Effects of Resource Availability on Consensus Decision Making in Primates

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Abstract There has recently been increasing interest in group decision making, and in particular the mechanisms through which a group of individuals can arrive at a consensus decision. In this paper we investigate the effects of resource availability upon consensus decision making in a primate group. We extend an existing agent-based model of primate decision making to incorporate a model of diminishing foraging returns, and show that the difficulty of obtaining energy from the environment has an impact on successful strategies for consensus decision making in such groups. Moreover, the introduction of diminishing returns also results in better agreement between the predictions of the model and field studies of a naturally occurring primate group.

1 Introduction

Many non-human animals live in social groups. The advantages of group living, including e.g. decreased risk of predation (Hill and Lee, 1998), depend on the group remaining cohesive. However differences in the drives and desires of individuals have the potential to result in group fragmentation, particularly when the group is presented with choice (Leca et al, 2003). Yet, groups routinely make decisions regarding which activity to pursue, where to pursue it, the direction of movement and the timing of departure (Conradt and Roper, 2003) without fragmenting. The mechanisms underlying such consensus decision making are an important but poorly understood aspect of group-level dynamics. Many factors may potentially affect how such decisions are made, including dominance hierarchy and social and familial affiliation (King et al, 2008), the consensus cost (relative to grouping benefits), the physical homogeneity of the group, the size of the group (relative to an optimal size) and the nature of possible activities (Conradt and Roper, 2007).

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Much of the data pertaining to group decision making in animals has been collected through observational field-based research. However, studies of this kind are frequently resource intensive and logistically complex making large scale/long term data collection impractical. It is often infeasible, and may be undesirable, to attempt to conduct behavioural research on animal groups within a laboratory setting. Yet without the controls provided by laboratory conditions we lack the consistency and repeatability necessary to draw strong conclusions from experimental findings (Eberhardt and Thomas, 1991). Given these difficulties, multi-agent simulation offers an attractive alternative to field or laboratory-based studies of group decision making mechanisms. The results of an agent-based model depend on the desires of 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 and Parker, 1991). Agent-based simulation has been successfully applied to the investigation of group decision making in animals across a variety of taxa and scenarios including nest selection in ants (Pratt et al, 2005), shelter selection in cockroaches (Garnier et al, 2005), and action selection in primates (Sellers et al, 2007).

In this paper, we investigate the effect of environmental features, and specifically resource availability on consensus group decision making. We extend an agent-based model of primate group decision making (Sellers et al, 2007) to include a model of diminishing resource returns whereby energetic (food) availability within a region is reduced proportionally to the degree of foraging activity. We study the implications of diminishing returns on the ability of group members to achieve their goals and its implications for group decision making, specifically its impact on the proportion of individuals required to effect 'consensus' (the quorum threshold). We show that as environmental conditions become less favourable, the value of the quorum threshold must adapt if the agents are to achieve their goals.

The remainder of this paper is organised as follows. In Section 2 we briefly present a theoretical framework for consensus decision making in animal groups. In Section 3 we summarise the agent-based model of consensus decision making in primates developed by Sellers et al (2007) which forms the basis of our work, and highlight some of the limitations of this model. Our model of diminishing resource returns is presented in Section 4 and in Section 5 we summarise the results of a replication and validation study of the Sellers *et al.* model. In Section 6 we present results of experiments with our model of diminishing returns, and compare these with with results of Sellers et al (2007) and field observations. In Section 7 we consider the implications of our work in the context of related literature. Finally we consider options for future work and expansion of this study in Section 8.

2 Group Decision Making

For a group of animals to remain cohesive, individuals must synchronise the timing and location of their activities. However, such synchronisation may require that an individual performs an activity which is not optimal for that individual (Leca et al, 2003). Biomechanical and physiological differences between individuals resulting from variations in age, gender, and reproductive status, can lead to divergent abilities and

motives, giving rise to conflicting needs amongst group members (Leca et al, 2003). In social species the outcome of collective decisions has implications for the fitness of each animal, yet individuals will defer to these decisions even where it may not be in their best interests to do so (Conradt and Roper, 2007). Decision making strategies employed by animal groups must maximise the welfare of the group overall without excessively compromising the requirements of each individual (Conradt and Roper, 2007). At present, we understand very little about the mechanisms by which such agreement can be reached, in a non-verbal way, and by animals of limited cognitive ability.

Conradt and Roper (2005) define a *consensus decision* as a choice between two or more mutually exclusive actions with the specific aim of reaching a consensus. All group members must abide by the outcome of this decision, however, not all group members need contribute to the making of the decision. In an *equally shared consensus decision* all members do contribute towards the decision (democratic), whereas in an *partially shared consensus decision* only a proportion of group members (e.g., all adult males) contribute to the decision, and in an *unshared consensus decision* the decision is made by a single individual (despotic). The latter form of decision making may occur either under *consistent leadership* where the same individual is always responsible for the decision or *variable leadership* where different individuals take this responsibility at different times.

For a shared consensus decision to be achieved a *quorum*, representing a required minimum number of group members, must agree. The quorum may be a *sub-majority*, a *majority*, or a *super-majority*, with thresholds for these being less than fifty percent, at least fifty percent and more than fifty percent of group members respectively. Where the needs of an individual conflict with the outcome of a consensus decision, that individual may bear a *consensus cost*, for example, to their fitness. Consensus decisions are typically made in respect of synchronised group activities, e.g., timing and direction of travel, and which activities are pursued and where they are pursued (Conradt and Roper, 2005).

3 A Model of Consensus Decision Making

Sellers et al (2007) present a multi-agent simulation of group decision making in a troop of 50 chacma baboons (*Papio hamadryas ursinus*), and compare the results of their simulation with data collected over a seven month period of field observation at the De Hoop Nature Reserve in South Africa. In this section, we briefly summarise the Sellers et al model and key results of their simulation experiments.

The simulation model consists of two components: the environment model and the baboon model. The environment model is based on the 200m × 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 (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). 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 baboon model simulates the activities of each baboon during daylight hours at a 5 minute timestep over a seven month period. 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. 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 a target score has been achieved, and when they are all zero the agent will opt to rest. Each agent selects its preferred activity stochastically from a distribution weighted according to the strength of these drives. At each timestep an agent can perform one of five actions corresponding to the activities recorded for the baboons at De Hoop: drinking, foraging, moving (travel foraging), socialising or resting. Performing an action updates the appropriate scores. For example, foraging updates the agent's energy score with the net energy gain, i.e., the difference between the amount and the type of food consumed (determined by the habitat type(s) of the current cell) and the energy cost of foraging. Foraging and travel-foraging also cause the food available in the grid cell containing an agent 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.

The model assumes equally shared consensus decision making. Agents, under the constraint that they must not separate, use a democratic voting mechanism to arrive at a consensus decision concerning the initiation and direction of group travel. 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 chooses a preferred action based on its drives. 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. 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.

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. Note that consensus decisions may result in a consensus cost for some agents, if they are not able to perform their individually selected action as a result of a group decision to move in a particular direction.

In (Sellers et al, 2007) Monte Carlo simulation was used to determine how well the model was able to duplicate the observed activity patterns of animals found in the field data, and to estimate the importance of decision parameters on the outcome. (See table 1 for the Monte Carlo parameters.) The quorum threshold (V) was found to be the most important determinant of both the fitness of each agent and the behaviour of the group as a whole. Thresholds of between 50% and 65% provided agents with the greatest chances of survival; outside of this narrow band the chances of an agent failing to meet its survival goals, measured in terms of food/water intake and time spent in social engagement, increased drastically.

However, while the Sellers *et al.* model successfully meets its requirements in terms of goal achievement in a large proportion of cases, it is less successful in predicting activity budgets and habitat utilisation (see Figures 3 and 5). The agents spend significantly less time foraging and significantly more time resting than the natural population. A similar pattern is seen in the habitat types used by the agents: the agents use the Vlei habitat significantly more than the natural population, and significantly under-utilise the Acacia Woodland habitat. Sellers *et al.* speculated that the poor fit to the data may be due in part to the agents foraging too easily. Agents uniformly deplete 200m × 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 this paper, we extend the Sellers et al (2007) model to include a simple model of the effects of diminishing foraging returns. Using Monte Carlo simulation we characterise this model in terms of its effects on the behaviour of the agents and its ability to improve the fit between simulated and observed outcomes. Lastly, we investigate the implications of diminishing returns for group decision making.

4 A Model of Diminishing Returns

We extend the Sellers et al (2007) model by introducing a new parameter, *occupancy penalty* (P_O). The occupancy penalty is used to compute the diminished energy resource in a habitat cell as a function of the daily total occupancy time of that cell, according to:

$$d = \frac{v}{1 + (t \times P_O)}$$

where d is the (diminished) available energy resource in a habitat cell, v is the available energy resource in the cell in the original Sellers *et al.* model, and t is the number of time steps that habitat cell has been occupied during the current simulated day. The occupancy penalty is inversely proportional to the half-life of the decay, e.g. an occupancy penalty of 0.1 means that a given constant will decay to half of its value in ten time steps. The effect of the occupancy penalty on a typical habitat cell is illustrated in Figure 1.

The occupancy penalty serves two purposes: firstly it provides a model of diminishing foraging returns; decreasing the rate at which agents obtain food from a given
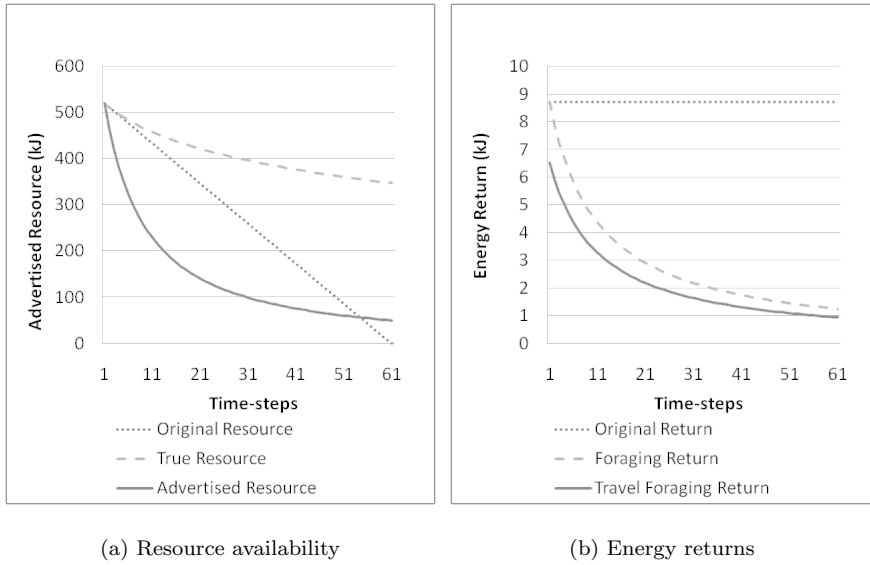
(a) Resource availability   (b) Energy returns

Fig. 1 Effect of occupancy penalty on resource availability and energy returns over time. Original Resource and Original Return represent the behaviour of the simulation prior to the introduction of the occupancy penalty. True Resource and Advertised Resource represent the actual and diminished resource of the habitat cell (as perceived by the agent), respectively. Foraging Return and Travel Foraging Return (foraging whilst on the move) represent the net energy returns from these activities after the introduction of the occupancy penalty. ($P_O = 0.1$)

location as a function of the time spent at that location; secondly, it reduces the apparent availability of food in cells previously occupied during the course of a simulated day.

With the exception of the model of diminishing returns, the revised model is identical in all respects to that of Sellers et al (2007).

5 Simulation Replication & Validation

To verify that our revised model was in fact identical to that in (Sellers et al, 2007) we performed a replication and validation study.

Replication is one of the tenets of cumulative science, yet the findings of simulation studies are rarely verified in this manner. However without independent replication, it is possible that the results of simulation experiments are partially or wholly attributable to implementation artefacts or simple programming errors (Axelrod, 1997). To validate the results of Sellers et al (2007), the original simulation was re-implemented (without the diminishing returns model) using the MASON simulation toolkit (Luke et al, 2005). MASON was chosen for its high performance relative to other Java based toolkits (Railsback et al, 2006).

During the re-implementation the code was refactored both to exploit the features provided by the MASON libraries, and to allow support for alternative models of group decision making. For example, the environment model was implemented using MASON

library classes for the representation of two-dimensional spatial structures. To facilitate future investigation of alternative decision making strategies, the classes were split into three main groups according to function: generic aspects of agent-based simulations, the group decision making model, and classes necessary to replicate the Sellers et al (2007) model. The generic aspects are implemented as 'manager' classes for time, geometry, populations, environment and logging. The group decision making process is implemented as a generic architecture that can be tailored to the needs of different models of group decision making, and includes classes representing groups, activities, policies, and decisions. The specific agent and habitat models are implemented as classes based on those in the Sellers et al (2007) model.[1] MASON's discrete event scheduler permits prioritisation of events scheduled at the same timestep. In the reimplemented model, operations which update the environment, e.g., seasonal re-growth, have highest priority, followed by the two-phase agent decision procedure, with updates to the states of the agents and the effects of agent actions on the environment having lowest priority.

A rigorous validation of the replicated simulation was undertaken. To account for stochastic elements within the model an identical stream of random numbers were used, in identical circumstances (isomorphically) (Will and Hegselmann, 2002) whilst executing both original and re-implemented simulations in parallel; this approach permits direct comparison of the complete internal state of both models. The re-implementation was shown to exhibit numerical identity (Axtell et al, 1996) when compared to (Sellers et al, 2007).

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. In addition, deterministic behaviour in the group decision making algorithm could also result in a bias towards moving in the direction of locations suitable for foraging in cases where a sub majority quorum threshold was used in the group decision making procedure.

These defects were corrected and the revised and original models were statistically compared using a two-tailed t-test for matched pairs. 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 Results

The diminishing returns model was incorporated into the new MASON simulation, and a Monte Carlo sensitivity analysis performed to determine the effects of introducing diminishing returns into the model.

Our initial trials focussed on calibrating the occupancy penalty parameter in order to determine suitable ranges for the Monte Carlo simulation. This was achieved through

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[1] The source code and complete technical documentation for the new simulation is available from http://www.openabm.org/model-archive/primate_gdm/.

observation of the effects of a range of values for P_O on the average times spent in each activity and habitat. We found that even a relatively modest occupancy penalty of $P_O = 0.1$ had a noticeable impact on both the average time the agents spent foraging and on the average time the agents spent moving, increasing the latter well above the observed level. With $P_O = 0.1$, the agents consume half the available food in a habitat cell in ten timesteps (50 minutes), and "prefer" to move into previously unoccupied cells than to continue foraging at the lower rates of return which result from the diminishing returns model. The willingness of the agents to move to forage is governed by the Foraging Move Threshold (T_F) parameter, which determines the degree to which an alternative cell must be better than the current cell for an agent to vote to move. In order to compensate for this effect, the range of the T_F parameter was extended to between 1 and 6 (compared to between 1 and 3 in (Sellers et al, 2007)).

Table 1 Monte Carlo parameters and ranges.

Parameter	Meaning	Lower Bound	Upper Bound
V	Proportion to win vote (quorum threshold)	0.1	0.9
S	Search radius	200	2200
W_F	Relative food importance	1	10
W_S	Relative socialising importance	1	10
W_D	Relative drinking importance	1	10
T_F	Foraging move threshold	1	6
T_S	Socialising move threshold	1	3
T_R	Resting move threshold	1	3
T_K	Resting/socialising risk threshold	0	0.25
P_O	Occupancy penalty	0	0.2

We analysed the predictions of the diminishing returns model in terms of how well it was able to duplicate the observed activity patterns of animals found in field data. The model was run 100,000 times sampling the decision parameters from Table 1 each time.

Table 2 Comparision of rates and reasons for unsuccesful outcomes for both the original Sellers *et al.* model and the model incorporating diminishing returns.

Attribute	Original	Diminishing Returns
Energy Intake	37.59%	56.59%
Water Intake	60.53%	70.80%
Social Activity	18.22%	29.11%
Unsucessful (overall)	60.60%	70.86%

In (Sellers et al, 2007) a simulation was considered *successful* if all of the agents simultaneously achieved their targets for energy intake (approximately 3500kJ per day dependant on activity pattern), water intake (agents must drink at least every two days) and time spent socialising (agents must socialise for at least two hours per day) over the entire seven month simulated period, and *unsuccessful* otherwise. As can be seen from Table 2, the introduction of diminishing returns not only increases the percentage of unsuccessful simulations attributed (in part or in whole) to failure to meet the agents' energy intake targets, but also increases failure rates for the water and social activity targets. Analysis of the effect of occupancy penalty on the proportion of successful

runs (see Figure 2) shows a clear trend: as P_O increases there is a decrease in the proportion of successful runs. However, the model is far less sensitive to parameter T_F in this respect.
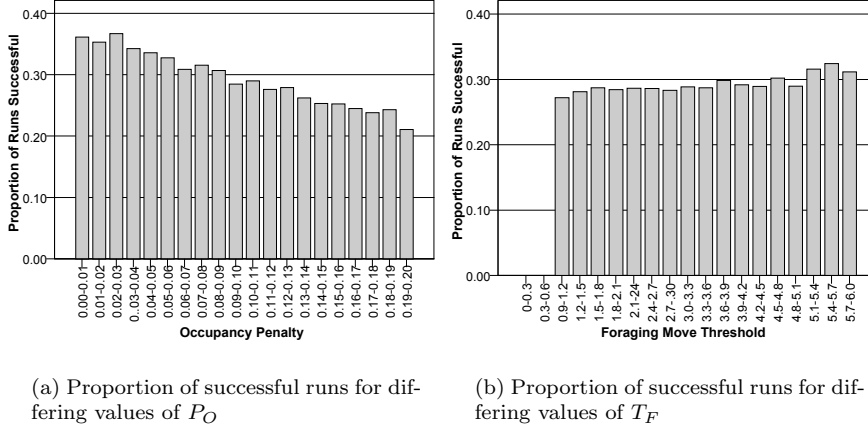

(a) Proportion of successful runs for differing values of P_O

(b) Proportion of successful runs for differing values of T_F

Fig. 2 Proportion of runs which were successfull for differing values of the occupancy penalty (P_O) and the Foraging Move Threshold (T_F).
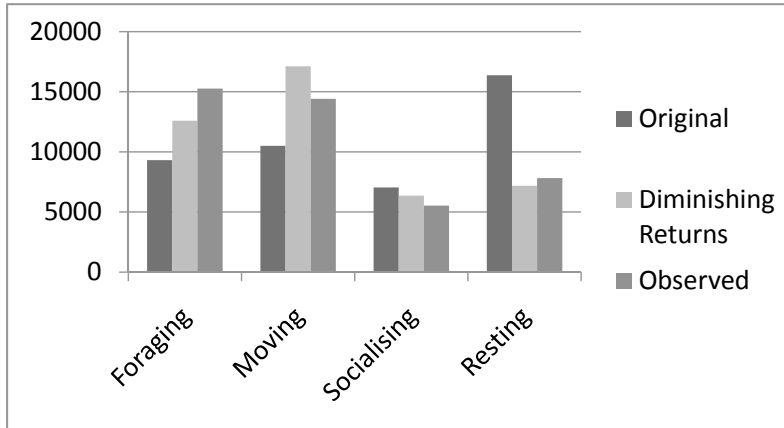

Fig. 3 Comparison of mean daily time spent in each activity for the original model, the diminishing returns model and field observation.

Figure 3 shows the average time spent by the agents in each activity over all 100,000 Monte Carlo simulations. For comparison, results from the original model of Sellers et al, the same model with T_F adjusted to the new range, and the observed activity budgets are also shown. As can be seen, the introduction of diminishing returns (and increasing the range of the T_F parameter) significantly improves the agreement

Table 3 Results of a logistic regression analysis, identifying which model parameters are significant determinants of success.

model	Nagelkerke r^2	-2 log L	χ^2	d.f.	p
	0.730	49026.070	71740.013	23	< 0.0001
variables included	r^2 change	B	Wald	d.f.	p
V	0.631	-	19302.124	15	< 0.0001
S	0.035	-0.001	2540.057	1	< 0.0001
W_F	0.026	-0.428	4481.035	1	< 0.0001
W_F	0.019	-0.060	106.384	1	< 0.0001
W_D	0.010	0.367	3441.515	1	< 0.0001
T_F	0.008	0.053	26.266	1	< 0.0001
T_S	0.000	0.063	5.782	1	< 0.0200
T_K	0.000	7.214	1150.363	1	< 0.0001
P_O	0.000	-9.774	1341.276	1	< 0.0001
variables excluded			score	d.f.	p
T_R			0.048	1	0.826

between the simulated and observed time for all activities compared to the original simulation in (Sellers et al, 2007).

Overall, these results tend to support the original hypothesis of Sellers et al (2007), that the poor fit between the simulated an observed activity budgets was due to the agents foraging too easily. Moreover, they indicate that even a very simple model of increased foraging costs is able to significantly improve predictions of the simulation.

A key result of the Sellers *et al.* model was that the quorum threshold, V, was the most important determinant of whether the agents successfully met their energetic, water and socialising targets. To determine if this was still the case in the diminishing returns model, we performed a forward logistic regression analysis to determine which of the model parameters have significant effects on the success and failure of each run (see Table 3). Since the relationship between success or failure of the model and the voting threshold was non-linear (see Figure 4), the quorum threshold was recoded as a categorical variable for analysis, with each category representing a proportional increase in threshold of 0.05. As can be seen from Table 3, although nine parameters are significant determinants of the success or failure of the model, it is clear that V still has the greatest effect.

We then analysed the data to determine the implications of the diminishing returns model for group decision making. A key finding from (Sellers et al, 2007) was that only intermediate quorum threshold values result in successful outcomes, with thresholds between 0.5 and 0.65 most consistently leading to successful runs of the model. In contrast, simulations with low or very high voting thresholds rarely resulted in the agents achieving their requirements, indicating that majority decision making is key to a successful foraging strategy within the model. A comparison of the relationship between success and the quorum threshold for both simulations (see Figure 4) indicates that whilst this relationship remains, the introduction of diminishing returns has narrowed the range of quorum thresholds resulting in successful runs to between 0.55 and 0.65, with a pronounced peak in the region between 0.55 and 0.60. This tends to suggest that, as resources become more difficult to obtain, group decision making needs to adapt to the more challenging situation.
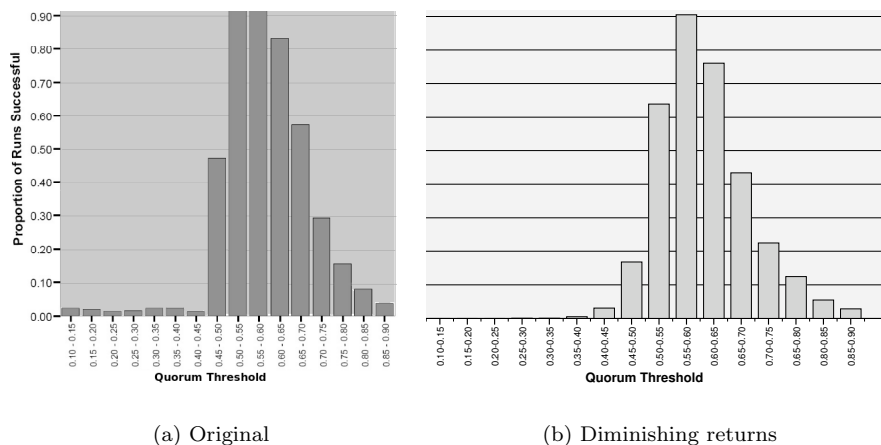
(a) Original   (b) Diminishing returns

Fig. 4 Proportion of successful runs against V for the original and diminishing returns models.

7 Discussion

We have investigated the effects of resource availability on consensus decision making in primates groups. Through replication we have verified an existing agent-based model of primate group decision making (Sellers et al, 2007) showing that, despite minor defects, the results of this model are not due to implementation artefacts. Further, we have extended the original work by providing a model of diminishing resource returns from foraging activity. We have shown that resource availability has a marked effect on the quorum threshold necessary for successful group decision making. The introduction of diminishing returns also increased agreement between the predictions of the model and the observed behaviour of a naturally occurring primate group.

It has been observed that "An unreplicated simulation is an untrustworthy simulation" (Edmonds and Hales, 2003). The replication conducted during this work identified some defects in the original model. Most notably, the use of deterministic group activity selection at sub-majority quorum thresholds may have been responsible for the failure of agents to achieve their goals in simulations where the quorum threshold was below 0.50, one of the key results of the original work. However, correction of this defect revealed that this is not the case, and although the results from the reimplemented model differ slightly from those of the original model, the findings of Sellers *et al.* are supported by this work. Access to the original model was also critical in detecting and correcting minor defects in the new implementation, and replication has therefore undoubtedly contributed to the fidelity of *both* models.

The introduction of diminishing returns affects the model in a number of ways. The occupancy penalty decreases the rate at which agents can obtain food from a given location as a function of the time they spend at that location. This in turn requires that agents must increase the proportion of time spent foraging in order to achieve their energy intake target. Reducing the advertised availability of food in cells previously occupied also discourages agents from revisiting foraging areas in the course of a simulated day, which, in turn, increases the proportion of time agents spend moving.

In these circumstances we might expect that the frequency with which agents fail to meet their energetic targets would increase, and this is confirmed by the results from the diminishing returns model. In comparision to the Sellers *et al.* model, the proportion of unsuccessful simulations in which the agents fail to meet their energy intake requirements increases by approximately 20%, while the proportion of failures due to achieve the agents' water and social targets, and the proportion of unsuccessful runs overall, increases by approximately 10%. Our results clearly show that introduction of diminishing foraging returns has created a more challenging environment for the agents, in which it is more difficult to achieve their survival targets.

The introduction of an occupancy penalty has also resulted in an improved fit between observed and simulated values for the time spent in each activity. Our work therefore supports the original hypothesis advanced in (Sellers et al, 2007), that discrepancies between the Sellers et al model and the field data were caused by the agents foraging too easily.

However, whilst the introduction of diminishing returns improved the predictions of the the average time spent in each activity, other discrepancies reported in (Sellers et al, 2007) remain. Specifically, the model fails to accurately predict time budgets for the utilisation of the various habitat types found in the De Hoop Nature Reserve. Figure 5 shows a comparison of the habitat utilisation predictions from the Sellers *et al.* model, the predictions of the diminishing returns model and observed values. Whilst the model with diminishing returns does provide a closer match to observed habitat utilisation times it is clear that the introduction of diminishing returns alone is insufficent to address this disparity.
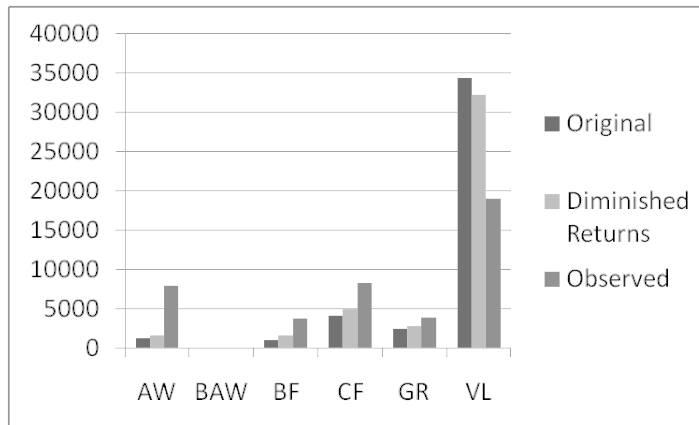

Fig. 5 Comparison of original, diminishing returns and observed mean daily habitat utilisation times. Habitat types are given as: AW - Acacia Woodland, BAW - Burnt Acacia Woodland, BF - Burnt Fynbos, CF - Climax Fynbos, GR - Grassland, VL - Vlei.

The introduction of the occupancy penalty also had a noticeable effect on the proportion of successful runs for a range of values of the quorum threshold. This suggests that environmental conditions, in this case resource availability, may influence the group decision making process in determining an appropriate value of the quorum threshold. Our results show that as environmental conditions become less favourable, the range of quorum threshold values which result in the agents achieving their goals

becomes smaller. This is reflected in the differences in the quorum response of the group (see Figure 4). Sub-majority values for the quorum threshold produce significantly fewer successful outcomes than in the original model where diminishing returns are not present. In particular, the lower bound of the quorum threshold which results in the greatest proportion of successful runs has increased from 0.50 (the majority threshold) to 0.55 (a super majority threshold) suggesting that greater commitment from the group is now required in order to prompt a change in activity.

Figure 6 shows the percentage of successful runs for each value of the occupancy penalty P_O for runs where the quorum threshold is greater than 0.55. As can be seen, the adoption of a super-majority decision strategy is increasingly successful as P_O increases, i.e., as the environment becomes less favourable. This behaviour is in
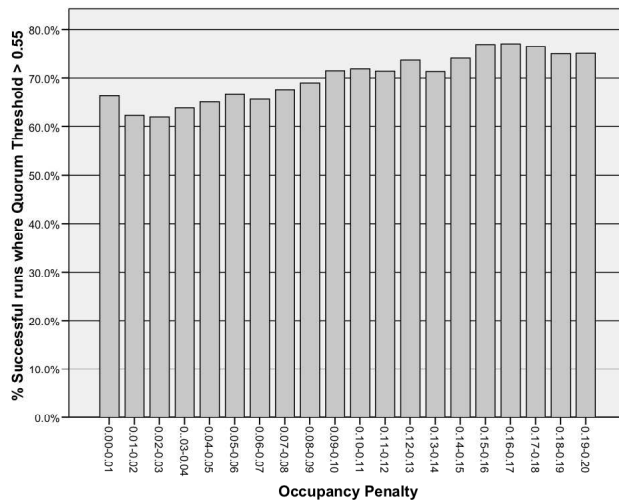

Fig. 6 Effect of P_O on the percentage of successful runs where $V > 0.55$.

agreement with the model of democratic decision making proposed by List (2004), who shows that for the same group under differing circumstances, contrasting quorum thresholds may be required. Specifically, List suggests that, where food resource is scarce, a strategy of super majority decision making, as exhibited by our model, will reduce the probability of making the wrong decision. To the best of our knowledge, this relationship between resource (un)availability and 'successful' values of the quorum threshold has not been addressed in previous work.

The introduction of diminishing returns has also reduced the range of values of the quorum threshold which result in successful outcomes for the agents, yet the process of democratic decision making employed in the model remains a stable strategy. Despite reduced resource availability agents were able to achieve their survival goals under a wide range of conditions (approximately 29% of the simulations). This result tends to confirm the view that democracy should be advantageous in a wide range of situations (Conradt and Roper, 2003).

Recent empirical research supports the view that the group decision making process in primates can indeed be influenced by resource availability (King et al, 2008). In this work, King et al introduced artificial foraging patches to wild chacma baboon troops in

the Tsaobis Leopard Park, Namibia. The distribution of food resource in these patches was designed to create a degree of resource contention amongst troop members. They found that resource contention can induce a group-fission event, where an otherwise stable naturally occurring group will divide into subgroups (based on social affiliation) and follow independent foraging patterns. Such behaviour was not witnessed under normal foraging conditions.

Stueckle and Zinner (2008) have observed leadership and decision making in a troop of chacma baboons as they embarked on their morning departure in the De Hoop Nature Reserve, South Africa. Their findings indicate that a partially shared consensus decision was used to establish both the timing and direction of departure, and that leadership was distributed, with most adult group members initiating group movement on different occasions. Stueckle and Zinner note that this latter finding confirms behaviour predicted in (Sellers et al, 2007) of similar baboons in a similar location, suggesting that the decision making model proposed in (Sellers et al, 2007) closely reflects the mechanism by which natural primate groups reach a consensus decision.

Field-based research reported in (King et al, 2008; Stueckle and Zinner, 2008) both consider groups of chacma baboons. However they reach different conclusions regarding the type of decision making utilised by their respective groups. Stueckle and Zinner conclude that consensus is achieved through a partially shared process, whereas King et al argue that despotic (unshared) decision making is "the norm". These studies were conducted in different locations and presumably under diverse environmental conditions, the effects of which, as shown here, are pronounced, and so may contribute towards this apparent disparity. We believe that agent-based modelling can be a useful approach to understanding such differences in group decision making in primates, as it permits fine-grained control of the entire system.

8 Future Work

Our current research qualitatively demonstrates some possible implications of resource availability on group decision making in primate groups. In future work we hope to extend this result through quantification of the relationship between resource availability and the quorum threshold. In addition, our results lead us to speculate that introducing further granularity in resource availability within the environmental model will increase agreement between observed and simulated results. In particular, we expect that more accurate modelling of resource availability within the Vlei habitat type will address the remaining discrepancies found in the agents' habitat utilisation.

In (Sellers et al, 2007) group cohesion is enforced such that group fission events, as recorded in (King et al, 2008) are precluded. Our re-implementation of the original model has been designed to allow investigation of more individually oriented models of group decision making. Such models would also provide opportunities to consider the effects of social and familial relationships upon the decision making process in primate groups.

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