterns are observed for the diminishing returns model, although the increased foraging costs in this model results in higher rates of failure on all criteria, with less than two thirds of simulations successful overall. It is clear, therefore, that the addition of a model of diminishing foraging returns has made it more challenging for the agents to achieve their goals. In the remainder of this section we examine parameters that account for the success and failure of each run and examine the degree to which the new diminishing returns model is able to predict observed time budgets and habitat utilisation for the De Hoop baboons.

Table 5 presents the results of a forward logistic regression analysis to determine which of the nine parameters in the model’s decision procedure have significant effects on the success and failure of each run. Since the relationship between success or failure of the model and the voting threshold was non-linear (see Figure 2), the vote to move threshold was recoded as a categorical variable for analysis, with each category representing a proportional increase in threshold of 0.05. As in (Sellers *et al.* 2007), despite seven parameters being significant determinants of the success or failure of the agents, it is clear that V , the proportion of agents required to vote in order to move, has the greatest effect. Furthermore, it is evident from Figure 2 that only intermediate vote to move threshold values produce successful outcomes, with thresholds between 0.40 and 0.70 consistently leading to successful runs of the model. In contrast, sim-

Model	Nagelkerke r^2	-2 Log L	χ^2	df	p
	0.585	73337.7	55040.2	21	< 0.0001
Variables included	r^2 change	B	Wald	df	p
V	0.437		23884.3	15	< 0.0001
W_D	0.083	0.049	8307.1	1	< 0.0001
W_F	0.026	-0.269	3021.3	1	< 0.0001
W_S	0.018	-0.224	2147.6	1	< 0.0001
T_F	0.017	0.981	2041.8	1	< 0.0001
T_K	0.004	3.757	448.4	1	< 0.0001
T_S	0.001	0.046	4.7	1	< 0.0001
Variables excluded			Score	df	p
S			2.05	1	0.152
T_R			0.89	1	0.346

Table 5: Results of a logistic regression analysis to determine which factors within the model have the greatest effect on whether the agents succeed or fail in achieving their goals.

ulations with low or very high voting thresholds rarely result in the agents achieving their requirements, indicating that majority decision making is the key to a successful foraging strategy within the model.

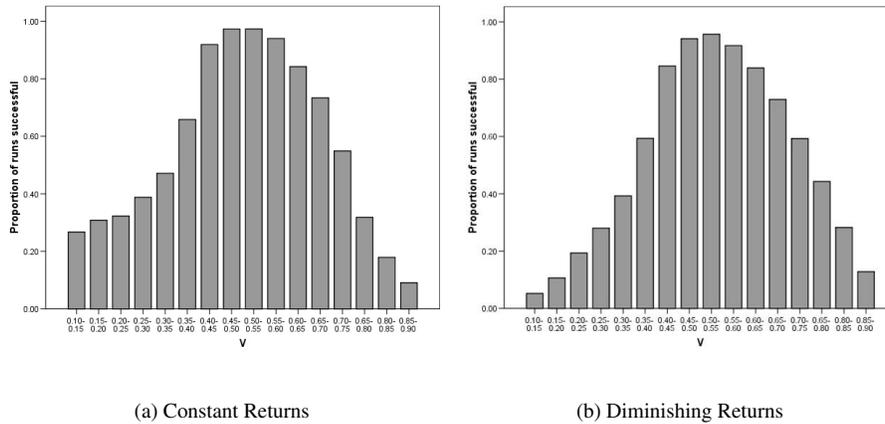
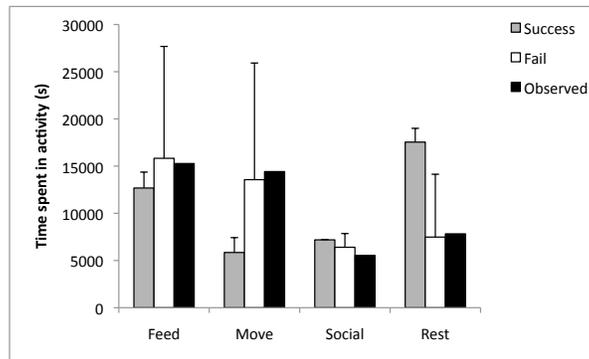


Figure 2: Proportion of runs resulting in the agents successfully achieving their goals against proportion of agents required in order to vote to move V .

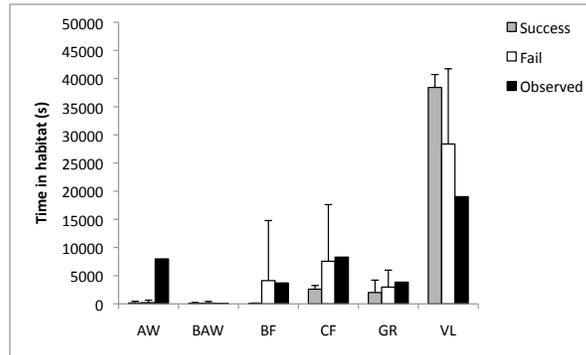
By comparing the distribution of successful runs with respect to V for constant and diminishing returns we can investigate the response of the model to the introduction of diminishing returns. From Figure 2 we can see that for values of V between 0.10 and 0.50, the agents are consistently more successful with constant returns than with diminishing returns. However, as V tends towards 0.5 the number of successful runs reduces

non-linearly, until the number of successful runs converge. Perhaps surprisingly, for values of V between 0.70 and 0.85 the agents are more successful in the diminishing returns model than the model with constant returns.

Further differences with the logistic regression model of Sellers *et al.* (2007) are also evident, however, with the search radius no longer a significant predictor of the success of the model. Interestingly, T_F is now significant, suggesting that the increased foraging requirements of the diminishing returns model place far greater significance on the move to forage threshold in determining the agents' ability to achieve their energetic requirements.



(a) Activity budgets



(b) Habitat use

Figure 3: Mean (+SD) duration of time spent in (a) each of the four activities and (b) each habitat type in successful and failed runs of the model compared with the values from the field data. AW — Acacia Woodland; BAW — Burnt Acacia Woodland; BF — Burnt Fynbos; CF — Climax Fynbos; GR — Grassland; VL — Vlei.

Although the factors underpinning the success of the model remain similar to those in (Sellers *et al.* 2007) it is clear that the diminishing returns model is better able to predict the observed baboon activity budgets (Figure 3(a)). In particular, the diminishing returns model results in a significant increase in time spent foraging (12679s compared to 6513s in the reimplemented model) although the observed value still lies over one standard deviation from the mean of the successful simulations. In turn this results in a reduction in resting time relative to the earlier model (17544s vs 23391s), although the simulated values still greatly exceed those observed. Similarly, as with (Sellers *et al.* 2007), the successful simulations predict the agents to move far less than observed and social time is in line with that predicted.

The diminishing returns model does little to improve the fit with the observed habitat use relative to the model of Sellers *et al.* (2007). Figure 3(b) illustrates that in the successful simulations the agents use the vlei habitat significantly more than observed within the field data, with the acacia woodland habitat significantly underutilised. Since the vlei habitat is both high in food availability and low in predation risk these results suggest that on average the agents are able to satisfy their foraging requirements without needing to move to the more distant and risky acacia woodland. Overall, therefore, it is clear that while the diminishing returns model represents a significant improvement in terms of matching the foraging costs in the observed data, the model still does not adequately capture all of the parameters constraining patterns of baboon activity and habitat use.

7 DISCUSSION

Although the diminishing returns model represents a significant improvement to the original model presented in (Sellers *et al.* 2007), it is nevertheless clear that it is still relatively easy for the agents to satisfy their energetic requirements over a broad range of parameter values. It is important to remember though that we would never expect a model to precisely match the observed activity patterns at even a monthly level, let alone daily or hourly time scale, although the results presented here do suggest that this should be possible. Nevertheless, further developments are clearly required if this is to be achieved.

Despite the diminishing returns model providing far greater ecological realism in terms of foraging costs, we noted in (Sellers *et al.* 2007) that the coarseness of our environmental model (where groups are foraging in $200\text{m} \times 200\text{m}$ patches) may prevent an accurate simulation of observed behaviour. Even with the diminishing returns model the agents are able to deplete the 200m grids evenly without additional moving costs, whereas in reality baboons will of course cause local resource depletion on a much finer scale with more rapidly diminishing foraging returns. As a consequence the animals are likely to make frequent movements over small distances between discrete food patches within a cell and these elements are currently not captured in our model. A significant improvement may therefore be achieved if we were to simulate baboon foraging at an appropriate temporal and spatial scale (such as 1m^2 at sub-minute intervals). Although our current ecological data do not permit such an approach, a number of studies have recently started to incorporate landscape dynamics and geographic in-

formation systems (GIS) data into individual-oriented models (Gimblett 2002; Topping *et al.* 2003). In future, coupling multi-agent simulation tools with GIS mapping data will offer opportunities for the production of highly realistic multi-agent simulations of individual behaviour and population processes within precise spatial contexts (Schüle *et al.* 2004).

While the need for more detailed environmental models is clear, there are a number of other areas where additional parameters could also be beneficially incorporated into the current model. Firstly, the incorporation of a full diet model may be essential. While the agents' preference for foraging within the vlei habitat may be explained in terms of its proximity to sleeping sites and the nature of resource depletion ensuring that it always offers high energetic returns, it may be equally true that in nature the baboons move on in order to seek a more diverse diet (Post 1982; Hill 2006b). In reality, the vlei has only limited diversity in terms of food types (Hill 1999), but since the model only examines energy intake this may explain why the more food species diverse habitats such as acacia woodland and burnt climax fynbos are underutilised in the simulations. A full diet model would be easy in modelling terms but difficult in terms of validation, since it would require much more detailed chemical and calorific analysis of what the baboons actually eat in different areas. While this is not possible with our existing ecological data it does serve to highlight the value of agent-based modelling in identifying areas of empirical data that are important for future field studies.

Some improvements in relation to foraging costs should nevertheless be achievable within the framework of the current model. Over 56% of food items consumed within the vlei are subterranean, compared to less than 1% in acacia woodland, the other high food availability habitat. Although subterranean items are often of high quality in terms of energy they are generally considered to be fallback items due to their high costs of excavation (Hill & Dunbar 2002). As a consequence, foraging within the vlei is likely to be more energetically expensive than in other habitats and this fact may account for why our simulations overestimate the time spent in this habitat. Although accurate estimates of the energetic costs of digging are not currently available for primates, it should still be possible to more accurately account for the different foraging costs for each habitat in a future iteration of the model. This alone should significantly improve the fit with the habitat usage observed for the De Hoop baboons.

Given the ease with which agents appear to be able to forage within our model, it is extremely interesting that the agents fail to achieve all of their goals simultaneously in over one third of simulations. The results of the Monte-Carlo sensitivity analysis indicate that while the agents are able to achieve their minimum requirements across a range of decision parameter values, unsuccessful runs are most likely to arise from individuals gaining insufficient access to water. The primary determinant of the success of the model, however, is determined not by W_D , the relative importance of drinking, but instead by the proportion of individuals voting to move. Only in situations where a majority is required for movement (and thus changes in activity and location) does the model consistently result in the agents achieving their minimum requirements. In fact, the voting threshold is also the primary variable underlying variation in the time spent in various behaviours and in the different habitat types (Sellers *et al.* 2005). This is almost certainly because democratic decision making tend to produce less extreme decisions (Conradt & Roper 2003) and it is certainly true that the unsuccessful runs produce

far more variable output (Figure 3). While all grid cells in the model contain at least some food, and many habitats are suitable for socialising and resting, water is restricted to just a few localities. As a consequence, while it is probably still possible for individuals to adequately forage, socialise and rest under less democratic voting thresholds because suitable habitats are still likely to be encountered, low (and to a lesser degree very high) voting thresholds can lead to more extreme variation in drinking intervals resulting in the agents being unable to meet their drinking requirements in many cases. The introduction of diminishing returns creates a more challenging environment for the agents, in that more time is required to achieve a similar energetic intake. Intuitively, one might expect that this would reduce the success rate for all values of V ; however, this is not the case. Although the introduction of diminishing returns does produce a noticeable (3.5%) reduction in overall success rates, this difference is almost entirely accounted for by runs in which V is less than 0.5. As it becomes more difficult for the agents to achieve their goals, super-majority ($V > 0.5$) decision strategies, which demand greater commitment from the group, are preferable to sub-majority ($V < 0.5$) decision strategies where lower group commitment is required.

Although the voting procedure employed in this paper might be considered unrealistic, anecdotal observations of wild baboons have reported voting behaviours where a simple majority determines changes in group activity based on movement (Byrne 2000), or where the majority of adults decides on the direction of travel through body orientation (Norton 1986). Perhaps most importantly, a recent study on the De Hoop baboons has shown the timing of departure and travel direction seemed to be a partially shared consensus decision with adult males contributing more to the decision outcome (Stueckle & Zinner 2008). While constraining a social group to remain together, the voting mechanism in our model may have greater similarities to natural systems than might be supposed. Nevertheless, while this study adds to the growing body of evidence that democracy and majority decision-making should be widespread across a range of animal taxa, it is clear that the questions of how animal groups coordinate movement and reach decisions are a fertile field for future research.

It would also be interesting to extend the model to explore the relationship between individual and group level action selection in more detail. For example, it would be straightforward to incorporate a weighted voting scheme in which the votes of some individuals have a greater effect on action choice (and in the limit some subset of individuals determines group actions). Such a modification would allow us to explore whether the empirical data reported by Stueckle and Zinner (2008), where males have greater voting weights, allow us to better predict the other elements of observed behaviour. It would be more interesting, however, to try to model the emergence of group level action selection from the sum of interactions between individual agent's action choices (i.e., without an explicit voting scheme). This would require a much finer grained model of baboon sensing and behaviour, and a greater time resolution of the model. Nevertheless, agent-based modelling offers the potential to address these issues, and the current model should provide a valuable springboard for examining the relationship between individual and group level action selection.

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