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Agent-based modelling as scientific method: a case study analysing primate social behaviour

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A scientific methodology in general should provide two things: first, a means of explanation and, second, a mechanism for improving that explanation. Agent-based modelling (ABM) is a method that facilitates exploring the collective effects of individual action selection. The explanatory force of the model is the extent to which an observed meta-level phenomenon can be accounted for by the behaviour of its micro-level actors. This article demonstrates that this methodology can be applied to the biological sciences; agent-based models, like any other scientific hypotheses, can be tested, critiqued, generalized or specified. We review the state of the art for ABM as a methodology for biology and then present a case study based on the most widely published agent-based model in the biological sciences: Hemelrijk's DomWorld, a model of primate social behaviour. Our analysis shows some significant discrepancies between this model and the behaviour of the macaques, the genus used for our analysis. We also demonstrate that the model is not fragile: its other results are still valid and can be extended to compensate for these problems. This robustness is a standard advantage of experiment-based artificial intelligence modelling techniques over analytic modelling.

Keywords: agent-based modelling; primate social behaviour; Hemelrijk; DomWorld; validation

1. INTRODUCTION

Agent-based modelling (ABM) is a method of testing the collective effects of individual action selection. More generally, ABM allows the examination of macro-level effects from micro-level behaviour. Science requires understanding how an observed characteristic of a system (e.g. a solid) can be accounted for by its components (e.g. molecules). In ABM, we build models of both the components and the environment in which they exist, and then observe whether the overall system-level behaviour of the model matches that of the target (or *subject*) system.

ABM is a sufficiently new technique that there is still some controversy in its use, and also some unevenness in its application and description in scientific papers. Most critically, there is not enough established methodological practice for incorporating modelling results into true scientific discourse. In this paper, we discuss ABM and the techniques for its analysis. We also present a case study in which we analyse, critique and extend the most extensively published ABM in biology: Hemelrijk's DomWorld (Hemelrijk 1999*a*,*b*, 2000, 2002*a*,*b*, 2004; Hemelrijk *et al.* 2003, 2005). DomWorld provides an explanation for systematic differences in social organization observed in closely related primate species. In this article, we focus on how well this model can be generalized to the genus *Macaca*.

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One contribution of 15 to a Theme Issue 'Modelling natural action selection'.

Section 2 reviews the current literature on analysing ABM and assesses how this applies to the specific case of modelling in the biological sciences. The background information necessary for understanding DomWorld is then provided: the literature describing the target system against which the model is tested (macaque social behaviour) as well as a thorough description of the model and its results. Section 5 describes our replication and analysis of DomWorld. Finally, we return to our earlier discussion of ABM as a scientific methodology, illustrating our points in the light of our analysis of DomWorld. We show that ABM is not a fragile analytic model, but rather a robust scientific hypothesis, open to critique, extension and circumscription.

2. ANALYSING AGENT-BASED MODELLING

In order for a methodology to be useful to science, it must provide two things: first, a means of explanation and, second, a mechanism for improving that explanation. The explanatory force of the model is the extent to which an observed meta-level phenomenon can be accounted for by the behaviour of its micro-level actors. Where models are running programs, they are tested by sampling their behaviour both over time and over a number of runs. Different experimental runs may use either the same parameters, in order to discover the range of possible results due only to the effects of random variation, or systematically varying parameter values, to test the significance of each parameter set or *condition*. The behaviour of the model system is then compared with that of the target system.

Axelrod (1985) founded ABM with his evolutionary simulations of cooperative behaviour (the first

publication being Axelrod & Hamilton 1981). He is still one of the area's main advocates as well as practitioners. In the appendix of a recent text on this topic, Axelrod & Testfatsion (2006) describe the following four research goals for the field.

— *Empirical*. 'Why have large-scale regularities evolved and persisted, even when there is little top-down control?'
— *Normative understanding*. 'How can agent-based models be used as laboratories for the discovery of good designs?'
— *Heuristic*. 'How can greater insight be attained about the fundamental causal mechanisms in social systems?'
— *Methodological advancement*. 'How [can we] best provide ABM researchers with the methods and tools they need to undertake the rigorous study of social systems… and to examine the compatibility of experimentally-generated theories with real-world data?'

The bulk of the present article focuses on the methodological question as applied to biology, which we believe essentially subsumes the heuristic question, at least with respect to ABM. The type of models we examine focus on empirical, not normative, problems. In this section, we primarily focus on the methodological issue of 'compatibility' between theory and data, which in the ABM literature is often called the problem of *validation*.

(a) *Validation and analytic solutions*

As ABM has become more prevalent in the social sciences and, particularly, in business and public policy, there has been an increasing emphasis on developing methods of verification and validation (Balci 1998; Kennedy *et al.* 2006). *Verification* is the process of making certain that a model runs as designed. In science, this is roughly equivalent to ensuring that good experimental practice has been followed. *Validation* is the process of making certain that the model actually models the target system. As we will argue more thoroughly in the following section, when ABM is used in biology, validation is equivalent to hypothesis testing. We will begin by discussing validation, and then return to verification.

There is a common perception that ABM is very complex (in the sense of having a large number of parameters), that it can be easily made to match any data or predict any outcome, but that having done so the system will have no capacity for generalization, and therefore no predictive power. In practice, however, building and debugging an agent-based model is a difficult skill, and matching datasets is not easy.

If a model is built to a set of justified assumptions, and *subsequently* matches a dataset with minimal adjustment, then it is generally considered to be at least partially validated. Of course, the more datasets it matches, the better validated the model becomes. As this notion of *better* validated implies, validation is not simply a state that either holds or does not for a model. Rather, like any other scientific hypothesis, the more the model becomes *probable*, the more it is validated,

but it never becomes perfectly certain (Box 1979). The only exception is when a model is understood to such an extent that it can be *proved* correct in a logical or formal analytic sense.

Many people view formal analytic models as preferable to ABM for this reason, but there are several reasons to prefer ABM. First, even formally correct models can be wrong if their premises or assumptions are incorrect (Bundy *et al.* 2005)—thus ABM with its more experimental approach can actually help *verify* a *valid* model. Second, ABM is sometimes more accessible or intuitive. Such models can consequently play an important role in scientific understanding, including *developing* a formal analytic understanding of a system by helping explore the space of possible solutions (Axtell 2000). And finally, there are large classes of dynamic systems that are not amenable to closed analytic solutions (Axelrod 1997; Axtell 2000). Particularly interesting to biologists are those involving the open-ended coevolution of multiple interdependent species.

Returning to the matter of verification, this issue is most nefarious in purely formal systems, where validation is not grounded on real-world data. Formal systems are used in mathematics and similar disciplines as a means of knowledge *discovery*, in which case verification is both more critical and more difficult. When validation is performed via hypothesis testing against real-world data, validation itself serves as a form of verification. To the extent a computational model reliably matches and predicts a target system's performance, then it *is* a model, in the formal sense.

Verification in this sort of scientific process is converted into an analogous but not identical process of *model understanding*. A part of this process can be simplifying or generalizing the model, or better determining the biological correlates of its components. This is true not only for ABM, but also for all sorts of formal modelling in biology. For example, Wynne (1998) provides a neat history of the development of ever-simpler models of transitive inference learning (see also Delius & Siemann 1998).

(b) *Agent-based models as scientific hypotheses*

For biology, there are only two important criteria for validation in ABM. These are the same as those for validating any behavioural model.

(i) Does the behaviour of the model match that of the target system within the standard metrics of hypothesis evaluation?
(ii) Do all the attributes of the agents and their environment have plausible biological correlates in the target system?

These 'standard metrics' depend largely on the success of previous explanatory efforts. If the literature contains no prior explanation or model, then it may be sufficient to show a qualitative similarity between the model and the target system. However, if there is another competing model, then we need to use standard statistical hypothesis testing to decide which will be the better match.

For the second criterion, the issue is whether the modeller has given the artificial agents any capacities that real subjects could not or arguably would not possess. For example, if we tried to explain the origin of theory of mind using artificial agents that actually had perfect access to each other's internal state, then we might have simply modelled the presumed end state of the system while providing no explanation for how that capacity came into existence. Note, however, that such a model might be useful if the true end state of the system was in doubt. For example, we might show that our 'perfect knowledge' theory-of-mind agents were actually less socially capable than the agents with imperfect knowledge. This might lead us to change some of our assumptions, e.g. from believing more-social agents must be more perceptive, to some other explanation, such as that more-social agents require a higher capacity for propagating social norms.

We recommend that the analysis of an agent-based model should be a three-phase process. The first phase is the *replication* of the ABM. This may not seem (or even be) strictly necessary if the model is publicly available—the results in that case can be checked just by rerunning the model on another computer. However, reimplementing the model from its description in the literature can be a valuable exercise, and may uncover important aspects of the model which the authors either took for granted, overlooked or even forgot about during the course of their research (King 1995; Axtell *et al.* 1996). As we mentioned earlier, an ABM may be valid without actually having been fully verified or understood. This is true of any scientific hypothesis; a part of the scientific method is improving the understanding of a theory as a community.

Once the critical attributes of the model are well understood, we can enter the second phase of ABM analysis, *model understanding*. Here, we carefully consider what the implied or the explicit correlates of those attributes are. Again just as in any other science, we go through a process of finding testable predictions and implications which result from our hypothesis. The third and final phase is *testing* these predictions and implications, looking first into the extant literature, and then (if necessary) proposing and executing new experiments.

Note that goodness of fit to data is not necessarily a sufficient metric for evaluating models. Computer science has shown that for large classes of computation there are an infinite number of mechanisms for achieving results that are all fundamentally equivalent (Turing 1936). In natural science, when we have two models that make equivalent predictions, we favour the simplest. Of course, when predictions are not precisely equivalent, trading off factors such as goodness of fit, simplicity and the capacity for generalization can actually be quite complicated (see further the literature on model selection, e.g. Myung *et al.* 2000).

In general, ABM tends to follow the principle of parsimony like any science. Complex individual behaviour is difficult to program, takes a long time to execute in simulation and is difficult to analyse. We may therefore have a strong bias towards looking for simple solutions. Our understanding of evolution

to some extent justifies the assumption that the simplest solution that achieves an adaptive purpose is most probable, because it is the most likely to be maintained genetically over time. Nevertheless, any bias, even where generally useful, can occasionally lead to problems.

3. PRIMATE SOCIETIES AND THE DOMWORLD MODEL

We now present a case study analysing DomWorld, a model which provides an explanation for the variety of social structures seen in different species of primates. We begin this study by providing background information on the data we intend to model.

(a) *Primate social structure*

Most primate species are highly social. They live in structured societies, and the structure of these societies is often characterized along a single axis. This axis is based primarily on social tolerance and conciliatory tendency. *Tolerance* is expressed when a dominant animal allows a subordinate to take advantage of a resource in its presence. *Reconciliation* is when animals that were involved in an aggressive interaction participate in affiliative behaviour (e.g. grooming or clasping) shortly after the incident. This appears to happen most frequently between animals that have strong affiliative relationships, such as kinship.

Tolerance is considered technically as one of the most basic forms of conflict resolution for a social species (de Waal & Luttrell 1989), though, of course, it 'resolves' the conflict by avoiding it in the first place. It might be difficult to see tolerance as an action to be selected, since tolerance may seem more like a form of *inaction*. However, if an agent is more inclined to preserve resources (including its own social rank), then expressing tolerance can require considerable inhibition of strong inclinations. In some species, this is achieved by the apparently deliberate averting of gaze in order to avoid witnessing a desired event. For example, a mother that desires to allow a juvenile throwing a tantrum to feed may look away from a particular morsel (de Waal 2000). This shift in visual attention is necessary if witnessing such an event would automatically trigger an emotional/species-typical response that would lead to conflict and prevent the completion of the feeding.

For the species at the low end of the tolerant/conciliatory axis, the vast majority of conflicts are unidirectional—that is, a subordinate makes no effort to retaliate against an attack by a dominant, and would almost never attack a dominant itself. Conflicts tend to be infrequent, but when they occur, high-intensity (e.g. biting) and conciliatory behaviour after the conflict is rare. On the other end of the spectrum, conflicts are both more frequent and bidirectional, the majority being met with protests or counter-attacks, but their aggressive intensity is typically low (e.g. vocalizations, slapping). In the most extremely conciliatory species, even unrelated participants reconcile after approximately 50% of conflicts (Thierry 2006). van Schaik (1989) refers to these two extremes as *despotic* for the low end and

egalitarian for the high. Although these terms are obviously anthropomorphic, they are well established and have a strong mnemonic value.

Thierry *et al.* (2004) propose that the macaques are a particularly good model genus for studying primate social organization (see also Thierry 1985; de Waal & Luttrell 1989; Preuschoft & van Schaik 2000). There are approximately 21 macaque species—the exact number depends on taxonomic dispute (Thierry *et al.* 2004)—all fairly closely genetically related. Thierry (2006) divides these species into four clusters on the tolerant/conciliatory axis. The familiar rhesus (*Macaca mulatta*) and Japanese (*Macaca fuscata*) macaques fall into the most despotic category. The stump-tailed macaques (*Macaca arctoides*) used by de Waal & Johanowicz (1993) in their well-known cross-rearing studies with rhesus are in the second-most egalitarian cluster, while the Tonkean (*Macaca tonkeana*) and crested (*Macaca nigra*) are in the most egalitarian cluster.

(b) *The DomWorld model*

The DomWorld model was originally based on the MIRROR agent-based model (Hogeweg & Hesper 1983; Hogeweg 1988), an ABM which among other things was used to model the emergence of party composition of chimpanzees and fission–fusion dynamics in primate societies in general (Te Boekhorst & Hogeweg 1994). The results of these older simulations were based on variables not seen in the basic DomWorld, such as food availability and the number of agents.

Hemelrijk was already a well-established primatologist when she published her first DomWorld paper in 1999 (Hemelrijk *et al.* 1992, 1999; Kummer *et al.* 1996; Hemelrijk 1999*b*). Although Hemelrijk (1999*b*) attributes DomWorld to Hogeweg (1988), Hemelrijk's paper appears to be the first full record of the dominance interactions. She also followed good methodological practice by reducing the complexity of the MIRROR model to its most essential components. Her later work reintroduced attributes such as food into the now better-understood system (Hemelrijk *et al.* 2003).

The only addition to DomWorld made between the 1999 and 2002 models this article focuses on is the addition of an 'attraction procedure' to the motion rules to simulate sexual attraction (Hemelrijk 2002*a*). We describe this addition in §4 on tumescence, not here as part of the basic model.

Describing the technical aspects of an agent-based model requires the description of the following three attributes: the environment, the agents' state and the agents' behaviour.

(i) *The DomWorld environment*

The DomWorld environment is flat and undifferentiated. On a computer screen, it looks like a square; however, the top and bottom edges of the screen are contiguous. That is, if an agent goes off the top of the environment, it will reappear at the bottom. Similarly, the left and right edges are connected. Consequently, the world is said to be a *torus* since building such a world in reality would require a doughnut shape. This is a standard simplifying assumption for abstract behaviour models (e.g. Laver & Schilperoord 2007), though models concerned with realistic environmental behaviour (such as Sellers *et al.* 2007) work with more realistic maps.

The DomWorld environment is typically populated by eight agents—four males and four females. The world is large enough (given the agents' visual range) that agents could in theory become 'lost' out of view of the troop. One task for their intelligence is to ensure that this does not happen (see §3*b*(iii)). The agents in DomWorld do not eat, die or reproduce. They only wait, move around and occasionally perform dominance interactions.

(ii) *DomWorld agents*

Agents have a set of characteristics or parameters that describe their individual differences. Some of these parameters are fully dynamic; that is, they change during an individual run. The *dynamic parameters* for each agent in DomWorld are as follows.

— Their x and y positions on the two-dimensional surface.
— Their *Dom* value. This determines the agent's dominance rank. Its initial value is determined by the sex of the agent, but it changes as a result of dominance interactions.
— A *waiting period*. When an agent stops moving, it will resolve to sit still for a brief random amount of time. This models foraging or resting in the wild. This period is shortened if there is a nearby dominance interaction (cf. Galef 1988).

Some parameters are determined per run of the experiment and therefore remain fixed over the course of that run. In DomWorld, these *run-dependent parameters* are as follows.

— The *sex* of each agent.
— Each agent's *StepDom*, which describes the level or intensity of aggression. This is species and sex specific: values are much higher for despotic than for egalitarian conditions and slightly higher for males than females.

Some parameters of an agent are set by the experimenter in the course of developing the system into something that is a reasonable model of the target system. Once determined by the modeller, these values are not changed at all over the course of the experiment. In DomWorld, these *static parameters* are as follows.

— The *field of view*: an angle that determines how much an agent sees around its direction of motion (the agents always look straight ahead).
— The *max view*: the furthest they can see.
— The *near view*: a distance within which the agents feel comfortably in the troop.
— The *personal space*: the minimum distance two agents can have between each other without engaging in a dominance interaction.

(iii) *DomWorld agent behaviour*

The basic motion dynamics of DomWorld are similar to Reynolds' (1987) boids. Coherence is provided by the fact that if an agent is more than near view away from the nearest agent it sees, it will move towards that agent. If an agent cannot see any other agent, it will rotate until it does. Separation is maintained by the fact that whenever two agents come within personal space of each other, they tend to engage in a dominance interaction (see below). The result of the interaction is that one agent will chase the other away from their joint location. There is no correlate in DomWorld of Reynolds' alignment; consequently, the troop as a whole does not move quickly or in any persistent direction. The DomWorld troop wanders randomly rather than flocking.

When an agent sees another within its personal space, it engages in an agonistic social interaction. As mentioned earlier, each agent has a certain dominance rank value, *Dom*, which is adjusted after any 'fight' involving that agent. This variable determines both the agent's rank and its probability of winning an interaction. The first step of the interaction is a 'mental battle' in which the acting agent compares its own *Dom* value with that of the other agent it has seen. If its own value is higher than or equal to the other's, the agent begins a full-scale dominance interaction. If not, the active agent will stay put. Owing to the limits provided by the field of view, it is possible that the dominant agent will move off from its current personal space without even 'seeing' the nearby subordinate agent.

The outcome of a dominance interaction is calculated with the following formula (from Hemelrijk 2002*a*, p. 734):

$$w_i = \begin{cases} 1 & \dfrac{Dom_i}{Dom_i + Dom_j} > Random(0,1) \\ 0 & otherwise, \end{cases} \qquad (3.1)$$

where Random (0,1) produces a random real value between 0 and 1.

In this calculation, w_i represents whether agent i has lost or won. Here, 1 means victory and 0 defeat. The relative dominance value between the two agents is compared with a randomly drawn number between 0 and 1. If the relative dominance is greater than the drawn number, the agent wins. This means that the higher an agent's rank is relative to its opponent, the more likely the agent is to win, while two similarly ranked agents each have an even chance of winning.

After a dominance interaction, the dominance values of both the agents are adjusted according to the interaction's outcome, using roughly the same information,

$$Dom_i = Dom_i + \left[w_i - \dfrac{Dom_i}{Dom_i + Dom_j} \right] StepDom$$

$$Dom_j = Dom_j - \left[w_i - \dfrac{Dom_i}{Dom_i + Dom_j} \right] StepDom \qquad (3.2)$$

The only exception to equations (3.2) is that the lowest possible *Dom* value is fixed at 0.01, keeping all the *Dom* values positive.

Hemelrijk calls this mechanism of determining dominance values a *damped positive feedback system*. For example, in the case of winning the dominance value of the higher ranking agent increases only slightly, but if the lower ranking agent wins, its dominance value undergoes a great change. For both the agents, the *Dom* is not changed much by an expected outcome, but it changes greatly for an unexpected one. The generally self-reinforcing nature of a positive reinforcement system has been shown empirically in many animal species (Hemelrijk 2000). However, if the *StepDom* is set high enough, significant changes in ranking can result from the unexpected outcomes.

The final step of a dominance interaction is a change in physical position. The winner moves slightly towards the loser, 'chasing' it, while the loser turns in a direction roughly opposite to that of the agent and 'runs' twice as far as it is chased. There is a small variation added to the angle the loser turns to reduce the probability that the two agents will meet again in the immediate future.

(c) *DomWorld results*

The contributions of DomWorld, reviewed by Hemelrijk (2004), can be summarized as follows.

(i) *Gradients of dominance hierarchy*

The primary result is a model of the difference in 'gradients' of dominance hierarchy. Hemelrijk proposes that having a larger difference between *Dom* values among a troop is equivalent to the troop being more despotic, whereas more similar values correspond to egalitarianism. Her hypothesis is essentially that there is no qualitative difference in how primates in an egalitarian society treat their superiors versus how those in a despotic one do, but rather that every individual will show an equal amount of respect for a troop-mate with twice its absolute (real-valued) dominance.

The main metric Hemelrijk uses for assessing this is the *coefficient of variation of dominance values*. This coefficient indicates the average variation between dominance ranks of the individuals in the troop. A large coefficient indicates despotism, a small one egalitarianism.

In DomWorld, the differences in position along the tolerant/conciliatory axis are accounted for entirely by the intensity of aggression. Aggression is modelled using *StepDom* (Hemelrijk 2002*a*). The principle result then is that high levels of *StepDom* lead to greater variations in *Dom* within the troop (figure 3). Note that this 'aggression' intensity value, *StepDom*, has no direct impact on whether a dominance interaction occurs or who wins it (see equation (3.1)). Rather, its only direct impact is on the adjustment to *Dom* *after* the fight, although this *StepDom* does have an indirect impact on future fight probabilities and outcomes.

(ii) *Troop spatial structure*

Another key result from DomWorld is the replication of the spatial organization of real troops. Macaque troops have been observed to have dominant individuals primarily in the centre of the troop (e.g. Hall & Fedigar 1997). Although this organization might be seen as a cognitive strategy, the dynamics of the DomWorld

motion behaviour already described produce this phenomenon with no additional cognition or search by the agents. The critical metric here is *centrality*, which is the sum of the unit vectors (that is a vector with a direction but only a fixed length) from an agent to every other agent in the troop. The shorter this summed vector, the more the directions of the other troop members cancel each other, and thus the more central the agent is.

In mentioning cognition, we do not mean to set up a false dichotomy between human-level awareness and simple reflexive response. The term *cognitive* is not well defined, and is applied to a large range of possible capacities. The most fundamental of these are mental representation of state not currently present in the environment, and mental search across alternatives (either of actions or of explanations/perceptions). Neither 'representation' nor 'search' in this context needs to be deliberate or even conscious. The significance of this result is that the agents need not have even an implicit model or perception of the centre of the troop. This is what we mean when we refer to the DomWorld centrality effect as the result of a 'non-cognitive' mechanism.

Centrality is not the main focus of this article's analysis, but it is a substantial result for DomWorld, and we will return to it while discussing the extension of this model in §5*d*.

(iii) *Sexual attraction and tumescence*
Finally, Hemelrijk (2004) reviews her work on the impact of sexual attraction. This was a later addition to DomWorld and requires further elaboration of the model, which is discussed in §4.

4. MODELLING BEHAVIOUR DURING TUMESCENCE

In most primate societies, males are more dominant than females. This is probably due to differences in body size and physical strength. Generally speaking, in a primate society, dominant animals have priority access to any desirable resources. This changes during females' receptive periods (i.e. when they are capable of reproduction). During these periods, females of most primate species develop genital swellings as an obvious physical signal. This is called *tumescence*. During tumescence, females are often the benefactors of special privileges, for example priority access to food, in apparent exchange for copulation opportunities (Yerkes 1940). This is frequently seen as a cognitive strategy by males, with the assumption that apparently altruistic acts directed towards receptive females lead not only to satisfying the males' reproductive drive but also to an increase in their total number of offspring (Goodall 1986; de Waal & Luttrell 1989; Stanford 1996).

Similar to the earlier discussion of centrality, one can easily construct cognitive explanations for male behaviour of extending preferential treatment to tumescent females. Although few would expect the males to be aware of the actual potential to propagate, some might imagine that the males *are* aware that the females exercise some extent of control over sexual access to themselves, and that the males may be particularly

motivated to achieve that sexual access when they see the signals of tumescence. Males might also be aware that certain behaviours are more likely to win access, and deliberately choose to perform those behaviours.

Hemelrijk proposed a much simpler explanation (Hemelrijk 2002*a*; Hemelrijk *et al.* 2003). She starts from a highly parsimonious theory that the only real difference in the animals' action selection is the apparent one—that at this time of the month, males are more likely to approach females. Owing to the dynamics of dominance interactions (as displayed in DomWorld), this leads to more fights between males and females, which in turn leads to a greater number of low-probability events, such as a female winning a fight against a higher-ranking male. Owing to the dynamics of equations (3.2), this can in turn lead to a female who has won several unexpected victories to outranking at least some males. In this case, the apparent shift in behaviour, where males are tolerating female access to resources, is in fact simply the normal respect a subordinate shows a dominant.

Yerkes (1940) himself first suggested that female chimpanzees may become dominant to males at this time. Hemelrijk's model is further supported by the results of her own field research. Hemelrijk *et al.* (1992), studying a captive population of chimpanzees, report no statistical evidence for exchanges for food during periods of tumescence. Hemelrijk *et al.* (1999), using DNA evidence on the same population, report that the males that do increase the amount of time they spend grooming females when they are tumescent have no better reproductive success than those that do not. Given these results, it may be reasonable to believe that there are no actual exchanges being made, intentional or not.

To model this theory, the only modification necessary to the standard DomWorld is the addition of one run-dependent parameter, *attraction*. The behaviour algorithm is modified such that when attraction is *on*, males move towards females when they are within the near view. The increased fighting that results from this attraction can indeed in some conditions lead to an increased number of females with high rank (see full results in §5*a*(i)). When a tumescent female does come to outrank a male, the males are still attracted towards the females, but then sit still once they have entered the dominant female's personal space, since she now outranks them.

5. THE ANALYSIS OF HEMELRIJK (2002*a*)

Critics of ABM are often sceptical that such simple models can have any explanatory value for real systems. People who work closely with apes feel that it is 'obvious' that the animals have substantial cognitive capacity, or at least that when humans express very similar behaviour, they subsequently report having had cognitive state. But human behaviour has also been replicated with relatively simple models (Cederman 2003; Laver 2005). On the other hand, science is biased towards looking for simplicity, not only as a matter of principle but also as a matter of practicality. Simple explanations are attractively easy to communicate and understand. Guarding against this bias for

overly simple explanations is just as important as guarding against its opposite.

We decided to evaluate DomWorld as a general explanation for the despotic/egalitarian continuum in primate behaviour. As reviewed earlier, this continuum is best documented in the genus *Macaca*. It has been proposed that this genus should serve as a model (in the biological sense) for primate social organization in general (Thierry *et al.* 2004). Therefore, we use this genus in our analysis.

Following §2, our approach to analysing this model consists of three phases. The first phase is the replication of the DomWorld experiments. This replication allows us not only to confirm their results but also to determine which aspects of the model are critical to its performance. The second phase of our analysis is to consider the correlations between these critical aspects of the model's agents and real primates (in this case, macaques), and thus make a series of predictions based on the consequences of the model. The third phase is to test these predictions against the primate social behaviour literature. The third phase *could* involve gathering more data in the field, but in this case it proves unnecessary as key questions derived in our second phase can be answered from extant studies.

(a) Replication

The original DomWorld was implemented in OBJECT PASCAL and BORLAND PASCAL v. 7.0 by Hemelrijk (2002a) and to date has not been made publicly available. We implemented our version in NETLOGO (Wilensky 2005). As a purpose-built modelling tool, NETLOGO provides a relatively easy high-level language for quickly constructing models and visualizing results.

We matched our parameter settings with those specified by Hemelrijk (1999a, 2000). The world's size was 200×200 units (note that time and space units here are abstractions—their exact value is not important as long as the relative proportions between parameters are maintained). Agents have real-valued (continuous) locations and can move in any of 360 (discrete) directions. Each agent can 'see' what is in its forward vision angle (field of view) of 120°—that is, it can attend to agents that are 60° to either side of its direction of forward motion—and within a maximum perception range (max view) of 50 units. When an experimental run starts, the agents are initially set at random locations within a 30×30 unit parcel of this space. Consequently, at the beginning of a run, each agent can find another by simply rotating. If an agent cannot see others, it rotates 90° and looks again. Because near view is only 24 units and the waiting period is never very long (see below), the property of never being more than max view from at least another troop member is maintained throughout the simulation. Occasionally, the troop splits, but the agents always reunite shortly thereafter.

Also at the beginning of a run, the waiting period for each agent is set independently to a random value between 0 and 10. For each program cycle, if an agent's waiting period is 0 the agent acts during that time unit, otherwise it reduces its waiting period by 1. If an

interaction happens within an agent's near view, the agent also reduces its waiting period by 1. Once an agent has acted, its waiting period is again set to Random(0, 10).

Each run of the simulation is given 32 000 time units. Hemelrijk specified 160 epochs of 200 activations each. We have slightly simplified this to be easier to implement in a standard, general-purpose ABM tool. The result is that our runs are a bit longer, but our dynamics appear to be identical (see §5a(i)). Hemelrijk specified that data points are taken at the end of each of the 160 epochs; hence, for the replication results in §5a(i), we also took data points every 200 time units.

With respect to the motion dynamics of the interactions, personal space in this model is set to 2 units. The fleeing distance is also 2 units and the pursuit distance 1 unit. Because interactions generally occur as soon as an agent is within personal space of another, this net increase in distance of 1 unit is generally but not always sufficient to move the loser out of the interaction range of the winner, particularly because the loser is probably now moving in a slightly different direction. The fleeing direction includes a random factor evenly drawn from between 0 and 45°.

With respect to the dominance dynamics of the interactions, *Dom* values of females are initially half those of males (females = 8 and males = 16). Also, females have only 80% of the 'aggressive intensity' (*StepDom*) of males. For experiments on despotic species, the *StepDom* values of males and females were 1.0 and 0.8, and for egalitarian runs, 0.10 and 0.08, respectively.

In our experience, the model does not appear overly sensitive to most of the parameter values, although at the same time none of them can be eliminated and still maintain the action-selection model. However, the model *is* sensitive to changes in the length of the waiting period. This may be because constant dominance interactions not only look unnatural but also make the troop so chaotic that spatial measurements of troop coherence and rank become less meaningful.

(i) Results

Our experiments were run in the same four conditions specified by Hemelrijk (2002a). For each of the despotic and egalitarian cases, 10 runs were made under each of two conditions of *sexual attraction*, where either there was none (a replication of the basic DomWorld) or all the males were attracted to all the females (the tumescent case). The total number of runs was therefore 40. Our results match with Hemelrijk's results to the extent that we used the same analysis, which we largely did in order to test the replication.

To match Hemelrijk's figures, we show typical individual exemplar results, rather than averaging over the 10 runs. Figure 1 replicates Hemelrijk's (2002a, p. 739) fig. 3A. It shows (over time in each of the four conditions) the sum over all females of the number of males which rank below that female. For example, if two females each outrank two males, one outranks one male and the other outranks no males, this value would be 5. We can see, as reported by Hemelrijk, that the female dominance in conditions
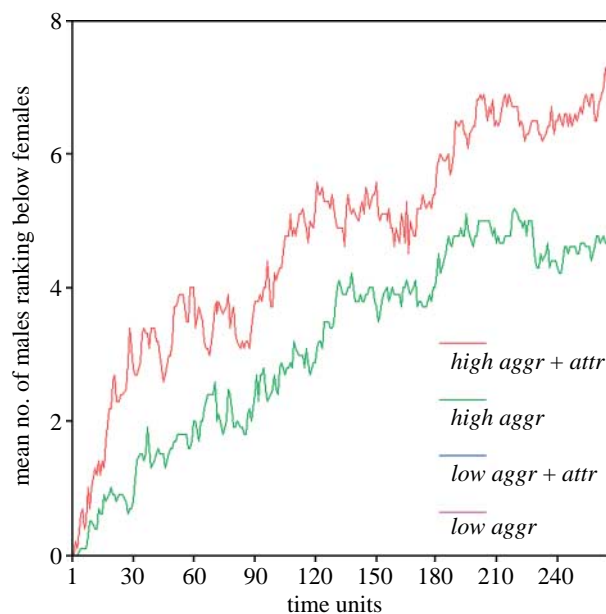
Figure 1. The dominance of females as shown from the sum of the number of males ranked below each female at different times under different conditions. Note that the egalitarian (*low aggr*) conditions are not visible because they are equivalent to the *x*-axis (i.e. constantly 0). *high aggr+attr*, despotic and tumescent; *high aggr*, despotic with no tumescence; *low aggr+attr*, egalitarian and tumescent; *aggr low*, egalitarian with no tumescence; aggr, aggression; attr, attraction.

with high *StepDom* increases over time, but stays constant in the egalitarian conditions with a low *StepDom*.

Figure 2 shows the classic DomWorld result concerning Hemelrijk's explanation of despotic and egalitarian species. In Hemelrijk (2002*a*), it replicates fig. 4*A* (p. 741). The figure shows the distribution of the coefficient of variation of dominance values for both the sexes (see discussion in §3). If *StepDom* is high, the difference between *Dom* values will be larger. By Hemelrijk's account, this models higher aggression leading to a despotic-style social structure. Sexual attraction amplifies this result, despite the fact that some females may outrank some males in this condition.

Figure 3 shows the change of dominance values for both the sexes under conditions with high and low levels of aggression. Again, here we have typical instances from single runs. In each figure, all four males initially have a *Dom* value of 16, while the four females have an initial *Dom* value of 8. Figure 3a corresponds to fig. 4*B* in Hemelrijk (2002*a*, p. 741). With high *StepDom*, the dominance structure is enormously dynamic, with an increasing coefficient of variation for each sex. Figure 3*b* corresponds to fig. 4*C* in Hemelrijk (2002*a*, p. 741). With a low *StepDom*, there is very little change in the dominance values. This creates a relatively stable hierarchy where the females never gain higher positions in the troop.

Figure 4 has no equivalent in Hemelrijk (2002*a*), but shows data derived from our replication, which is significant to our analysis (§5*b*). In this figure, the total number of aggressive interactions initiated by virtual females is compared for all four different conditions
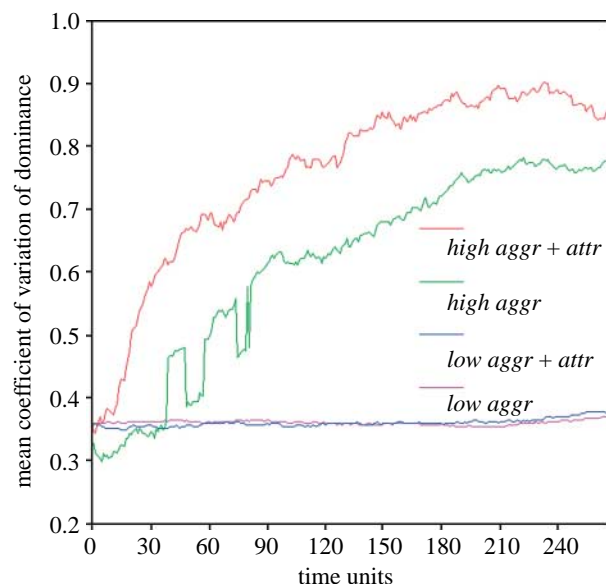
Figure 2. Distribution of the *coefficient of variation* of dominance values under different conditions for both the sexes. The definitions are the same as given in figure legend 1.
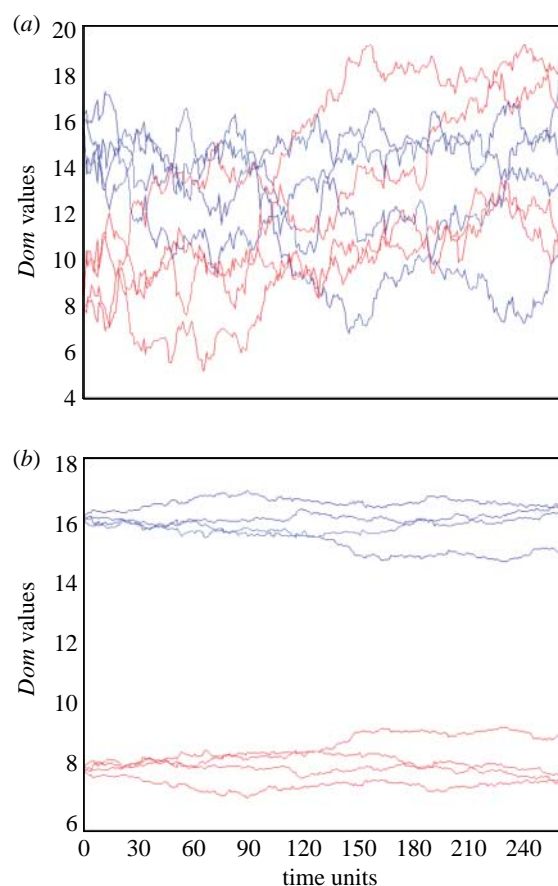

Figure 3. Distribution of *Dom* values at a (*a*) high and (*b*) low level of *StepDom*. In both the conditions, the males (blue) have initially twice the *Dom* value of the females (red).

used in the experiment, and averaged across all the 10 runs in each condition. We can see that the number of virtual female dominance interactions increases significantly in conditions with sexual attraction in both intensities of aggression (low: Mann–Whitney, $N = 10$, $U = 0$, $p < 0.001$, two tailed; high: Mann–
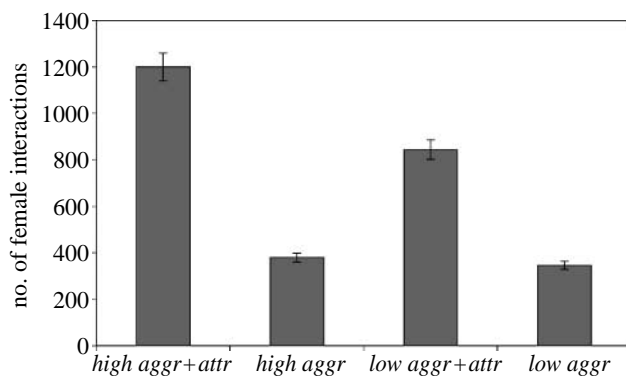
Figure 4. Total number of female interactions under different conditions. The definitions are the same as given in figure legend 1.

Whitney, $N = 10$, $U = 0$, $p < 0.001$, two tailed). This means that females are involved in considerably more interactions when they are attractive. The *StepDom* level also amplifies the result, though this effect is rather weak (Mann–Whitney U-test, $N = 10$, $U = 24$ $p < 0.049$, two tailed).

(b) *Analysis of model correlates*

Having successfully replicated DomWorld and achieved a good understanding of its components and their dynamics, the next phase of our analysis is to consider what the natural analogues of those components and behaviours are, and what they imply, explain or predict about real primate behaviour. For example, the most basic model results show that only in groups with a high *StepDom* are females able to gain higher *Dom* values than males. Sexual attraction amplifies this effect, but plays a secondary role. Hemelrijk uses *StepDom* to model intensity of aggression and *Dom* to model dominance rank. If we examine real animals substituting these terms into the results, will the results hold?

As described in §2, the second phase of the analysis should consist of considering the correspondences assumed by the model, and compiling from these and the model itself a list of testable claims. We have compiled a list of questions based on the model but rephrased in primatological terms, which are as follows.

(i) If one agent defeats another that vastly outranks it in a dominance interaction, does this have more impact on its rank than if it defeats a near peer? In other words, is a more unexpected outcome from a fight likely to have a more significant effect? If this is true, it would validate the use of relative dominance values in equation (3.2).

(ii) Within species, if a fight is more violent (e.g. if blood is drawn compared to mild beating, or if there is mild beating compared to a non-physical interaction), does it have more impact on the dominance hierarchy? If this is so, then we can rightly refer to *StepDom* as 'intensity of aggression' (since the level of aggression would determine the increment of *Dom*) and it would further validate its use in equation (3.2).

(iii) Are females more likely to engage in fights when they are tumescent? If not, this model cannot account for their increased tolerance during that period (figure 4).

(iv) Do females only become dominant during their tumescence in despotic species? Given that the prime indication in Hemelrijk's model of increased dominance for the females is the males' increased tolerance of them, discriminating an increase in rank in an egalitarian species may be difficult, since these species are definitionally more tolerant towards all group members. However, if there is any increase in favouritism towards egalitarian females, this model does not account for it.

(v) When an animal in an egalitarian species is *clearly* outranked by another animal, are those two animals' interactions similar to two more nearly ranked animals in a less egalitarian species? Or is there a qualitative difference in how different species behave with respect to dominance hierarchies? The answer to this question will serve to validate whether the coefficient of variance is a good indicator of location along the tolerance/conciliation axis—is it sufficient to discriminate an egalitarian from a despotic species?

Each of these questions seeks to validate or invalidate some part of the DomWorld model. When we framed these questions, we could not be certain what data would be easy or hard to come by, therefore some of these questions test the same parts of the model but in different ways.

Of course, we realize these questions may sound naive in one important respect. Establishing a dominance hierarchy is never easy, particularly in egalitarian species (Flack & de Waal 2004). It is not clear that every animal will agree on the current hierarchy, and indeed some animals will behave differently with respect to others depending on what other animals are present (Harcourt 1992) or how strongly motivated they are by a particular resource. However, we attempted to frame our questions broadly enough that at least some of them could be answered from accessible data.

(c) *Evaluating the model*

When answering questions of the sort just posed, there are two obvious possible outcomes: either existing data may answer a question decisively or, if there is not sufficient existing data, the question may motivate a new field study. However, at least three of the questions fall into a third category. Existing data are not sufficient to answer the questions conclusively, but this is not because insufficient studies have been run. Rather, the type of social events over which the predictions are made are so rare in real animals that no statistically significant comparison can be performed. Thus, a question that appears to be well posed from the perspective of the model is not answerable. However, the discrepancy between the model and the target system that leads to the problematic question is itself data to be taken into account when evaluating the model. Pragmatically, however, if a non-domain expert

modeller uncovers this sort of problem through querying domain experts or studying the literature, the results must be treated with care. One must be certain that the apparent lack of correspondence is not in fact a failure of communication.

Question (i) in §5*b* is an example of this third category. In despotic macaque species, unexpected outcomes are so rare that there can be no statistically significant results concerning them. Despotic conflicts are almost always unilateral, from a dominant to a subordinate. To obtain a statistically significant result, either for or against the model, we would need to see a reasonable number of subordinate animals becoming superordinate as a result of unlikely 'wins' in dominance interactions, and then determine how the rate of their ascension correlates with their number of improbable outcomes. However, in macaques at least, changes in dominance ranking are very infrequent. Most variation comes as a consequence of ageing (both juveniles becoming stronger and aged adults becoming weaker) or new arrivals in a troop. In both these rare cases, dominance rank change tends to be gradual, with the formerly subordinate animals normally challenging troop members nearest their own rank, working gradually up the hierarchy. Thus, the unlikely outcomes that drive the volatility in ranks in the model would almost never occur in nature.

If we consider the situation of DomWorld as shown in figure 3*b*, there are four females with an average *Dom* of approximately 8 and four males with an average of approximately 16. A very average male and female might be expected to be separated by three or four individuals (the high-ranking females and low-ranking males), yet if they engage in a dominance interaction, the female would have a one-in-three, $8/(8+16)$, chance of defeating an agent very much its superior. This high number of 'improbable' outcomes is what creates the dynamicism of the ranking system in DomWorld. The difference between the two conditions, despotic and egalitarian, is a direct consequence of a larger multiplier (*StepDom*) exaggerating the effects of these outcomes.

The fact that dominance order for adult macaques almost never changes makes question (ii), in §5*b*, equally difficult to answer, at least from observations of captive troops. It further calls into doubt the plausibility of results such as those shown in figure 3*a*, and thus in figure 2. The large and widening coefficient of variation comes not from an increasing and well-delineated order in the dominance ranking of the despotic species, but rather from high-gain random fluctuations. These problems call into question the DomWorld account of *Dom* values and therefore its explanation of the difference between despotic and egalitarian social orders.

One question that *can* be answered is question (iii) in §5*b*. Aujard *et al.* (1998) show that egalitarian macaque females in tumescence are involved in, if anything, *fewer* agonistic interactions, not more. Aujard *et al.* (1998) document a large range of behaviours with respect to the female reproductive cycle. Social grooming and 'affiliative interactions' with males all peak at or just before tumescence. For conflict/agonistic interactions, there is no significant change but a downward trend

throughout this period, followed by a sharp increase several days *after* tumescence (Aujard *et al.* 1998, particularly fig. 2, p. 293, and discussion therein). This work was done with semi-free-ranging Tonkeans, one of the species that Thierry (2006) puts in the most egalitarian cluster.

As we showed in figure 4, the Hemelrijk (2002*a*) model of female preference predicts increased fighting for both egalitarian and despotic females. Further, DomWorld results indicate that there should be no increase in preferential treatment of females of egalitarian species. Thus, the above results counter not only our question (iii), but also the basic hypothesis that preferential behaviour towards females can be explained in this manner, at least in macaques.

On the other hand, Eaton *et al.* (1980) document an increase in dyadic inter-sex and male-on-male violence in a similarly semi-free-ranging troop of Japanese macaques (*M. fuscata*) during their breeding season. Thierry (2006) assigns *M. fuscata* to the most highly despotic category. There is, however, a significant downturn of aggression by either females on females or groups on females during this period, though there is an increase in violence of groups on males. Because this study does not include hormonal analysis, it is difficult to be certain whether this violence is occurring during the fertile period of individual animals or shortly after, as was reported by Aujard *et al.* (1998). Also, this species does not technically experience a period of tumescence—the female's fertility in Japanese macaques is not signalled by genital swelling. Nevertheless, if the level of violence *does* increase in periods of tumescence but only in despotic species, then this is further evidence that DomWorld is not a sufficient model of the difference between egalitarian and despotic species. If on the other hand, increase in the despotic species' violence occurs after the females are no longer fertile, as it does in the egalitarian Tonkeans, then the results for the despotic agents shown in figure 4 are also invalid.

Aujard *et al.*'s (1998) data for the egalitarian Tonkeans also have a bearing on question (iv). While Aujard *et al.* (1998) do not specifically document tolerance of food access, the significant increases in affiliative behaviour *other* than (as well as) grooming and sexual behaviour does seem an indication of the sort of favouritism the Hemelrijk (2002*a*) extension of DomWorld is intended to explain. There is another problem with the question of female dominance rising in despotic species: other than the behaviours Hemelrijk calls 'tolerant', there is no indication that a tumescent female's dominance rank really changes. In many species, dominance can be recognized by a set of social signals (Preuschoft & van Schaik 2000). With respect to these and other indicators, there is no change in a female's troop standing during her tumescence. In particular, other females treat a tumescent female no differently, and after tumescence, males treat them just as they did before (Samuels *et al.* 1987; B. Thierry 2005, personal communication). DomWorld does not account for a female returning to its exact previous rank after tumescence.

With respect to our final question, (v), again it is difficult to gather quantitative data on this point. For
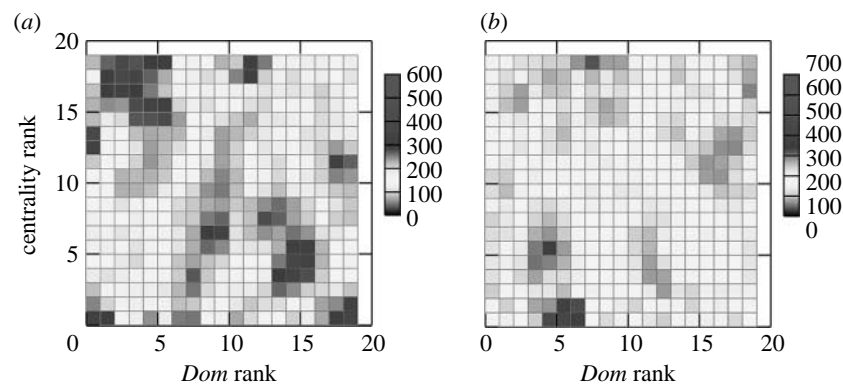
Figure 5. The correlation between centrality and *Dom* in two conditions: (*a*) fleeing and pursuing and (*b*) just fleeing. More-dominant animals have a higher *Dom* value, but agents closer to the centre have a lower centrality index. The darker regions show the higher correlations.

one thing, dominance hierarchies in extremely egalitarian species are not well defined except at the very top ranks. But the answer again seems to be 'no'. There are many affiliative and conciliatory behaviours that all members of egalitarian species engage in and no members of despotic species do, for example clasping (Thierry 1985; de Waal & Luttrell 1989; Thierry *et al.* 2004). Thus, absolute difference in *Dom* alone probably does not account for all the discrepancies between egalitarian and despotic species. However, this question is not really a good evaluation, because it neglects the level of abstraction of the model. It is possible that a more complete model based on the same basic interactions could show the evolution of extra conciliatory behaviours. It is not really justified to ask a model to explain data outside its remit.

In summary, while DomWorld does account for several primate social phenomena—including the propensity for dominant animals to be in the middle of the troop, the difference between egalitarian and despotic species and the special treatment given to females during their tumescence—we have found several failures of correspondence between this model and our target genus, the macaques. In particular, despotic species are not well characterized by rapidly fluctuating dominance rankings, neither type of macaque species experience reliable numbers of victories by significantly subordinate animals in disputes, and females in at least some species of macaques are not subject to significantly more agonistic interactions during their periods of tumescence.

(d) *An extension*

This paper aims to review the use of ABM as a methodological tool in science, as well as to present a case study for the analysis of a well-published model, DomWorld, with respect to macaques. Our analysis has shown some significant failures of correspondence between DomWorld and live macaque data. However, an agent based mode, like most scientific models, is not fragile—unlike analytic models or mathematical proofs. Even if a flaw is found in some aspects of a model, it does not necessarily invalidate the entire construction. While occasionally scientific theories are totally abandoned, more often scientific progress is gradual, and theories are refined and improved.

We continue our case study now by demonstrating that DomWorld has this property of robustness. We show that some DomWorld results, particularly the centrality result, still hold despite our criticisms, with only a slight modification to the model. The modification is simple—we assume that the *motion dynamics* aspects of dominance interactions are just as described earlier. However, we change our *interpretation* of those dynamics with respect to their correlations with the target system. Also, we assume that dominance levels are entirely stable—we do not update any *Dom* values. While this new model does not account for what changes *do* occur in dominance structures, it may be a better representation of average daily lives for most macaques.

In this modification of the DomWorld model, interactions are less likely to represent actual fights than *displacement* (sometimes called *supplantation*). Displacement is a common behaviour observed in macaques and other species where a dominant animal will come towards a subordinate, and the subordinate will get up and move out of the way (Rowell 1966). The dominant will then sit in or near the location previously occupied by the subordinate. This behaviour may be seen simply as a power move, an assertion of dominance, but it is also possible that a dominant may take advantage of resources discovered by the subordinate.

In a further replication of DomWorld (see electronic supplementary material, A), we show that centrality remains a characteristic of behaviour dynamics that are otherwise identical to DomWorld even if *Dom* values are held constant.

In this replication, we have tested which aspects of the behaviour dynamics of a dominance interaction are necessary to maintain this centrality result. We thought that the 'fleeing' aspect of the motion might be sufficient to explain the effect, but this is not the case, as shown in figure 5. These statistics were gathered for 20 individuals in steps 1000–5000 of a simulation otherwise as described previously, except that the *Dom* values were set as run-dependent parameters with each agent given a unique *Dom* from 1 to 20. These results show that displacement is a sufficient explanation for centrality, but only if it involves the dominant animal coming closer to the subordinate's former position than it would have by chance wandering.

In general, these results demonstrate the robustness of agent-based models, and their suitability for being not only replicated but also extended.

6. CONCLUSIONS

This paper has discussed one of the leading paradigms for experiments studying action selection, i.e. ABM. In addition to our case study, three other articles in this issue demonstrate some of the sorts of current action-selection research that are also being explored using ABM (Laver & Schilperoord 2007; Sellers *et al.* 2007; Seth 2007). The main theme of this paper has been to fully describe ABM as a *scientific* modelling technique. Our main point, that agent-based models can and should be treated as any other scientific hypotheses, can be extended from ABM to cover most, if not all, of the experiment-based techniques demonstrated in this issue.

This paper also presented a thorough analysis of one of the most widely published agent-based models in biology: Hemelrijk's DomWorld, a model of primate social dynamics. We have examined this model through a three-phase process: first, replicating the model and, in the process, coming to understand its dynamics and important parameters; second, producing a list of testable predictions or assumptions by considering these important model attributes in terms of their target system analogues; and third, evaluating these predictions and assumptions in the light of the extant primate literature.

We found several points where this model did not correspond to the behaviour of the target system chosen, the genus *Macaca*. We chose this genus because it has previously been presented as a well-documented model for the sorts of primate social behaviour DomWorld models (Thierry *et al.* 2004). The problems we found were that the rate of change of the dominance rankings was exaggerated, as was the probability of success of subordinate animals in aggressive interactions, and the account for female favouritism was not predictive of actual observed behaviour. Of course, the model was not originally built to model macaques (Hemelrijk herself is an expert in analysing chimpanzee behaviour), but it has been proposed as a general model of egalitarianism and despotism in primates (Hemelrijk 2004).

As we have argued, agent-based models are not fragile analytic proofs that collapse in the face of an error in a premise. Like any other theories, the model can be augmented, extended or restricted. We have already shown that if the part of the model disputed (the mechanism for changing dominance rank) is excised, one of the other significant results (the emergent centrality of dominant animals to the troop) still holds. It would also be interesting to find whether, in species that do have relatively dynamic dominance patterns, the model holds better. In free-ranging baboons, for example, although the ranks of females are remarkably stable, the dominance ranks of males can change as often as once a month, owing to the frequent migrations of males between troops (Kitchen *et al.* 2005).

We should emphasize that our perspective on artificial intelligence (AI) models as an ordinary part of the scientific method is not a universal one, although its acceptance seems to be spreading. However, some practitioners are less willing to take such an absolute stance. For example, although Axelrod (1997) described ABM as 'a third way to do science' (induction and deduction being the other two), he also stated that 'the purpose of ABM is to aid intuition. ABM is a way of doing thought experiments' (Axelrod 1997, p. 4). Despite the fact that Hemelrijk validated her data statistically against real animal behaviour, she also took this perspective (C. Hemelrijk 2006, personal communication).

We believe that this perspective does not take ABM seriously enough, or in other words, takes the rest of science as something more certain than it really is. No model describes all the known phenomena about a target species, but neither does any other scientific theory. Models and other theories are necessarily abstractions, constrained by the cognitive capacities of the scientists that hold and attempt to communicate them. In fact, some AI models might be criticized because they have become *too* precise and detailed to be comprehensible or communicated by individuals (related claims have been made about computer-generated mathematical proofs, cf. Bundy *et al.* 2005). This leads us into an interesting position as a scientific community, analogous to what happens to story telling and history as cultures develop the innovation of literacy. AI models can of course be communicated perfectly through digital copies without human comprehension. Thus, the process of validating and understanding them can become an evolutionary process similar to the scientific process itself. Whether such an approach is *desirable* is, however, an open question.

Given our conviction that ABM is just a special case of ordinary scientific method, we return finally to the matter of replication. Many modellers are reluctant to make their models available, because they both represent an enormous development effort and fear that other researchers will take better advantage of their work than they can themselves. King (1995, 2003) has addressed an equivalent concern in the social and political sciences, involving the datasets scientists gather at great cost and effort. King (1995) argued that replication is a necessary part of the scientific process, and while data can be withheld sometimes either temporarily (to ensure the right of first publication) or permanently (due to confidentiality or national security issues), in general, withholding such work is detriment to both the discipline and the individual scientists. King's argument has now become a matter of policy for many political science journals (Gleditsch & Metelits 2003). Further, Gleditsch *et al.* (2003) demonstrate empirically that there is an individual advantage of knowledge sharing, by performing an extensive piece of meta-analysis. Providing replication material actually improves the career of a scientist, as their reputation and citation rate both tend to be increased.

We believe that ABM is becoming a standard mechanism not only for experimental methodology,

but also for clearly communicating well-specified theories of action selection between scientists and laboratories. We hope that shared models can become catalysts for scientific progress in the study of social behaviour.

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NOTICE OF CORRECTION

The paper is now presented in its correct form.   20 April 2007