Biorealistic Simulation of Baboon Foraging using Agent-Based Modelling

W. I. Sellers
University of Loughborough
Department of Human Sciences
Loughborough UK
W.I.Sellers@lboro.ac.uk

R. Hill
University of Durham
Department of Anthropology
Durham UK
r.a.hill@durham.ac.uk

B. Logan
University of Nottingham
School of Computer Science & IT
Nottingham UK
bsl@cs.nott.ac.uk

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 the De Hoop Nature Reserve in South Africa. We analyse the predictions of the model in terms of how well it was 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. The model predicts reasonable yearly average values for energy intake, time spent socialising and resting, and habitat utilisation, but is unable to account for month by month variation in the field data. However even at the current stage of model development we are able to show that, across a wide range of decision parameter values, the baboons are easily able to achieve energetic and social time requirements. This suggests that these particular animals are strongly influenced by other factors such as predation risk or thermal load in deciding their activity patterns.

1 Introduction

Agent-based modelling is a powerful tool for ecological modelling and is especially suitable for situations where individual strategy and planning may be important as is commonly assumed to be the case when considering primates. However for this technique to be useful it is necessary to confirm that the model is sufficiently complex to represent observed behaviour patterns and to identify the environmental and behavioural measures that need to be collected to (a) build a successful model and (b) validate the predictions of the model against experimental data. In this paper we consider these issues using a set of field data from a single troop of chacma baboons (Papio hamadryas ursinus) with associated environmental data collected at the De Hoop Nature Reserve in South Africa. We present an agent-based model designed to simulate the key activities of the troop and analysed its predictions in terms of how well it was able to duplicate the observed activity patterns of the animals and also in terms of the relationship between the parameters that control the agent's decision procedure and the model's predictions.

The construction of the model itself identified some key items of information that were missing from the field data that would need to be collected in subsequent fieldwork. The simulation results identified decisions concerning movement (group action selection) as having the greatest influence on the outcomes and whilst the model was able to produce reasonable estimates of yearly average outcomes, it was unable to produce month by month estimates suggesting that considerably more work needs to be done to successfully model baboon behaviour at this level of granularity. However the model was able to show that, across a wide range of decision parameter values, the baboons were easily able to achieve their targets in terms of food and social time in the vast majority of cases. This suggests that these particular animals are strongly influenced by other factors such as predation risk or thermal load in deciding their activity patterns.

The remainder of the paper is organised as follows. In section 2 we motivate our approach to agent-based modelling and our choice of group behaviour as the focus of this paper. In section 3 we briefly summarise the field data on which our model is based and in section 4 we outline our agent-based model and the decision procedure which the agents use to choose their activities. In section 5 we present the results of a Monte-Carlo sensitivity analysis of the parameters used in the agent's decision procedure. In section 6 we discuss the results and in section 7 we briefly outline some related work. In section 8 we conclude and outline directions for future work.

2 Agent-based modelling

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 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).

The outcome of this process depends on the set of desires and goals within the individual, its current internal state, an internal world model, and sensory information. This reliance on individual choice makes this technique especially useful when dealing with intelligent organisms 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]. The justification for this approach is that whilst 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. This means that such a model can 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.

Agent-based modelling has become a popular technique for modelling social and spatial interactions in humans and non-human primates: virtual worlds populated by decision-making agents have been used to investigate topics as diverse as primate social hierarchies [Hemelrijk, 2002] and Mesolithic hunter-gatherer behaviour [Mithen, 1994]. However 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.

No model can accurately predict all aspects of primate behaviour.[1] In this paper, 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. 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. A great deal of ecological theory has been generated to investigate grouping strategies and to identify the optimal group size given various ecological parameters [Cheney, 1987; Dunbar, 1996]. We focus on measures such as range size, daily travel distance, energy and time budgets, as these are good candidates for testing agent-based approaches: they have measurable numerical values

and so can be tested objectively, and they are highly dependent on the activities and choices of the individual within the population. Modern common 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 and Dunbar, 2002].

Our long term aim is a robust model of baboon behaviour which is valid across a wide range of habitats and baboon species (including extinct species). Our methodology is to first build a model that can successfully predict the behaviour of a particular group of baboons and then attempt to generalise, conserving the decision procedure while tailoring the decision parameters to a particular species or habitat type. The work reported in this paper is the first step in this process, namely the modelling of a particular group of baboons in a particular habitat.

3 Field Data

The model is based on data from De Hoop Nature Reserve in South Africa. De Hoop Nature Reserve (20°24′E, 34°27′S) is a coastal reserve within the Overberg region, in the Western Cape Province. 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. Vegetation is dominated by coastal fynbos, a unique and diverse vegetation type comprising Proteacae, Ericaceae, Restionaceae and geophyte species. Seven distinct habitat types were classified on the basis of vegetation structure within the home range of the baboons (Table 1: see [Hill, 1999]) for detailed descriptions and further information on the ecology of the reserve).

De Hoop has a mean annual rainfall of 428 mm, with a mean annual temperature of 17.0°C. Both rainfall and temperature show considerable seasonal variation and shade temperature in the summer months regularly exceeded 25°C. Due to its southerly latitude, De Hoop also experiences significant day length variation (from 9.8 to 14.2 hours) that has important implications for the behavioural ecology of this population [Hill et al., 2003].

Data were collected over a 7-month period (June to December 1997) from a single troop of chacma baboons (*Papio hamadryas ursinus*) 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 12-13 adult females sampled for a minimum of five full days each month. At each sample point, information was recorded on the iden-

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[1]Even if it could, it is unlikely that it would be useful, as one of the primary functions of a model is abstract the key features of the system of interest.

Habitat Type	Proportion of Range (%)	Bush Cover (%)	Tree Cover (%)	Food Availability	Shade Availability	Predation Risk
Acacia Woodland	15.8	55.8	34.4	High	Very high	High
Burnt Acacia Woodland	1.2	3.2	0.4	Low	Low	Intermediate
Burnt Fynbos	27.6	3.6	0.0	Low	Low	Intermediate
Climax Fynbos	25.7	54.0	3.4	Low	High	High
Grassland	11.0	1.6	1.2	Intermediate	Low	Low
Vlei	18.7	0.0	0.0	High	Very low	Low
Cliffs	0	—	—	Very low	Low	Very low

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

tity, 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].

4 Agent-Based Model

The model consists of two components: the environment model and the baboon model. The environment model was based on the 200 by 200 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 (primarily cliffs), and refuges. Each habitat type was characterised by a maximum food availability, energy intake rate when foraging and foraging on the move and replenishment rate, and these varied month by month. For reasons of space, we do not report the values in this paper, which can be found in [Hill, 1999]. The actions of the agents affect the environment: food consumed is depleted from the grid square containing the agent. Food consumed is replaced at the replenishment rate for current simulation month for each of the habitat type(s) occurring in the grid square. The energy value of the food available was estimated at $13.98\,\mathrm{kJg}^{-1}$ [Stacey, 1986]. The environment model is illustrated in the simulator's graphical output shown in Figure 1.

The baboon model models each baboon as an agent with physical parameters based on well-known baboon physiology. In addition, each agent maintains an individual score for thirst, energy and social time. These scores function as 'drives' or 'desires' in biasing the agent's choice of preferred activity at each timestep.

At each timestep, each agent can choose one of four actions corresponding to the activities recorded for the baboons at De Hoop: feeding, moving, socialising or resting. In addition, an agent can perform an instantaneous drinking action which can be combined any of the other activities (assuming the agent is in a cell which contains a water source). Each action has an associated energy cost. These were calculated using the formulae given in [Tucker, 1970] for an average adult female baboon with a body mass of 16.1 kg (the heavier males offset by the lighter infants and juveniles) and assuming that the
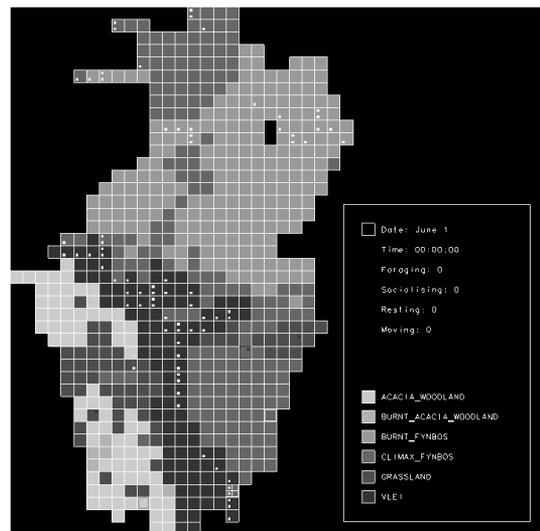

Figure 1: Graphical output from the simulator showing the habitat types and distributions.

baboons moved relatively slowly ($0.5\,\mathrm{ms}^{-1}$) since they customarily foraged whilst moving. Thus foraging uses 36.71 W; moving 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 treated as approximate. In addition to its energy cost, each action updates the appropriate scores. Feeding causes food to be depleted from the grid square containing the agent and increases the agent's energy score depending on the type of food consumed. The agents also forage while moving, which depletes food from the grid square at a lower, travel foraging, rate.[2] Socialising increases the agent's social time score by the length of the timestep. Drinking adds one to the agent's thirst score. Any action other than socialising causes the social score to decrease by the length of the timestep, and not drinking causes the agent's drinking score to decrease by the reciprocal of the timestep.

The agents have two hard constraints: they must return to a sleeping site to rest each night and they must drink (i.e., visit a grid square constraining a water source) at least once every 2 days. Otherwise they have 2 goals: to maintain their

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[2]In some habitats there is no food to be gained by foraging on the move.

energy balance (i.e., to eat sufficient food to make up for the energy expended each day) and to spend 2 hours a day in social activity. Each agent is equipped with a simple decision procedure designed to allow it to exploit the habitat subject to physiological constraints to achieve its goals. However the actions of each individual are constrained by actions selected by the other baboons in the manner explained below.

The model uses a fixed timestep of 5 minutes. At the end of each timestep each baboon chooses a preferred action to perform at the next timestep and whether it would prefer to move to allow it to perform the action more effectively. If the number of agents which vote to move is higher than a given threshold, V, then the whole group moves in the most commonly preferred direction. If the group does not move, agents which voted to move have the opportunity to choose an alternative action which can be performed in the current grid square. The agent then spends the next 5 minutes performing its chosen action and its scores in terms of energy balance, thirst and social time adjusted accordingly. Drinking is considered an instantaneous action that occurred whenever the agent occupied a grid square containing a water source.

The complete decision procedure can be summarised as follows:

```
Decision procedure:
    for each agent:
        if (!Automatic Action):
            Choose Preferred Action
            and Preferred Cell;
            if Preferred Cell != Current Cell:
                Vote to Move;

    if (Votes to Move / no. agents > V):
        for each agent:
            Move in the most commonly
            preferred direction;
    else:
        for each agent:
            Check Preferred Action;
            Perform Action;
```

`Automatic Actions` are the hard constraints (resting at night, drinking) which can preempt the choice of `Preferred Action` and `Preferred Cell`. For example, the requirement that the agents must return to a sleeping site to rest each night constrains the choice of `Preferred Cell` so that the agent can always reach a sleeping site in the time remaining before nightfall. If the `Automatic Action` step has not determined the agent's choice of action at this timestep, the agent's `Preferred Action` is determined using a weighted random function with weights proportional to the current desire to drink, forage and socialise. Desires are linear functions of the corresponding scores with gradients proportional to user defined relative importance values for each action: W_D (the relative importance of drinking), W_F (the relative importance of foraging), and W_S and 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 scores at zero, the agents will drink on average once per day, and socialise on average 2 hours per day.

Parameter	Min	Max
V	0.1	0.9
S	200	2200
W_F	1	10
W_S	1	10
W_D	1	10
T_F	1	3
T_S	1	3
T_R	1	3
T_K	0	0.25

Table 2: Key parameters in the decision procedures showing the ranges used in the Monte-Carlo sensitivity analysis.

The agent will `Vote to Move` if it can perform its desired action more effectively in one of the neighbouring cells. This is determined by evaluating all the grid squares within the search radius, S, of the agent's current location. For drinking it is assumed that the agent knows where the nearest water source is, irrespective of search radius. The agent will vote to move if the best grid square is more than a user defined threshold better than the current square. 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. The votes for all the agents are counted and the group will only move if more than V vote in favour of moving. If fewer than V agents opt to move, then the agents which preferred to move choose their most preferred action for the current cell at the `Check Preferred Action` stage. This is because it is impossible to drink if there is no water in the current cell and undesirable to socialise or rest if the predation risk is greater than T_K. Finally all agents either move in chosen direction or get to `Perform Action`, which is whatever non-move action was decided upon after the preferred action was checked.

The difficulty is that we do not currently have suitable values for the parameters used in the decision process. Some we may be able to estimate empirically with much more detailed field observations (especially factors to do with predation risk) however others are essentially unknowable. To overcome this we choose plausible ranges for each decision parameter and performed a Monte-Carlo sensitivity analysis [Campolongo *et al.*, 2000] where the simulation was repeated a large number of times and the values of the parameters randomly sampled from the range for each run. This allows us to both estimate the importance of a particular parameter on the outcome and to allow us to calculate the range of possible outcomes. The parameter ranges used in the analysis are shown in Table 2.

5 Results

The model was run 100,000 times sampling the decision parameters from Table 2 each time. Figure 2 (a) and (b) show the distribution of outcomes in terms of the goal states (daily energy intake and daily social time). These values are highly consistent between runs and almost always adequately high suggesting that almost no matter what combination of decision parameters we use the agents are able to achieve their

goals. However if we look at the match between the model's predicted outcome and the recorded monthly activity summaries from the field data we can see that there is a very large amount of variation in the model's predictions and not particularly good agreement with the field data. This is shown in Figure 3 where the predictions in terms of time spent in different activities are compared with the experimental data. Figure 4 which shows the time spent in different habitats shows a similar picture. In particular it shows that the baboons spent a great deal of time in the Burnt Fynbos in August (and to some extent in September). This is very hard to explain in terms of food availability and it is not surprising that it is not matched by the model. In terms of the whole year the model is much better able to match the observed findings. Figure 5 shows the mean daily activity pattern for the whole year. Figure 6 shows the occupancy rates for different habitat types which also show a similar pattern, although the in the simulation the time spent in Acacia Woodland is consistently less than that spent by the actual baboons. The Burnt Fynbos usage over the whole year matches the baboon data even though it cannot mimic the September peak.

The linear effects of the decision parameters were analysed using Stepwise Multiple Regression in SPSS. Table 3 shows the regression terms identified by this process. The clearest relationship is between the V parameter and the time spent moving. V also had a reasonably strong effect on the time spent foraging, the energy intake, and the time spent in Acacia Woodland. The time spent in Grassland is quite strongly influenced by the search radius, S. In no case does the second term add much to the overall relationship.

6   Discussion

The data show that the model is able to approximate the behaviour of the De Hoop baboon troop in general terms. However it is where the model and the real data differ that is most informative. It is commonly supposed that the requirement to obtain sufficient food is the key factor that produces primate movement. The energetic aspects of the model are probably its most reliable features: we have reasonably good data for daily food requirements and nutrition physiology. The fact that even this simple model is able to obtain sufficient food (there is no planning of optimal routes or intelligent choice of when to feed) suggests that it is actually relatively easy for these animals to obtain sufficient food and that there must be other drives that have a strong influence on movement. Hill and Lee [Hill and Lee, 1998] have suggested that predation risk may actually be the primary influence and this is one area where the current model is weak. The model contains no free-ranging predators and the predation risk is simplistically modelled based on visibility rather than any actual data on predation rates (such data is notoriously difficult to obtain). Other factors that might be important include the fact that, although energy is plentiful in the environment, particular nutritional components such as protein may be much rarer. This might explain the high usage of the otherwise undesirable Burnt Fynbos habitat in August and September, if the food items available there (mostly subterranean tubers and roots) contain specific, rare dietary elements. More detailed
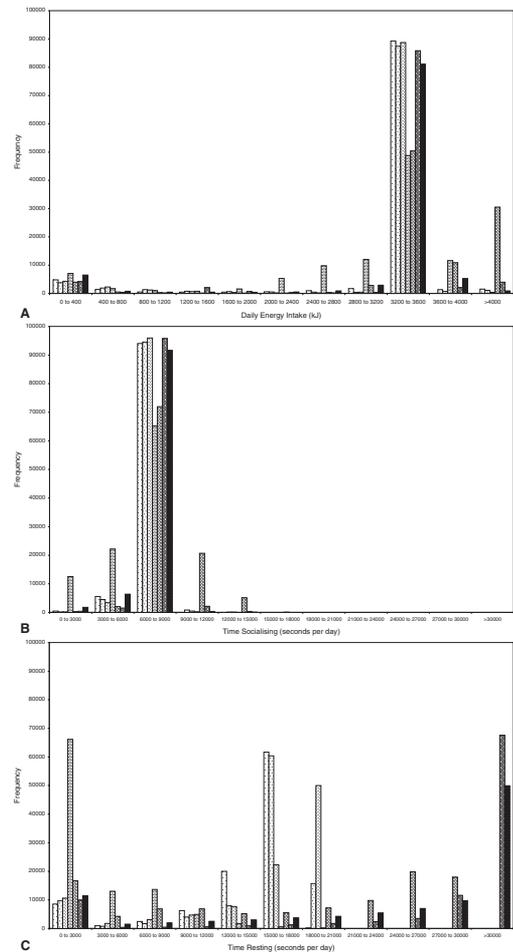

Figure 2: Frequency of the primary outcomes for 100,000 repeats of the simulation with the input parameters randomly sampled from the ranges in Table 2. (A) Daily energy intake (target approx. 3500 kJ depending on activity pattern); (B) Time spent socialising (target value is 7200 s); (C) Time spent resting.

experimental and observational data will be needed to answer this, and the dietary component of the model will need to become more complex accordingly.

The Monte-Carlo analysis revealed that the model has very little clear, linear dependence on any of the input parameters. The V parameter is involved only in the decisions to move and its influence it almost certainly entirely due to its strong effect on the time spent moving. This is one of the least realistic parts of the model since clearly baboons do not actually vote to move.[3] However they do always move in more or

[3]Conradt and Roper [Conradt and Roper, 2003] have shown that under certain assumptions, "democratic" decision-making results in lower costs to the group as a whole than "despotic" decision-making. They give as empirical examples of 'voting' behaviours the use of specific body postures, ritualised movements, and specific vocalisations, whereas 'counting votes' includes adding-up to a majority of cast votes, integration of voting signals until an intensity threshold is reached, and averaging over all votes. They cite anecdotal reports

Dependent Variable	Predictor 1	R square 1	Predictor 2	R square 2
Time Foraging	V	0.412	W_F	0.423
Time Resting	T_F	0.043	W_F	0.060
Time Moving	V	0.755	T_F	0.827
Time Socialising	W_F	0.018	V	0.028
Energy Intake	V	0.255	W_F	0.264
Acacia Woodland	V	0.368	T_F	0.490
Burnt Acacia Woodland	V	0.111	S	0.187
Burnt Fynbos	V	0.061	W_F	0.063
Climax Fynbos	V	0.063	W_D	0.069
Grassland	S	0.304	V	0.330
Vlei	V	0.054	S	0.064

Table 3: The first two terms of a linear stepwise regression using the Monte Carlo parameters as independent variables and the behavioural outcomes as the dependent variables using the combined 100,000 runs as the data source.
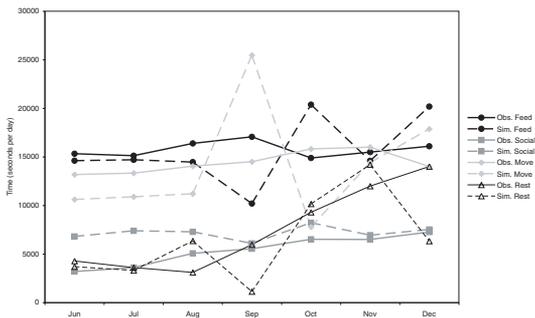

Figure 3: The daily duration of the 4 activities observed in the field and in the best matching run obtained in 100,000 repeats using randomly sampled decision parameters.
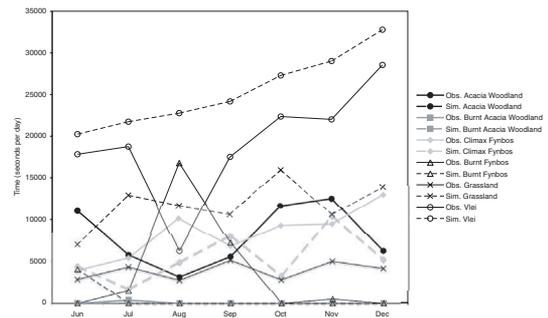

Figure 4: The daily amount of time each agent spends in a particular habitat observed in the field and in the best matching run obtained in 100,000 repeats using randomly sampled decision parameters.

less coherent groups (it is extremely hazardous to be a lone baboon) so some sort of coordination mechanism must be at work and this is one area where the model would benefit from elaboration. Large values of S reflect a better knowledge of the environment. Low values of S lead to more time being spent in grassland, suggesting that the agents are then failing to find better habitat in these cases.

7 Related Work

Agent and individual-based modelling is an increasingly popular approach to the study of primates. In this section we briefly review some of this work and sketch its relationship to the model described in this paper.

Robbins and Robbins [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. Hemelrijk [Hemelrijk, 2002] presents a model of primate social be-

haviour in which agents have two tendencies: to group and to perform dominance interactions. By varying group cohesion she shows that denser grouping can induce female dominance over males. Bryson and Flack [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 investigated the effect of a 'tolerance behaviour' on the amount of time spent grooming.

For want of better terminology, we can distinguish between individual-based and agent-based models. An *individual-based* model takes individuals as the basic unit and tracks them without the individuals interacting in a meaningful way. We reserve the term *agent-based* for models in which the individuals interact with an environment and/or each other.[4] For example, the model proposed by Robbins and Robbins is individual-based in that the gorillas don't 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 contrast the models by Hemelrijk and Bryson and Flack are agent-based in that they focus on the interaction

of voting behaviours in baboons where a simple majority determines changes in group activity based on movement, or a majority of adults or adult males decide on the direction of travel based on body orientation or position on a resting rock.

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[4]Note that this usage is not consistent with that in the literature generally or even the papers summarised in this section.
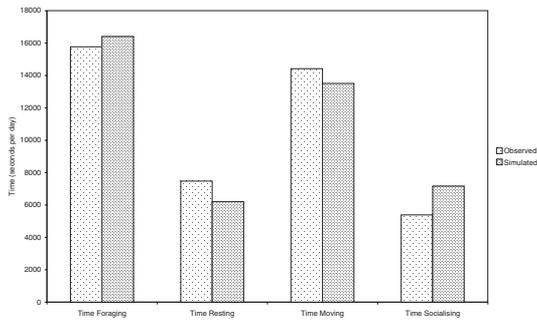
Figure 5: The daily duration of the 4 activities averaged over the seven month sample time observed in the field and in the best matching run obtained in 100,000 repeats using randomly sampled decision parameters.
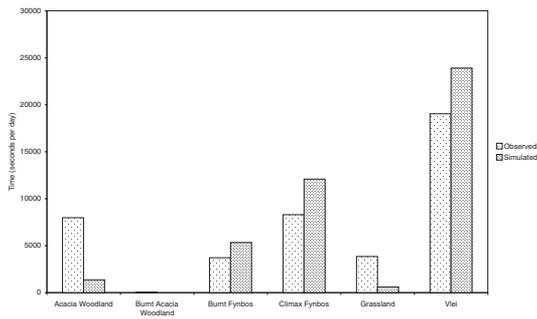

Figure 6: The daily amount of time each agent spends in a particular habitat averaged over the seven month sample time observed in the field and in the best matching run obtained in 100,000 repeats using randomly sampled decision parameters.

of the individuals in the simulation. In particular, both 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 an agent.

Our approach is intermediate between individual-based and agent-based: baboons are modelled as individuals which choose actions and interact with their environment based on their individual state, but their interactions with each other are limited to group level decisions, specifically whether to move, and the constraints this places on their individual choice of action. 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.

There is also a substantial body of work on joint action in AI, for example [Grosz and Sidner, 1990; Cohen and 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 ac-

tion which is performed by all agents but which only serves the interests of a subset. It seems unlikely that baboons have joint intentions, or the shared plans and models of teamwork necessary to achieve them.

8 Conclusion

This study shows the potential value of agent-based modelling in primatology. It clearly demonstrates that for this population factors other than food are important for ranging and the construction of the model identifies key areas where the available field data is missing and so is extremely useful for planning future studies. It also shows the non-linear nature of the problem and indicates useful ways that the model could be elaborated to investigate more complex issues such as predation and planning.

The fact that the model is able to match the yearly activity and occupancy profiles suggest that even a simple model is perfectly adequate to simulate primate behaviour recorded at this time scale. However it is clearly unable to match the detailed activity at even a monthly, let alone daily or hourly time scale, although the results presented here do suggest that this should be possible. There are a number of areas where additional detail could be beneficially added to the model. Firstly the incorporation of a full diet model may be absolutely necessary. This 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. Secondly since it seems likely that predation is a major driving force of primate ranging behaviour this would need to be incorporated specifically in the model. Fortunately this is precisely where agent-based modelling reveals its power and generality since the predators can be modelled as agents themselves. The difficulty here is that we know considerably less about the behaviours of any of the predator species than we do the prey animals, so that validation may be extremely difficult. Thirdly it seems likely that primates, and in particular baboons because of their larger than normal brains (for equivalent sized mammals) [Jerison, 1973], do have some sort of a mental map of their home range and do plan their daily activities to some extent. It is obviously almost impossible to know how a baboon might view the world but an agent-based model is an ideal way of investigating possible approaches and can certainly quantify the costs and benefits associated with various levels of planning.

It would also be interesting to explore the relationship between individual and group level action selection in more detail. It would be straightforward to extend our model 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). However it would be more interesting 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.

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