Agent-based models as scientific methodology: A case study analysing the DomWorld theory of primate social structure and female dominance

Joanna J. Bryson, Yasushi Ando and Hagen Lehmann
Artificial models of natural Intelligence
Department of Computer Science
University of Bath, Bath, BA2 7AY. UK

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Abstract

A scientific methodology must provide two things: first a means of explanation, and second, a mechanism for improving that explanation. It is also advantageous if a methodology facilitates communication between scientists. Agent-based modelling (ABM) is a method for exploring the collective effects of individual action selection. The explanatory force of the model is the extent to which an observed meta-level phenomena can be accounted for by the behaviour of its micro-level actors. But to demonstrate ABM is truly a scientific method, we must demonstrate that the theory it embodies can be verified, falsified, extended and corrected. This chapter contains a case study demonstrating ABM as biological science. We show that agent-based models like any scientific hypotheses can be tested, critiqued, generalised or specified. After first reviewing the state of the art for ABM as a methodology, we present our case: an analysis of Hemelrijk's DomWorld, a widely-published model of primate social behaviour. Our analysis shows some significant discrepancies between the model and the behaviour of the genus we compare it to, the macaques. We then demonstrate that the explanation embodied in the DomWorld model is not fragile: its other results are still valid and can be extended to compensate for the problems identified. This robustness is a significant advantage of experiment-based artificial intelligence modelling techniques over purely analytic modelling.

1 Introduction

Agent-Based Modelling (ABM) is a method for 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 over-all 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 still 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 chapter, we discuss ABM and the techniques for its analysis. We also present a case study where we analyse, critique and extend one of the most extensively-published ABM in biology, Hemelrijk's DomWorld (Hemelrijk, 1999, 2000, 2002; Hemelrijk et al., 2003; Hemelrijk, 2004; Hemelrijk et al., 2005, 2008). DomWorld provides an explanation of systematic differences in social organisation observed in closely related primate species.

Section 2 reviews the recent literature on analysing ABM, and assesses how this applies to the specific case of modelling in the biological sciences. We then provide the background information necessary for understanding DomWorld: the literature describing the target system we test the model against (macaque social behaviour) and a thorough description of the model and its results. In section 4 we analyse DomWorld. Finally, we conclude by illustrating our earlier discussion of ABM as a scientific methodology in light of our analysis of DomWorld. We show that ABM produces not fragile analytic models, but rather robust scientific hypotheses, open to critique, extension and circumscription.

2 Analysing ABM

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 phenomena 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 use systematically varying parameter values, to test the significance of each parameter set or *condition*. The behaviour of the model system is then compared with the behaviour of the target system.

Axelrod (1985) is credited with founding ABM with his evolutionary simulations of cooperative behaviour (Axelrod and Hamilton 1981; though see Hogeweg and Hesper 1979). He is still one of the area's main advocates. In the appendix of a recent text on the topic, Axelrod and Testfatsion (2006) describe four research goals for the ABM field:

1. *empirical:* "Why have large-scale regularities evolved and persisted, even when there is little top-down control?"

2. *normative understanding:* "How can agent-based models be used as laboratories for the discovery of good designs?"

3. *heuristic:* "How can greater insight be attained about the fundamental causal mechanisms in social systems?", and

4. *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 chapter focuses on the fourth, methodological question as applied to biology. In the present volume, science in general subsumes Axelrod's third heuristic question — we achieve greater understanding by doing science. The type of models we examine focus primarily on empirical rather than normative problems, as best suits biology. In the present section we focus primarily on the methodological issue of "compatibility" between theory and data, which in the ABM literature is often called the problem of *validation*.

2.1 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 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 the model actually models the target system. Our main thesis for this chapter is this: when ABM are used for biology, validation is equivalent to hypothesis testing. We will begin by discussing validation, then return to verification shortly.

There is a common perception that ABM are so complex (that is, have so many parameters) that they can be made to easily match any data or predict any outcome, but that having done so the system will have no capacity for generalisation, and therefore no predictive power. In practice, however, building and debugging ABM is a difficult skill, and matching datasets is not easy. While it is true that ultimately most datasets can be matched, the principle value of the model is expressing what aspects need to be changed in order to generate these various outcomes. Where the data is behavioural, the model aspects that determine it are the model's theory of action selection.

If a model is built first 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 hold for a model. Rather a model, like any scientific hypothesis, becomes more *probable* (given the data) the more it is validated. But a model never becomes perfectly certain

(Box, 1979). The only exception is if a model becomes understood to such an extent that it can be *proven* correct in a logical or formal analytic sense.

Many people see formal analytic models as preferable to ABM for this reason, but there are several reasons to use 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 model by proving it *valid*. 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 which are not amenable to closed analytic solutions (Axelrod, 1997; Axtell, 2000). Particularly interesting to biologists are those involving the open-ended co-evolution of multiple interdependent species.

Returning to the matter of verification, this issue is most nefarious in purely formal systems, where validation is not grounded in real-world data. Formal systems are used in mathematics and similar disciplines as a mechanism of knowledge *discovery*, and therefore 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 of the word.

Verification in this sort of scientific process becomes a process of *model understanding.* Part of this process can be simplifying or generalising the model, or better determining the biological correlates of its components. This verification-like process is useful not only for AI modelling, but for all sorts of formal theories in biology. For example, Wynne (1998) provides a neat history of the development of ever-simpler models of transitive inference learning (see also Delius and Siemann, 1998).

2.2 ABM as Scientific Hypotheses

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

1. Does the behaviour of the ABM match the behaviour of the target system within the standard metrics of hypothesis evaluation?
2. Do all the attributes of the agents and their environment have plausible biological correlates in the target system?

Regarding the 'standard metrics', these 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. The model is now a theory explaining the data, and as the first one it is necessarily the best. 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 origins of theory of mind by 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 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 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 a *replication* of the ABM. This may not seem (or even be) strictly necessary in the case where the model is publicly available — the results in that case can be checked just by rerunning the original model on another computer. However, reimplementing the model from its description in the literature can be a valuable exercise. Reimplementation may uncover important aspects of the model that the model's original 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; part of the scientific method is improving this 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 science, we go through a process of finding testable predictions and implications that 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) to proposing and executing new experiments.

3 Primate Societies and the DomWorld Model

We now present a case study. We analyse DomWorld, a model which provides an explanation for the variety of social structures we see in different species of primates. We begin this study by providing background information on the target biological systems and features that DomWorld is intended to model.

3.1 Primate Social Structure

Most primate species are highly social. They live in structured societies. The structure of these societies is often characterised along a single axis 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 which have strong affiliative relationships, such as kin.

Tolerance is considered technically as one of the most basic forms of conflict resolution for a social species (de Waal and 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 *in*action. However, if an agent is 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 who desires to allow a tantrum-throwing juvenile 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 desired result (the juvenile feeding).

For 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 initiate an attack on a dominant. Conflicts tend to be infrequent, but when they occur, high-intensity (e.g. biting). Conciliatory behaviour after the conflict is rare. On the high 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. vocalisations, slapping). In the most extremely conciliatory species even unrelated participants reconcile after around 50% of conflicts (Thierry, 2006). van Schaik (1989) refers to these two extremes as as *despotic* for the low end and *egalitarian* for the high. Though these terms are obviously anthropomorphic, they are well-established and have strong mnemonic value.

Thierry et al. (2004) propose that the macaques are a particularly good model genus for studying primate social organisation (see also Thierry, 1985; de Waal and Luttrell, 1989; Preuschoft and van Schaik, 2000). There are approximately twenty-one 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. Rhesus (*M. mulatta*, familiar from zoos and laboratories) and Japanese (*M. fuscata*) macaques fall into the most despotic category. The stumptailed macaques (*M. arctoides*) used by de Waal and Johanowicz (1993) in their seminal cross-rearing studies with rhesus are in the second-most egalitarian cluster, while the Tonkean

(*M. tonkeana*) and crested (*M. nigra*) are in the most egalitarian cluster.

3.2 The DomWorld Model

The DomWorld model was originally derived from another seminal ABM, the Hogeweg and Hesper (1983) MIRROR model (Hogeweg, 1988; Hemelrijk, 1999). MIRROR is 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 and Hogeweg, 1994). The results of these older simulations were based on variables not seen in basic DomWorld like 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; Kummer et al., 1996). DomWorld follows good methodological practice by reducing the complexity of the MIRROR model to its most essential components. Later work reintroduces attributes such as food into the now better-understood system (Hemelrijk et al., 2003).

The only addition to DomWorld made between 1999 and the 2002 model this analysis focuses on is the ‘attraction procedure’ added to the motion rules to simulate sexual attraction (Hemelrijk, 2002). We describe this in §3.3.3, which is on tumescence, not here as part of the basic model.

Describing the technical aspects of an ABM requires describing three things: the environment, the agents’ state, and the agents’ behaviour.

3.2.1 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 et al. (2009), though models concerned with realistic environmental behaviour such asHill et al. (2010) 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 this does not happen. Agents in DomWorld do not eat, die or reproduce. They only wait, move around, and occasionally perform dominance interactions.

3.2.2 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's 'lifetime' during an experimental run. The dynamic parameters for each agent in DomWorld are:

- Their **x, y** position on the 2-D 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 (c.f. 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:

- 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 egalitarian conditions, and slightly higher for males than females.

Some parameters of an ABM are set by the experimenter in the course of developing the system into 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:

- 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,
- **near view**, a distance within which the agents feel comfortably in the troop, and
- **personal space**, the minimum distance two agents can have between each other without engaging in a dominance interaction.

3.2.3 DomWorld Agent Behaviour

The basic motion dynamics of DomWorld are very like those described by Reynolds (1987) as necessary for flocking. The attractive force that provides coherence for the groups is the fact that an agent moves towards the nearest other agent it sees if that agent is more than **near view** away. If an agent can't see any other agent, it will rotate until it does. Separation (or *repulsion* as Reynolds terms it) 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. DomWorld troops mill around rather than truly flocking.

When one agent sees another within its **personal space** it engages in an agonistic social interaction. Each agent's dominance rank value, **Dom**, is adjusted after any fight involving that agent. This variable determines both the agent's rank and its probability of winning a given fight. The first step of the interaction is a 'mental battle' in which the acting agent compares its own **Dom** value with the **Dom** 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. Because of the limits provided by the **field of view**, it is possible the dominant agent currently in its **personal space** will move off without ever having 'seen' the nearby subordinate agent.

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

$$w_i = \left[\begin{array}{ll} 1 & \frac{Dom_i}{Dom_i + Dom_j} > Random(0,1) \\ & \\ 0 & otherwise \end{array} \right. \tag{1}$$

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 agents are adjusted according to the interaction's outcome, using roughly the same information:

$$\begin{array}{l} Dom_i = Dom_i + \left[w_i - \frac{Dom_i}{Dom_i + Dom_j} \right] StepDom \\ Dom_j = Dom_j - \left[w_i - \frac{Dom_i}{Dom_i + Dom_j} \right] StepDom \end{array} \tag{2}$$

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

Hemelrijk calls this mechanism of determining dominance values a *damped positive feedback system*, since if a higher-ranking individual wins its dominance value increases only slightly, but if the lower-ranked agent wins its dominance value undergoes a greater change. For both agents the **Dom** is not changed much by an expected outcome, but it changes greatly for an unexpected one.

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 of the agent and 'runs' a more significant distance away. 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.

3.3 DomWorld Results

The contributions of DomWorld can be summarised as follows.

3.3.1 Gradients of Dominance Hierarchy

The primary result is a hypothetical explanation of variation and the tolerance / conciliation social axis. Hemelrijk proposes that having a larger difference between **Dom** values among a troop is equivalent to the troop being more despotic, whereas more similar dominance values correspond to egalitarianism. This hypothesis implies 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. She uses a topographical metaphor to describe this, saying that despotic species have a steeper dominance profile. The main metric Hemelrijk uses for 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 a steep gradient and therefore despotism, a small one egalitarianism.

In DomWorld, these differences in position along the tolerant/conciliatory axis are accounted for entirely by the intensity of aggression. Aggression is modelled using **StepDom** (Hemelrijk, 2002). The principle result then is that high levels of **StepDom** lead to greater variations in **Dom** within the troop (figure 3). Notice though that this aggression intensity value, **StepDom**, has no direct impact on whether a dominance interaction occurs or who wins it (see Eq. 1). Rather, its only direct impact is on the adjustment to **Dom** *after* the fight. Through this mechanism though, **StepDom** does have an indirect impact on future fight probabilities and outcomes.

3.3.2 Troop Spatial Structure

Another key result from DomWorld is a replication of the spatial organisation attributed to real troops (Hemelrijk, 2004). Hamilton (1971) suggests that one selective pressure for dominance might be protection of the highest-quality individuals by keeping them central to a group. There is almost no field evidence of primates adopting this strategy, though Hall and Fedigan (1997) report observing it in wild capuchins. The dynamics of DomWorld motion behaviour already described produce this phenomena with no additional cognitive strategy required for the agents. *Centrality* is measured as the sum of the unit vectors (vectors with accurate direction but fixed length) from an agent towards 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. This is the same metric used in Hemelrijk's DomWorld papers.

Independently, Christman and Lewis (2005) have shown it is the most reliable metric for centrality. In DomWorld, centrality correlates with **Dom**.

Centrality is not a main focus of our present analysis, but it *is* a primary result for DomWorld and we will return to it while discussing the extension of this this model in §4.4.

3.3.3 Sexual Attraction During Tumescence

In most primate societies, most males are more dominant than most 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 though 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 beneficiaries 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 and Luttrell, 1989; Stanford, 1996).

Hemelrijk proposes a much simpler explanation (Hemelrijk, 2002; 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 the time of tumescence males are more likely to approach females. Due 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 higher-ranking male. Because of the dynamics of equation 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.

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 inside of **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, though on average no more than half of them would be (see full results below). 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.

3.3.4 Female Dominance over Males

In most species of primates, dominant animals tend to be male, though some females may outrank some males. However, in a few species (particularly lemurs) females routinely and sometimes even entirely outrank males. Hemelrijk et al. (2008) claim that DomWorld can entirely account for these species — the model shows that the proportion of dominant females in a troop increases as the proportion of males in a population increases. This result required no change to the standard DomWorld model other than altering the proportion of males in a run.

4 The Analysis of DomWorld

We now evaluate DomWorld as a general explanation of the despotic/egalitarian continuum in primate behaviour. As reviewed earlier, this continuum is best documented in the genus *Macaca*. We adopt the proposal of Thierry et al. (2004) that this genus should serve as a model (in the biological sense) for primate social organisation in general.

Following the approach described in §2, our analysis is in three phases. The first phase is a 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 considers the correlations between these critical aspects of the model's agents and real primates, and makes a series of predictions based on the consequences of the model. The third phase tests these 'predictions' against the primate social behaviour literature. The third phase could involve gathering more data from the field, but in the present case the extant literature proves sufficient to answer the key questions derived in the second phase.

4.1 Replication

The original DomWorld was implemented in Object Pascal and Borland Pascal 7.0 Hemelrijk (2002) and has to date 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 visualising results. The exact parameter settings of our model are matched to those in the previously published accounts of DomWorld. The details of our replication are described in Bryson et al. (2007); the code including these parameter settings is available as an electronic supplement of that article and from the authors' Web pages.

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* particularly 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. The documentation of the waiting period is not as conspicuous in Hemelrijk's papers as other aspects of her model (e.g. it is not mentioned in her flow diagrams of her control system), so this sensitivity may account for why some modellers have reported difficulty replicating her results.

4.1.1 Results

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

To match Hemelrijk's figures, we show typical individual exemplar results, rather than averaging over the ten runs. Figure 1 replicates the Hemelrijk (2002, p. 739) fig. 3*A*. 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 2 females each outrank 2 males, 1 outranks 1 male and the other outranks no males, this value would be 5. We can see that, as reported in Hemelrijk, the female dominance in conditions with high **StepDom** increases over the 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), it replicates fig. 4*A* (p. 741). The figure shows the distribution of the coefficient of variation of dominance values for both sexes (see discussion in §3.3.) 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, and females are more likely to outrank some males in this condition.

Figure 3 shows the change of dominance values for both the sexes in conditions with high and with low levels of aggression. Again, here we show 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 3(a) corresponds to fig. 4*B* in Hemelrijk (2002, 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* by Hemelrijk, p. 741. With a low **StepDom** there is very little change in the dominance values. This creates a relatively stable hierarchy, thus no females gain higher positions in the troop.

Figure 4 has no equivalent in (Hemelrijk, 2002) but shows data derived from our replication which is significant to our analysis (§4.2). In this figure the total number of aggressive interactions initiated by female agents is compared across the four different conditions used in the experiment, and averaged across all ten runs in each condition. The number of female dominance interactions increases significantly in conditions with sexual attraction at both intensities of aggres-

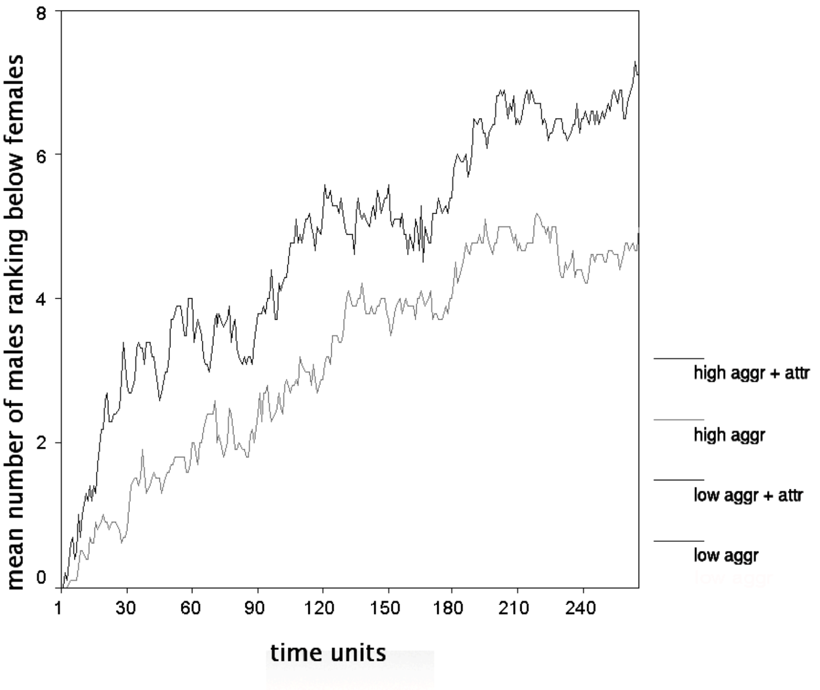


Figure 1: The dominance of females as shown from the sum of the number of males ranked below each female at different times in different conditions. The egalitarian (*low aggr*) conditions are not visible because they are equivalent to the X axis — that is, they are constantly zero. $highaggr + attr$, despotic and tumescent; $highaggr$, despotic with no tumescence; $lowaggr + attr$, egalitarian and tumescent; $lowaggr$, egalitarian with no tumescence; $aggr$, aggression; $attr$, attraction.

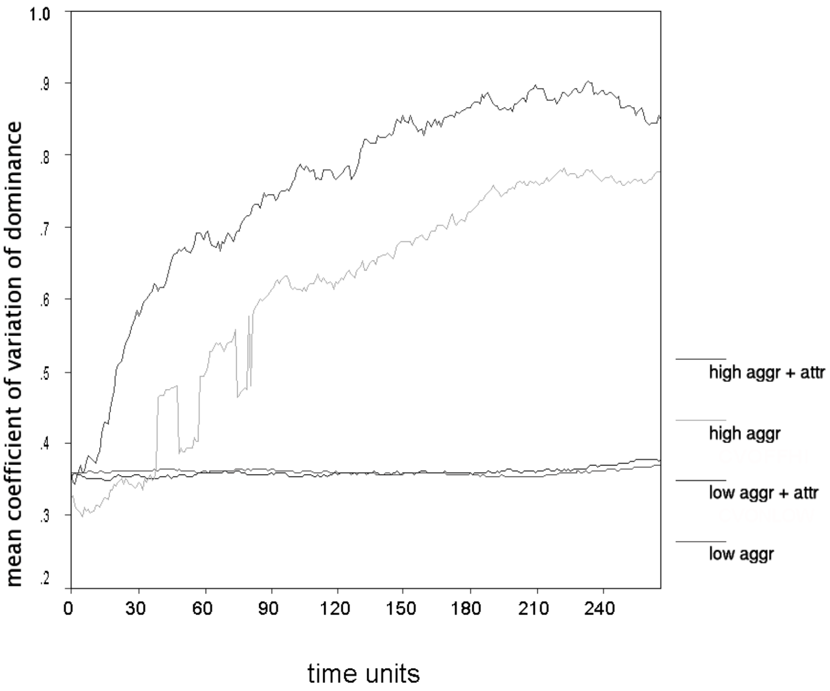
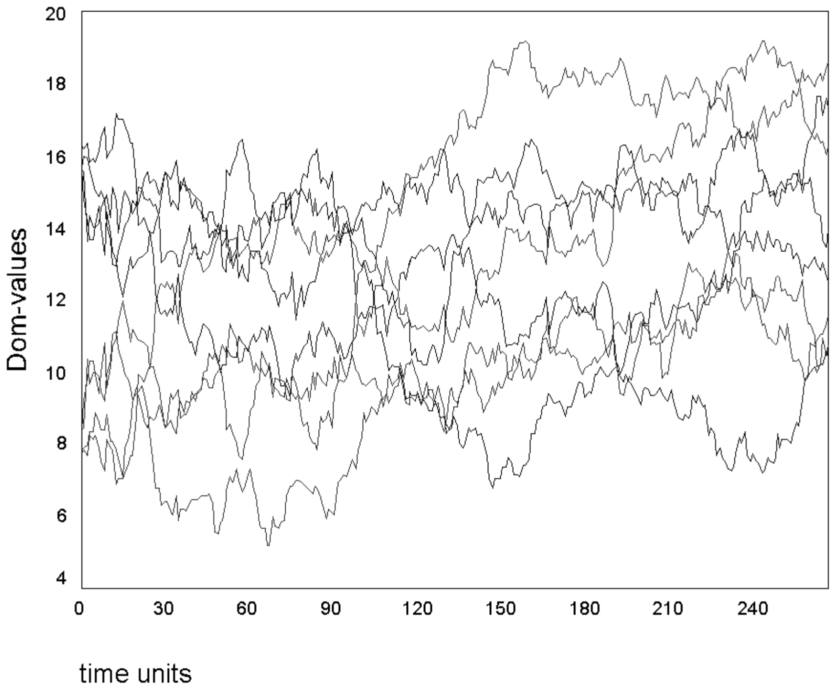


Figure 2: Distribution of the *coefficient of variation* of dominance values in different conditions for both sexes. The definitions are the same as given in figure legend 1.

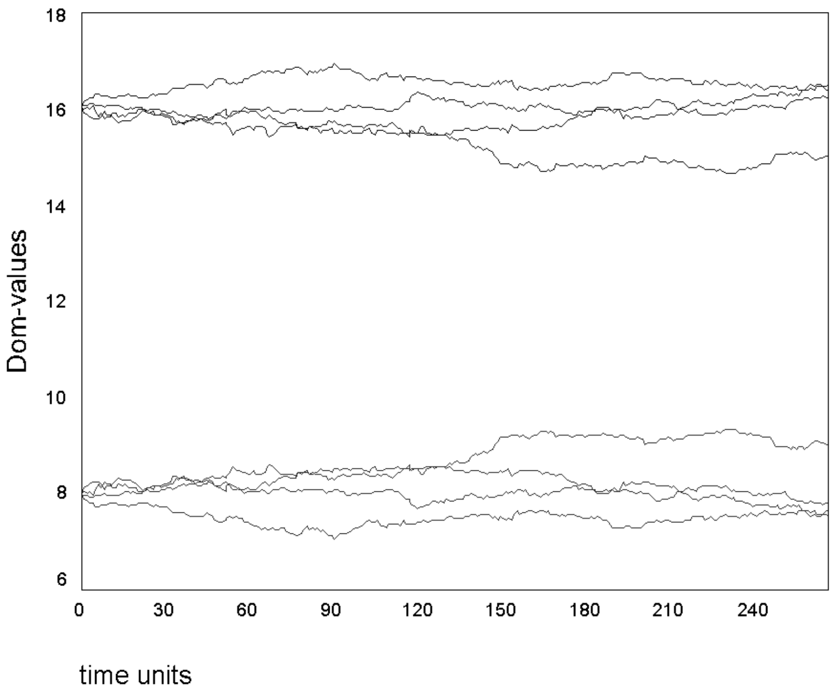
sion (low: Mann-Whitney, $N = 10, U = 0, p < .001$, two-tailed; high: Mann-Whitney, $N = 10, U = 0, p < .001$, two-tailed). This means females are involved in considerably more interactions when they are attractive. Higher **StepDom** amplifies this result, though this effect is rather weak (Mann-Whitney U-Test, $N = 10, U = 24p < .049$, two-tailed).

4.2 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



(a) High StepDom



(b) Low StepDom

Figure 3: Distribution of Dom values at a high level and at a low level of StepDom. In both conditions, the males initially have twice the Dom value of the females.

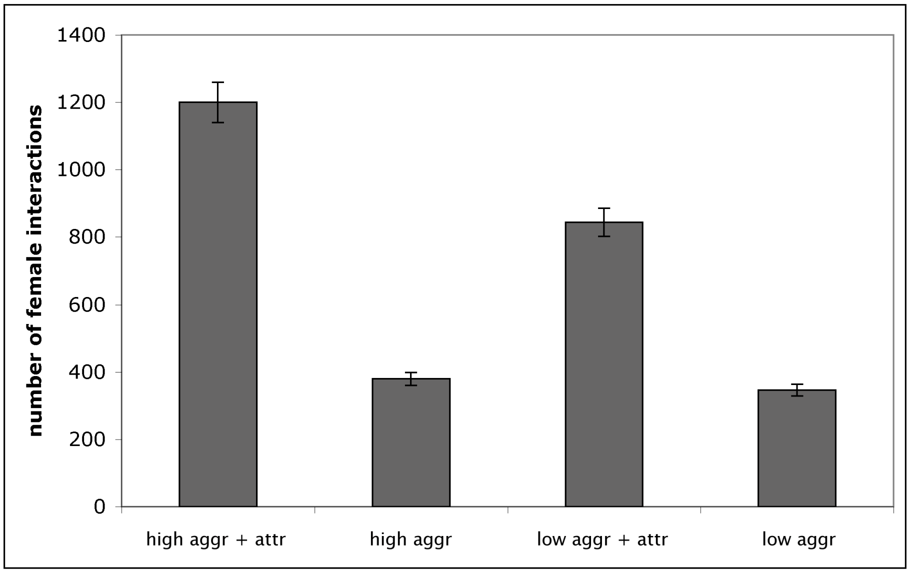


Figure 4: Total number of female interactions under different conditions. The definitions are the same as given in figure legend 1.

animals substituting these terms into the results, will the results hold?

For ths phase of our analysis, we compiled the following list of questions based on the model but rephrased in primatological terms:

1. 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 2.

2. 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 the fight have more impact on the dominance hierarchy? If so, then it makes sense to refer to **StepDom** as 'intensity of aggression', since the level of aggression would determine the increment of **Dom**) and it would further validate it's use in Equation 2.

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

4. 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 of 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.

5. 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 more despotic 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 first framed these questions (Lehmann et al., 2005), 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.

4.3 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 above fall into a third category. Existing data is not sufficient to answer the questions conclusively, but this is not because insufficient studies have been run. Rather, in order for data to give stastically-significant indications, particular types of social events would have to occur at a frequency which is not observed in real animals. Thus a question that appears to be well-posed from the perspective of the model is not directly answerable. However, the discrepancy between the model and the target system that leads to the problematic question is itself information useful for evaluating the model.

Question 1 in §4.2 is an example of this third category of question. Particularly in despotic macaque species, unexpected outcomes in conflict 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. For there to be a statistically-significant result either for or against the model, we would need to see a reasonable number of subordinate animals becoming superordinate (dominant) as a result of unlikely 'wins' in dominance interactions, then determine how the rate of their ascension correlates to their number of improbable outcomes. However, in macaques at least, changes in dominance ranking are very infrequent. Most variation comes as a consequence of aging (both juveniles becoming stronger and 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 challenging sequentially the troop members just above their own rank, working their way gradually up the hierarchy. Thus the unlikely outcomes that drive the rank volatility in DomWorld are not a feature of the target system 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 1-in-3 ($\frac{8}{8+16}$) chance of defeating an agent very much her 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 improbable outcomes.

The fact that dominance order for adult macaques almost never changes makes question 2 above equally difficult to answer, at least from observations of captive troops. It further calls into doubt the plausibility of results such as are shown in figure 3(a), and therefore in turn the results shown 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.

Standard DomWorld results like those shown in figures 1 and 2 are simple consequences of the fact that DomWorld's damped positive feedback system (§3.2.3) ultimately produces a perfectly random dominance hierarchy. **StepDom** functions as a gain, determining how fast this process takes place. Thus the analysis performed by Hemelrijk (2002) — and subsequently in (Hemelrijk et al., 2008) (replicated in figure 1) is deceptive. While appearing to show a steady increase in female dominance, in fact this increase will always asymptote when the females' ranks are randomly distributed with the males'. The rise is the consequence of having started from order, with the females all more lower ranked, then moving to disorder. The randomising process is accelerated in the female-attraction (tumescent) condition because there are more interactions involving the initially-lowest-ranked members of the troop (figure 4).

Contrary to Hemelrijk et al. (2008), DomWorld could never account for complete female dominance, unless the starting condition had the females already in a dominant position, and **StepDom** was too low to randomise their position during the number of time units allocated for the experiment. The apparent rise in female dominance is only a trend towards complete randomness. Adding males to the system increases the rate at which random order is acheived because males have a higher **StepDom** than females and thus the average amount of 'violence' per interaction increases with the proportion of males. Since the experimental run times are truncated at an arbitrary but fixed period of time before the ordering of agents is perfectly random, the rate of change determines the proportion of dominant females.

One question that *can* be directly answered is question 3 in §4.2. Aujard et al. (1998) show that egalitarian macaque females in tumescence are involved in, if anything, *fewer* agonistic interactions, not more. Aujard et al. document a large range of behaviours with respect to the female reproductive cycle. Social grooming with males and 'affiliative interactions' with males all peak at or just before tumescence. For 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 Figure 2, p. 293, and discussion *f.*). This work was done with semi-free-ranging Tonkeans, one of species Thierry (2006) puts in the most egalitarian cluster.

As we showed in Figure 4, the Hemelrijk (2002) 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 3, but also the basic hypothesis that preferential behaviour towards females can be explained in this manner.

Eaton et al. (1980) do document an increase of dyadic inter-sex and male-on-male violence in a similarly semi-free-ranging troop of Japanese macaques (*Macaca fuscata*) during their breeding season. Thierry (2006) assigns *M. fuscata* to the most highly despotic category. There is however a significant downturn of aggression either by females on females or by groups on females during this period, though there is an increase of violence in 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 would be 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 despotic agents shown in figure 4 are also invalid.

The Aujard et al. (1998) data for the egalitarian Tonkeans also bear on question 4. While Aujard et al. do not specifically document tolerance of food access, the significant increases of affiliative behaviour *other* than (and as well as) grooming and sexual behaviour does seem an indication of the sort of favouritism the Hemelrijk (2002) extension of DomWorld is intended to explain. Thus egalitarian tumescent females *should* also be accounted for in DomWorld, but are not.

There is a further problem with DomWorld's model 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 recognised by a set of social signals (Preuschoft and 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 her just as they did before (Thierry, 2005; Samuels et al., 1987). DomWorld does not account for a female returning to her exact previous rank after tumescence, nor for her difference in rank in the eyes of male and female agents.

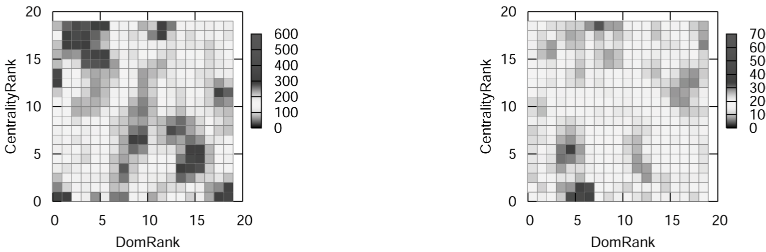
Our final question 5, about the difference between egalitarian and despotic species, is again difficult to answer with quantitative data. For one thing, dominance hierarchies in extremely egalitarian species are not well defined except at the very top ranks. But the answer again seems to be “no”. There 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 and 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 fair evaluation of DomWorld, 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 behaviour. It is not really justified to ask a model to explain data outside its remit.

In summary then, 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 females during their tumescence — we have found several failures of correspondence between this model and our target genus, macaques. In particular, despotic species are not well characterised by rapidly fluctuating dominance rankings, but these are the main mechanism DomWorld uses to explain both the tolerant/conciliatory access and female favouritism during tumescence. In nature, neither type of macaque species experience significant numbers of victories by significantly subordinate animals in disputes, yet this is what drives the rank fluctuations in DomWorld. Finally, females in at least some species of macaques are not subject to significantly more agonistic interactions during their periods of tumescence, and again these are essential to the Hemelrijk (2002) account.

4.4 Partial Recovery of the Model

This chapter has two aims: to review the use of ABM as a methodological tool in science, and to present a case study for the analysis of existing models. Our analysis has shown some significant failures of correspondence between DomWorld and live macaque data. However, agent-based models, like most scientific models, are not brittle — unlike analytic models or mathematical proofs. Even if a flaw is found in some aspect 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 (Kuhn, 1970).

We continue our case study now by demonstrating that DomWorld has this property of robustness. We show that DomWorld’s centrality result still holds even if our criticism is addressed with 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 (§3.2.3). However, we change our *interpretation* of those dynamics with respect to their correlations to the target



(a) Fleeing and Pursuing

(b) Just Fleeing

Figure 5: Correlation between centrality and dominance in two conditions: (*a*) fleeing and pursuing and (*b*) just fleeing. More dominant animals have a higher *Dom* rank, while agents closer to the centre have a lower centrality rank. The darker regions show the higher correlations.

system. Also, we assume that dominance levels are entirely stable — we do not update any **Dom** values. While this new model no longer accounts 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 the only study reporting centrality in primates we were able to find in the literature, Hall and Fedigan (1997) report that in capuchins the central position was held with no visible conflict, and conclude that subordinates simply avoid dominants.

In a further replication of DomWorld, Ando et al. (2007) 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 what aspects of the behaviour dynamics of a dominance interaction are necessary to maintain this centrality result. We originally hypothesised that the 'fleeing' aspect of the motion might be sufficient to explain the effect, but as figure 5 shows, this is not the case. These statistics were gathered for 20 individuals in time units 50–250 of a simulation otherwise as described above, except that the **Dom** values were set as run-dependent parameters with each agent given a unique **Dom** from 1–20. 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.

Taken in general, these results demonstrate the robustness of agent-based models, and their suitability for being not only replicated but also extended. This supports our position that ABM are a form of scientific hypothesis.

5 Conclusions and Discussion

This chapter examines a leading paradigm for furthering the scientific understanding of actions selection: agent-based modelling. In addition to the extended case study in this chapter, four other chapters in this book demonstrate the diversity of action-selection research that are being explored using ABM (Seth, 2009; Laver et al., 2009; Hill et al., 2010; Rands et al., 2009). The main theme of the present chapter has been to emphasise ABM as a *scientific* modelling technique. Models are a vector for communicating theory between scientists, as well as a mechanism to check ramifications of our theories that go beyond the computational ability of individual rational consideration (Kokko, 2007). The main argument, that agent-based models can and should be treated like any other scientific hypothesis, can be extended from ABM to cover most if not all of the experiment-based techniques demonstrated in this volume.

To demonstrate and communicate our point, we have 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 had originally expected to motivate novel research to test the predictions, but in fact the existing literature was sufficient to answer the questions once they were well-specified.

5.1 DomWorld as a Model of Primate Social Behaviour

We found several points where DomWorld did not correspond to the behaviour of the target system we chose for analysis, 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 main problems we found were:

- the rate of change of the dominance rankings is quite exaggerated, and many of the effects claimed for the system were entirely based on this e.g. increased female dominance (Hemelrijk, 2002; Hemelrijk et al., 2008);
- the probability of success of subordinate animals in aggressive interactions is also exaggerated — this generates the first inconsistency, the size of

the effect is determined by the StepDom, a proxy for the violence of the aggression in the interaction;

- the Hemelrijk (2002) account of special treatment for tumescent females (increased ordinary rank) is not predictive of actual observed behaviour (number of fights, return to previous rank after tumescence concludes);
- the Hemelrijk et al. (2008) account of female dominance is false because DomWorld cannot explain more than 50% of females being dominant on average in the long run.

Of course, the model was not originally built to model macaques. MIRROR was built to model social insects, and Hemelrijk originally applied it to her principle area of expertise, chimpanzee behaviour. However, DomWorld has been proposed as a general model of egalitarianism and despotism in primates (Hemelrijk, 2000; Hemelrijk et al., 2008).

Agent-based models are not fragile analytic proofs which collapse in the face of an error in a premise. Like any conventional biological theory, an ABM can be augmented, extended or restricted. We have demonstrated that if the part of the model we dispute (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, because of the frequent migrations of males between troops (Kitchen et al., 2005).

5.2 ABM as Hypotheses and Vectors of Scientific Communication

Our perspective on artificial intelligence (AI) models as an ordinary part of the scientific method is not universally held, although its acceptance seems to be spreading. However, some practitioners are less willing to take such an absolute stance. For example, although Axelrod (1997) describes ABM as “a third way to do science” (induction and deduction being the other two), he also states that “the purpose of agent-based modelling is to aid intuition. Agent-based modeling is a way of doing thought experiments.” (Axelrod, 1997, p. 4). Despite the fact that Hemelrijk validates her data statistically against real animal behaviour, she has also taken this perspective (Hemelrijk, 2006).

We believe this perspective is not taking modelling seriously enough, or put another way, is taking the rest of science as something somehow more certain or special than it really is. No model describes all the known phenomena about a target species, but neither does any other form of 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 criticised 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, c.f. 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 too large to be held in any one mind can still be communicated perfectly through digital copies without human comprehension. The process of validating and understanding them could thus become an evolutionary process similar to the scientific process itself. It is an open question whether such an approach would be *desirable*. It might for example increase our ability to make predictions, but reduce the probability of innovations based on insight.

Many modellers are in fact reluctant to make the digital versions of their models publicly available. This is primarily because models represent an enormous development effort. Some researchers are reluctant to fully share the outcomes of this effort, fearing perhaps that others might 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 these scientists gather at great cost and effort. King (1995) argues that replication is a necessary part of the scientific process. Thus while data can sometimes be withheld either temporarily (to ensure the right of first publication) or permanently (due to confidentiality or national security issues), in general withholding such work is a detriment both to the discipline *and* to the individual scientists. King's argument has now become a matter of policy for many political science journals (Gleditsch and Metelits, 2003). Further, Gleditsch et al. (2003) demonstrate empirically that there is an individual advantage of knowledge sharing, by performing extensive meta-analysis. Providing replication material actually improves the career of a scientist as their reputation and citation rate are both increased. Thus researchers both benefit their own careers and accelerate scientific advance by sharing data sets, and presumably also agent-based models. Hopefully biology journals will follow suit with the social sciences and begin to require publication either in public repositories or as electronic supplements to an article any model on which a publication is based.

In conclusion, agent-based modelling is becoming a standard mechanism not only for conducting experiments into the consequences and validity of biological theories, but also for clearly communicating well-specified theories of action selection between scientists and laboratories. They provide a robust, algorithmic framework for expressing theories that can be described in terms of the consequences of an individual animal's behaviour in given contexts. We hope that sharing such models can further catalyse scientific progress in the study of social behaviour.

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