

# Chapter 22

## Simulating Complexity of Animal Social Behaviour

Charlotte Hemelrijk

**Why Read This Chapter?** To get an overview of simulation models aimed at understanding animal social behaviour, such as travelling, foraging, dominance, or task division. The chapter also provides an analysis of the kinds of insight each simulation provides, how specific these insights are and whether they are testable.

**Abstract** Complex social phenomena occur not only among humans, but also throughout the animal kingdom, from bacteria and amoebae to non-human primates. At a lower complexity they concern phenomena such as the formation of groups and their coordination (during travelling, foraging, and nest choice) and at a higher complexity they deal with individuals that develop individual differences that affect the social structure of a group (such as its dominance hierarchy, dominance style, social relationships and task division). In this chapter, we survey models that give insight into the way in which such complex social phenomena may originate by self-organisation in groups of beetle larvae, in colonies of ants and bumblebees, in groups of fish, and groups of primates. We confine ourselves to simulations and models within the framework of complexity science. These models show that the interactions of an individual with others and with its environment lead to patterns at a group level that are emergent and are not coded in the individual (genetically or physiologically), such as the oblong shape of a fish school, specific swarming pattern in ants, the centrality of dominants in primates and the task division among bumble bees. The hypotheses provided by these models appear to be more parsimonious than usual in the number of adaptive traits and the degree of cognitive sophistication involved. With regard to the usefulness of these simulations, we discuss for each model what kind of insight it provides, whether it is biologically relevant, and if so, whether it is specific to the species and environment and to what extent it delivers testable hypotheses.

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## 22.1 Introduction

Many complex social phenomena of human behaviour are also observed in animals. For instance, humans coordinate their movement while searching for the right restaurant. They also make and follow paths on lawns in between different university buildings in order to cross between them. This resembles the path marking and following behaviour of ants as they forage and select different food sources. Furthermore, a division of tasks is found in both human social organisations and in large colonies of social insects, such as honey bees. Human social relationships are diverse, and so are the social relationships of primates. In groups of humans and animals, competition results in stable relationships in which one individual consistently beats the other. Within a group, individuals can be ordered in a dominance hierarchy. Furthermore, dominant relationships are also found between groups and between classes of individuals, such as between the sexes. Further, societies may differ in their dominance style, such as whether they are egalitarian or despotic. In summary, despite the hugely inferior cognitive capacities of animals they show a number of complex social phenomena that resemble those of humans. From this the question arises whether or not these complex phenomena originate by self-organisation in the same way as both humans and animals. Therefore, it is important to survey complex social behaviour in animals in addition to that of humans.

We divide the chapter in subsections dealing with different (groups of) complex phenomena ordered in increasing complexity: From group formation (which is simple in animals) and coordination under various circumstances (such as during travelling, foraging, selection of shelter and nest site) we continue to the social organisation of the group (its dominance hierarchy, dominance style, dominance classes, social relationships, personality style and task division).

We mainly confine ourselves to individual-based models that are spatially explicit. Individuals in the model are steered by behavioural rules that are fixed or that are based on parameters that change (compare self-organisation with(out) structural changes, Pfeifer and Scheier 1999); they react to their local environment only. The environment may contain only other individuals, or may also contain food. Food may be continuously abundant, or it may be depleted and may re-grow or not after being eaten.

In general, we discuss for each model whether it has led to a new perspective in the study of the phenomenon; whether this perspective is more ‘parsimonious’ than previous explanations in terms of cognitive sophistication and the number of specific behavioural adaptations; whether the new explanation concerns a general principle or is specific to a certain species or environment; and whether it produces hypotheses that can easily be tested in real animals. In the evaluation we also provide literature for further reading and indicate important areas for future modelling.

## 22.2 Group Formation and Coordination

Everywhere in nature groups are formed. They are formed among individuals of all kinds of species in all stages of their lives and in a few cases groups contain several species. Groups may differ in size, longevity, the degree of heterogeneity and also in the way they are formed. We distinguish two processes of group formation, namely social and environmental processes. Social processes concern forms of social attraction, and environmental processes relate to attraction to food resources, shelter and the like. Below we discuss models for each process separately and for their combination.

### 22.2.1 *Social Attraction*

Attraction is often mediated through visual and chemical cues. Visual attraction is important in many species of fish and birds. Chemical attraction (through pheromones) occurs among single celled individuals (such as bacteria and amoebae), ants and beetle larvae.

One of the simplest aggregation processes has been studied in certain experiments and models of cluster formation of beetle larvae (Camazine et al. 2001). In their natural habitat, these beetle larvae live in oak trees and grouping helps them to overcome the production of toxic resin by the host tree. They emit a pheromone and move towards higher concentrations of this chemical. In the experimental setup, larvae are kept in a Petri dish. In the model, the behavioural rules of following a gradient are represented in individuals that roam in an environment that resembles a Petri dish. It appears that both in the model and in the experiment the speed of cluster growth and the final number and distribution of clusters depend on the initial distribution and density of the larvae. By means of both model and experimental data it has been shown that cluster growth can be explained by a positive feedback. A larger group emits more pheromone and therefore attracts more members. Consequently, its size increases in turn emitting more pheromone, etcetera. This process is faster at a higher density, because individuals meet each other more frequently. Thus clusters appear sooner. Furthermore, growth is faster at higher densities, because more individuals are available for growing.

The location of the clusters has been studied. After starting from a random distribution of individuals, a single cluster remains in the centre of the Petri dish. This location is due to the higher frequency with which individuals visit the centre than the periphery. Starting from a peripheral cluster, there is an attraction to both the peripheral cluster and the centre. Thus, there is a kind of competition between clusters to attract additional individuals. The final distribution of clusters may consist of one cluster (at the centre, the periphery or at an intermediate location), or of two clusters (peripheral and in the centre). The final distribution depends on

self-organisation and on three factors, namely, the initial density of individuals, initial distribution of clusters, and whether there is social attraction. Although the model is devised for the specific experimental setup and species, the mechanisms of group formation and growth shown in the model are found in many animal species. For instance, similar patterns are observed in models and experiments of cockroaches.

Cockroaches aggregate by sensing the relative humidity. They tend to move towards lower humidity. Here larger groups grow faster, because individuals have a higher tendency to stop and form a group if they collide with a larger number of others. Besides, they rest longer if more individuals are resting close by. They use the relative humidity as a cue to estimate the number of individuals. A lower relative humidity correlates with a higher number of individuals close by (Jeanson et al. 2005). Despite the different underlying process of social attraction (pheromonal, visual or based on relative humidity) pattern formation is similar to that of beetle larvae.

### **22.2.2 Foraging**

A model that deals with group formation solely through environmental causes concerns the splitting and merging of groups as it is found in the so-called fission-fusion system of primates, in particular that of spider monkeys (Ramos-Fernández et al. 2006). It relates the pattern of group formation to various distributions of food, because particularly in these fission-fusion societies, the food distribution may have an effect on grouping. In the model, the food distribution is based on a distribution of resources in forests that follows an inverse power law as described by Enquist and co-authors (Enquist and Niklas 2001; Enquist et al. 1999). The foragers maximise their food intake by moving to larger food patches that are closer by (they minimise the factor distance divided by patch size). Further, they do not visit patches that they have visited before. Individuals have no social behaviour and they meet in groups only because they accidentally visit the same food patch. For a distribution with both large and small trees (patches) in roughly equal numbers the model leads to a frequency distribution of subgroup sizes that resembles that of spider monkeys. Results hold, however, only if foragers have complete knowledge of the environment in terms of patch size and distance. The resemblance is not found if individuals only know (a random) part of the environment. Furthermore, if they have complete knowledge, individuals meet with certain partners more often than expected if the choice of the food patch is a random choice. In this way, certain networks of encounters develop. Another serious shortcoming of the model is that food can only be depleted; there is no food renewal and individuals do not return to former food patches. The main conclusion is that the ecological environment influences grouping: Ecologies that differ in the variation of their patch sizes (high, medium or low variance) also differ in the distribution of subgroup sizes. This model delivers mainly a proof of principle.

### ***22.2.3 Combination of Social and Environmental Processes***

The relation between ecology and sub-group formation is also shown in a simulation study of orang-utans in the Ketambe forest in Indonesia (te Boekhorst and Hogeweg 1994a). The predictions for and resemblance to empirical data that are delivered in this model (te Boekhorst and Hogeweg 1994a) are more specific than those in the model of spider monkeys discussed above (Ramos-Fernández et al. 2006). Here, realistic patterns of grouping arise from simple foraging rules in interaction with the structure of the forest and in the presence of two social rules. The environment and population are built to resemble the Ketambe area in the composition of the community and the size of the habitat. Two main categories of food trees are distinguished, figs (very large and non-seasonal) and fruit trees (small and seasonal). There are 480,000 trees of which 1,200 bear fruit at the same time, once a year for ten consecutive days unless depleted earlier by the individuals. The crop size and spatial distribution of trees are specified: fig trees are clustered and fruit trees distributed randomly. Furthermore there are randomly distributed sources of protein. These are renewed immediately after being eaten. In the fruiting season extra individuals migrate into the area. With regard to the behavioural rules, individuals first search for a fig tree. If this is not found, while moving approximately in the direction of others, because other individuals may indicate the presence of food on a distant fig tree, individuals look for fruits close by. Upon entering a tree, the individual feeds until satiated or the tree is emptied. Next the individual rests close by and starts all over again later on. A further social rule causes adult males to avoid each other.

The resulting grouping patterns in the model resemble those of real orang-utans in many respects: Temporary aggregations are found in the enormous fig trees. This happens because in these big trees individuals may feed until satiated and then leave separately. However, when feeding in the much smaller fruit trees, food is insufficient and therefore individuals move to the next tree. This causes them to travel together. Thus, travelling bands develop mainly in the fruit season. In this season parties are larger than when fruit is scarce. Groupings emerge as a consequence of simple foraging rules in interaction with the forest structure. Thus, the model makes clear that differences between forest structures will lead to different grouping patterns in apes. This is a parsimonious explanation, because it is not necessary to think in terms of costs and benefits of sociality to explain these grouping patterns, rather they arise as a side effect of feeding behaviour. The empirical data analysis and ideas for the model of orang-utans were inspired by findings in another model on grouping in chimpanzees.

This model of chimpanzees concerns both foraging and social attraction and is meant to explain group formation, in particular the fission-fusion society (te Boekhorst and Hogeweg 1994b). It offers new explanations for the relatively solitary life of females and the numerous and large subgroups of males. Subgroups of males had so far been supposed to form in order to join in defending the community. To explain such cooperation, males were believed to be genetically

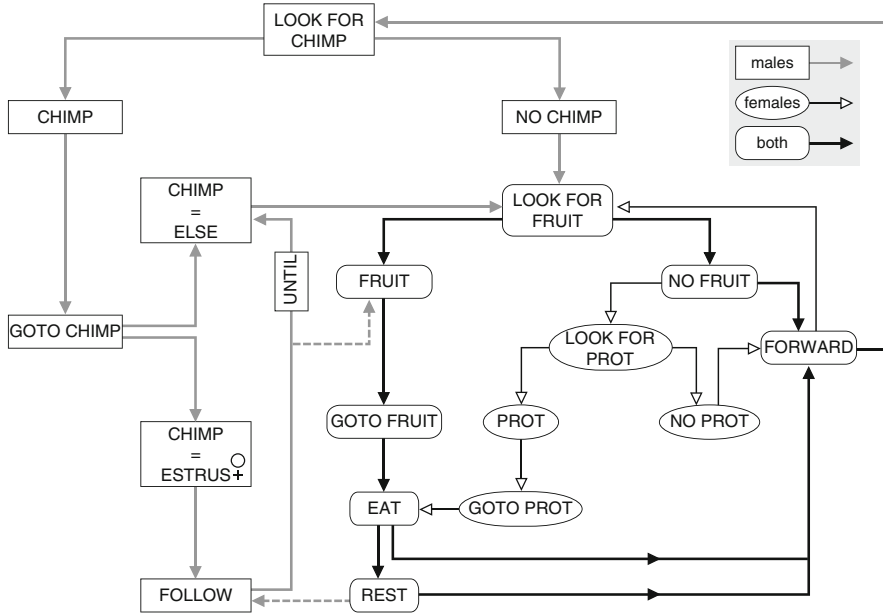


Fig. 22.1 Behavioural rules of artificial chimpanzees (te Boekhorst and Hogeweg 1994b)

related to each other. Further, the solitary life of females was attributed to competition for food. However, the model shows that their patterns of grouping may arise in an entirely different way: they may result from a difference between the sexes in diet and in the priority of foraging versus reproduction. The model resembles a certain community of chimpanzees in Gombe in its community composition (number of males and females, 11 and 14 respectively, and the number of females that are synchronously in oestrus) and its habitat size (4 km<sup>2</sup>), its number of trees, the number of trees that bear fruit at the same time, the length of their fruit bearing, their crop size, and the speed of their depletion. The number of protein resources is modelled more arbitrarily, approximating such forests. With regard to their behavioural rules, individuals of both sexes look for fruit and when satiated have a rest close to the tree (Fig. 22.1). If not satiated they move towards the next fruit tree. They continue to do this until they are satiated. If there is no fruit on a specific tree, females (but not males) look for proteins before searching another fruit tree. Males have one priority over finding food: finding females. Whenever they see a chimpanzee, they approach it to investigate whether it is a female in oestrus. If this is the case, males in the model follow her until she is no longer in oestrus.

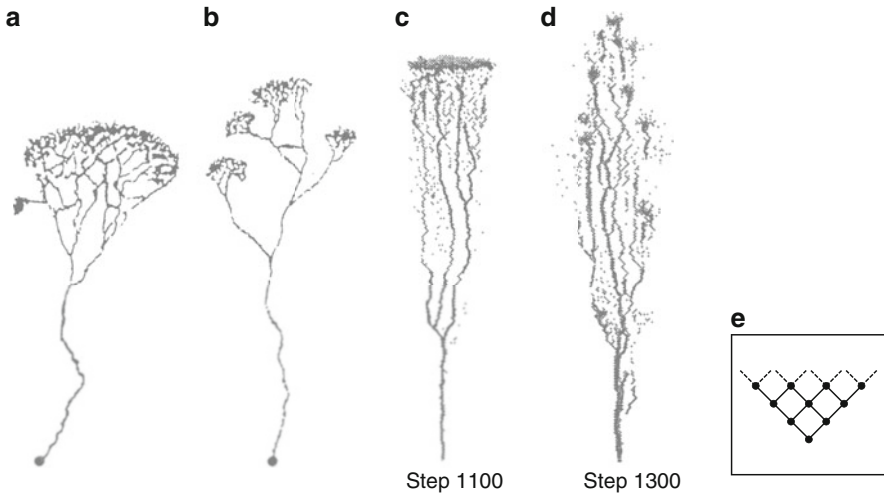
In the model, patterns of grouping resemble those of real chimpanzees. Male groups emerge because all males have the same diet which differs from that of females and because they will follow the same female in oestrus together. Furthermore, in the model, as in real chimpanzees, males appear to travel over longer distances per day than females. They do so because they are travelling in larger

groups and this leads to faster depletion of food sources and therefore they have to visit a larger number of trees in order to become satiated. This interconnection between the number of trees visited, group size and distance covered led to the hypothesis for orang-utans that different kinds of groupings (aggregation and travel bands) originate in different trees (fig and fruit). Note that these results were robust for a large range of different ecological variables and different compositions of the community. Here, a difference between the sexes in their diet and their priorities for sex and food appeared essential. With regard to the chimpanzee community, the authors conclude that, to explain its fission-fusion structure, the genetically based theory that kin-related males are jointly defending the community is not needed. In fact, in subsequent DNA studies no special genetic relatedness was found among cooperating male chimpanzees in Kibale (Goldberg and Wrangham 1997). Instead, chimpanzee-like party structures may emerge by self-organisation if chimpanzees search for food and for mates in a forest. Besides, the model can be used to explain the frequent bi-sexual groups observed in bonobos as being caused by their prolonged period of oestrus. Whereas these models have been controversial among primatologists for a long time, their usefulness is slowly becoming accepted (Aureli et al. 2008).

#### ***22.2.4 Group Coordination and Foraging***

Groups of social insects, for instance ants, are remarkably efficient in foraging. They collectively choose a food source that is closer rather than one (of the same quality) that is further away (Deneubourg and Goss 1989). Their choice is made without comparing the distance to different food sources. Experiments and models show that ants use trail pheromones as a mechanism of collective ‘decision’ making: Individuals mark their path with pheromone and at crossings follow the path that is more strongly marked. As they return to the nest sooner when the food source is close by, they obviously imprint the shorter path more often with pheromones. This results in a positive feedback: as the shorter path receives stronger markings, it also receives more ants, etcetera. Thus, the interaction between ants and their environment results in the adaptive and efficient exploitation of food sources. The ‘preference’ for a food source nearby rather than one further away is a side-effect of pheromonal marking. This marking also helps a single ant to find its way and may initially have been an adaptation to cause the ant to return to its nest. It is actually more than just that, because its intensity is adapted to the quality of the food source. The process of marking and following may also lead to mistakes. For instance, if a path is initially developed to a food source of low quality, and later to a food source of high quality is introduced elsewhere, due to ‘historical constraint’ the ants may remain fixated on the source of low quality even if it is further from the nest.

Army ants live in colonies of 200,000 individuals; they are virtually blind; they travel in a swarm with about 100,000 workers back and forth to collect food.

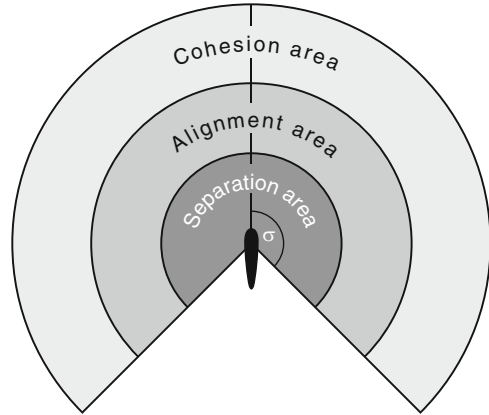


**Fig. 22.2** Foraging patterns of two species of army ants, *Eciton burchelli* and *Eciton rapax*, empirical data and models. Empirical data: *Eciton burchelli* (a) and *Eciton rapax* (b); models: (c) a few food clumps, (d) frequent occurrence of single food items, (e) network of nodes (After Deneubourg and Goss 1989)

Different species of army ants display highly structured patterns of swarming that may be species specific (Fig. 22.2a, b). For example, *Eciton burchelli* has a more dispersed swarm than *E. rapax*. Such species-specific differences in swarming are usually regarded as a separate adaptation, which is assumed to be based on corresponding differences in the underlying behavioural tendencies of coordination. Deneubourg and co-authors (Deneubourg and Goss 1989; Deneubourg et al. 1998), however, give a simpler explanation. In a model, they have shown that such markedly different swarming patterns may arise from a single rule-system of laying and following pheromone trails when ants are raiding food sources with different spatial distributions (Fig. 22.2c, d). The authors have shown this in a model in which ‘artificial ants’ move in a network of points (Fig. 22.2e), and mark their path with pheromones. When choosing between left and right, they prefer the more strongly marked direction. By introducing different distributions of food in the model (either uniformly distributed single insects or sparsely distributed colonies of insects), different swarming patterns arise from the interaction between the flow of ants heading away from the nest to collect food and the spatial distribution of the foragers returning with the food. These different swarm types are remarkably similar to those of the two species of army ants mentioned above (for empirical confirmation see Franks et al. 1991). Therefore, these different swarm forms reflect the variation in diet of the different species. Thus, the explanation of the model is more parsimonious than if we assume the different swarm forms to arise from a specific adaptation in rules of swarming. In summary, this model teaches us the effects of the environment on swarm coordination.



**Fig. 22.3** Behavioural areas of avoidance (separation), alignment and attraction (cohesion) with a dead ('blind') angle at the back (From Hemelrijk and Hildenbrandt 2008). The separation angle is indicated as  $\sigma$



With regard to its evolution, natural selection shapes the necessary traits for the successful marking and following of trails depending on the size of the food source and other environmental characteristics (for an evolutionary model of this, see Solé et al. 2001).

### 22.2.5 Group Coordination in a Homogeneous Environment

Even in environments (such as the open sea, savannah and sky) that are virtually uniform without environmental structure, remarkable coordination is observed in the swarms of many animal species, e.g. of insects, fish, birds and ungulates. Coordination appears flexible even in swarms of a very large size (for instance, of up to ten million individuals in certain species of fish). Swarming behaviour has been modelled in several ways. The most simplistic representations of emergent phenomena have used partial differential equations. Slightly more complex behaviour has been obtained using particle-based models derived from statistical mechanics in physics (Vicsek et al. 1995). These models have been used to explain the phase transition of unordered to ordered swarms in locusts (Buhl et al. 2006). Yet the biologically most relevant results come from models wherein individuals coordinate with their local neighbours by following only three rules based on zones of perception (Fig. 22.3): They avoid neighbours that are close by (separation), align to others up to an intermediate distance (alignment) and approach those further away (cohesion). These models have been applied to describe herds of ungulates (Gueron et al. 1996), schools of fish (Couzin et al. 2002; Hemelrijk and Kunz 2005; Huth and Wissel 1992, 1994; Kunz and Hemelrijk 2003; for a review see Parrish and Viscido 2005), and swarms of birds (Hildenbrandt et al. 2010; Reynolds 1987; Hemelrijk & Hildenbrandt 2011; Hemelrijk & Hildenbrandt 2012).

Through these models we obtain insight into a number of important biological aspects of swarming, which have mainly been related to schools of fish.

Firstly, we get insight into the *coordination* of schools. Schools coordinate with remarkable flexibility even into the absence of a *leader* and without a directional preference. The direction of their movement is merely the consequence of the location and heading of others in the school. With regard to the question whether there is a leader in a swarm, such a leader fish is supposed to be located at the front (Bumann and Krause 1993). However, neither in such models of fish schools nor in real swarms individuals appear to have a fixed location. Instead frontal locations are continuously switched in the model on average every 2 s, in real fish every 1.4 s (Gnatapogon elongates, Huth and Wissel 1994). Thus, there cannot be consistent leaders.

Furthermore, if a number of individuals have a directional preference (for instance, for certain food sources or breeding locations), but most of them do not, those with such a preference will automatically lead the school. Huse and co-authors (Huse et al. 2002) showed that even if the percentage of individuals that has a certain preferred direction is very small (though above 7 %), this may influence the direction of the entire school.

If individuals prefer a different direction, for instance, because they aim to go to different food locations, the school may react differently depending on the degree to which two preferred directions differ (Couzin et al. 2005): If the directions differ little, the group will follow the average direction between the two ('a compromise'). If the angle between both directions is large, the group will either follow the direction that is preferred by the majority or in the absence of a 'convincing majority' it will randomly choose one of the two. In these examples of swarming the models help us to understand the processes that determine the direction in which a school is heading.

Secondly, we obtain insight into the *segregation* of individuals that differ in a certain trait. In a school, individuals may be segregated, for example, according to size. Usually this is attributed to an intentional or genetic preference for being near individuals of the same size or body form. Models show, however, that this segregation may also arise directly as a side-effect of differences in body size without any preference (e.g. see Couzin et al. 2002; Hemelrijk 2005; Kunz and Hemelrijk 2003). This may, for instance, arise because larger individuals due to their larger body have a larger range at which they avoid others who are too close. Thus, by avoiding smaller individuals more often than the reverse, large individuals may end up at the periphery leaving the small ones in the centre (as has been found in water insects (Romey 1995)).

Thirdly, natural schools of fish show a number of traits that are believed to be helpful in the *protection against predators*: Their shape is oblong and their density is highest at the front. Bumann et al. (1997) argue that an *oblong form* and *high frontal density* protect against predation: the oblong shape reduces the size of the frontal area, where predators are supposed to attack and high frontal density protects individuals against approaching predators. Hemelrijk and co-authors (Hemelrijk and Hildenbrandt 2008; Hemelrijk and Kunz 2005) have noted that it

is unlikely that individual fish actively organise themselves so as to create these two patterns. Therefore, the authors studied in a model whether these patterns might arise by self-organisation as a side-effect of their coordinated movements. This indeed appeared to be the case and their emergence appeared to be robust (independent of school size and speed). These patterns come about because, during travelling, individuals avoid collisions mostly by slowing down (as they do not perceive others to be directly behind them, in the so-called blind angle, Fig. 22.3). Consequently, they leave a gap between their former forward neighbours and subsequently these former neighbours move inwards to be closer together. Thus, the school becomes oblong.

Furthermore, when individuals fall back, a loose tail builds up and this automatically leaves the highest density at the front. In the model it appears that larger schools are relatively more oblong because they are denser and so more individuals fall back to avoid collision. Faster schools appear to be less oblong. This arises because fast individuals have greater difficulty to turn, thus, the path of the school is straighter, the school is more aligned (polarised) and, therefore, fewer individuals fall back. Consequently, the core of a faster school is denser and the tail is looser than they are in slower schools. Recent tests in real fish (mulletts) confirm the specific relationships between group shape, and its size, density, and polarisation as found in the model (Hemelrijk et al. 2010). Although this indicates that the shape in real schools develops in a similar way, it is still necessary to investigate shape and frontal density in more species and to study the effects of different speeds on these traits.

Fourth, in real animals predation and attacks on swarms result in a spectacular range of behavioural *patterns of evasion by schooling prey*. These patterns are supposed to confuse the predator. They have been labelled ‘tight ball’, ‘bend’, ‘hourglass’, ‘fountain effect’, ‘vacuole’, ‘split’, ‘join’, and ‘herd’. They have been described for schools of several prey species and predators (Axelsen et al. 2001; Lee 2006; Nottestad and Axelsen 1999; Parrish 1993; Pitcher and Wyche 1983). Most of these patterns may be obtained in a model by simple behavioural rules of prey and predator (e.g., see Inada and Kawachi 2002). Many of the different patterns of evasion result in self-organisation in models of schooling which are built in such a way that upon detecting the predator, individuals compromise between their tendency to avoid the predator, and to coordinate with their group members. Though these models do not exactly fit real data, they give us insight into how specific collective evasion patterns may arise.

### 22.3 Social Organisation

Although groups may be beneficial for their members in so far as they provide protection against predation, they also result in competition for food, mates and space. If individuals meet for the first time, such competitive interactions may initially have a random outcome. Over time, however, a dominance hierarchy

develops, whereby certain individuals are consistently victorious over others and are said to have a higher dominance value than others (Drews 1993). Individuals may perceive the dominance value of the other from the body posture of the other (in primates) or from their pheromone composition (in insects).

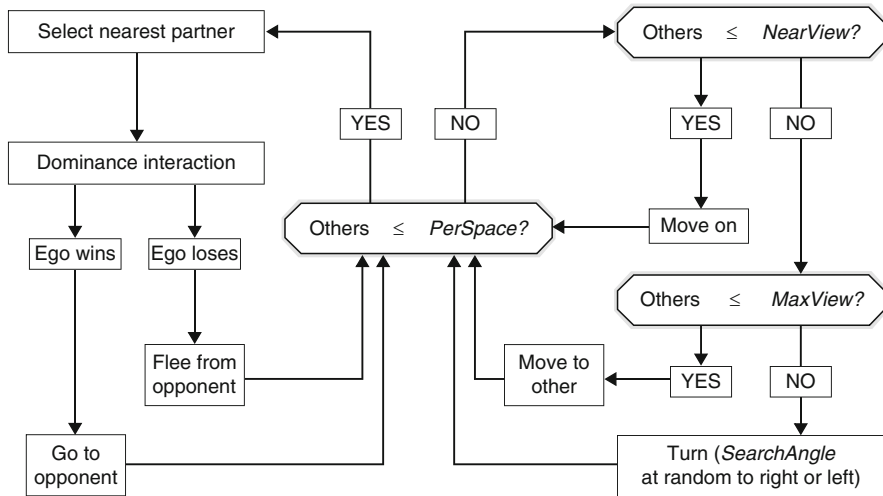
With regard to the question which individual becomes dominant, there are two extremely opposing views: dominance as a fixed trait by inherited predisposition and dominance by chance and self-organisation. While some argue for the importance of predisposition of dominance by its (genetic) inheritance (Ellis 1991), others reject this for the following reasons: Experimental results show that the dominance of an individual depends on the order of its introduction in a group (Bernstein and Gordon 1980). Dominance changes with experience, because the effects of victory and defeat in conflicts are self-reinforcing, the so-called winner-loser effect. This implies that winning a fight increases the probability of victory in the next fight and losing a fight increases the probability of defeat the next time. This effect has been established empirically in many animal species and is accompanied by psychological and physiological changes, such as hormonal fluctuations (Bonabeau et al. 1996a; see Chase et al. 1994; Hemelrijk 2000; for a recent review, see Hsu et al. 2006; Mazur 1985).

The self-reinforcing effects of fighting are the core of a model called *DomWorld*, which concerns individuals that group and compete (Hemelrijk 1996, 1999b; Hemelrijk and Wantia 2005). It leads to a number of emergent phenomena that have relevance for many species, in particular for primates and more specifically macaques.

### 22.3.1 *The Basic DomWorld Model*

The model *DomWorld* consists of a homogeneous world in which individuals are grouping and competing. It does not specify what they compete about. Grouping is implemented by making individuals react to others in different manners depending on the distance to the other (Fig. 22.4). An individual is attracted to others far away (within *MaxView*), it continues to follow its direction if it perceives others at an intermediate distance (within *NearView*), and it decides whether or not to perform a competitive dominance interaction if it encounters others close by (within *PerSpace*) (Hemelrijk 2000). After winning a dominance interaction, it chases away the other and after losing a fight, it flees from it.

Dominance interactions are implemented after the *DoDom* interactions by Hogeweg (Hogeweg and Hesper 1985), which were extended to reflect differences in the intensity of aggression between species and between the sexes and with the decision whether or not to attack depending on risks involved (Hemelrijk 1998, 1999b). Each individual has a dominance value which indicates the individual's capacity to win. At the beginning of a competitive interaction both individuals display their dominance value and observe that of the other. The outcome of the fight depends on the relative dominance of both partners and on chance.

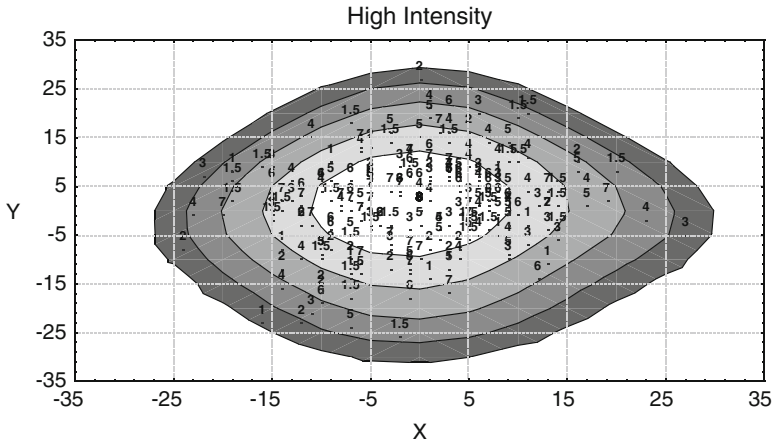


**Fig. 22.4** Flowchart of the behavioural rules of individuals in DomWorld. PerSpace, NearView and MaxView indicate close, intermediate and long distances, respectively

The probability of winning is higher the higher the dominance value of an individual in relation to that of the other. Initially, the dominance values are the same for all individuals. Thus, during the first encounter, chance decides who wins. After winning, the dominance of the winner increases and that of the loser decreases. Consequently, the winner has a greater chance to win again (and vice versa) which reflects the self-reinforcing effects of the victories (and defeats) in conflicts of real animals.

We allow for rank reversals; when, unexpectedly, a lower-ranking individual defeats a higher-ranking opponent, this outcome has a greater impact on the dominance values of both opponents, which change with a greater amount than when, as we would expect, the same individual conquers a lower-ranking opponent (conform to detailed behavioral studies on bumble bees by van Honk and Hogeweg 1981). Furthermore, in their decision whether or not to attack, we made individuals sensitive to the risks, i.e. the ‘will’ to undertake an aggressive interaction (instead of remaining non-aggressively close by) increases with the chance to defeat the opponent, which depends on the relative dominance ranks of both opponents (Hemelrijk 1998).

We also represented the intensity of aggression in which primate societies differ (in some species individuals bite, in other species they merely approach, threaten and slap) as a scaling factor (called StepDom) that weighs the changes in dominance value after a fight more heavily if the fight was intense (such as biting) than if the fight was mild (involving threats and slaps, or merely approaches and retreats) (Hemelrijk 1999b). In several models, we distinguished two types of individuals representing males and females (Hemelrijk et al. 2003). We gave males a higher initial dominance value and a higher intensity of aggression (reflecting their larger



**Fig. 22.5** Spatial-social structure. *Darker shading* indicates areas with individuals of decreasing dominance rank

body size, stronger muscular structure and larger canines than those of females). In fights between both types of individuals, the intensity of the fight was determined by the initiator (the attacker).

### 22.3.2 *Spatial Structure*

The major advantage of group life is supposedly to be protection against predators. Central positions are supposed to be safest, because here individuals are shielded off by other group-members from predators approaching from the outside. Therefore, according to the well-known ‘selfish herd’ theory of Hamilton (1971), individuals have evolved a preference for a position in the centre, the so-called ‘centripetal instinct’. If competition for this location is won by dominants, dominants will end up in the centre. This is thought to be the main reason why in many animal species dominants are seen to occupy the centre. However, in DomWorld this spatial structure emerges, even though such a preference is lacking and there is no ‘centripetal instinct’ nor threat of predation (Hemelrijk 2000).

The spatial configuration, with dominant individuals in the centre and subordinates at the periphery of the group (Fig. 22.5), emerges in the model due to a feedback between the dominance hierarchy and the spatial location of the individuals of different rank. During the development of the hierarchy, some individuals become permanent losers. Such low-ranking individuals must end up at the periphery by being constantly chased away. This automatically leaves dominants in the centre. Also, in real animals, such a spatial structure may occur although its members have no centripetal instinct nor experience a threat of predation. For instance, in the elegant experiments with fish by Krause (1993),

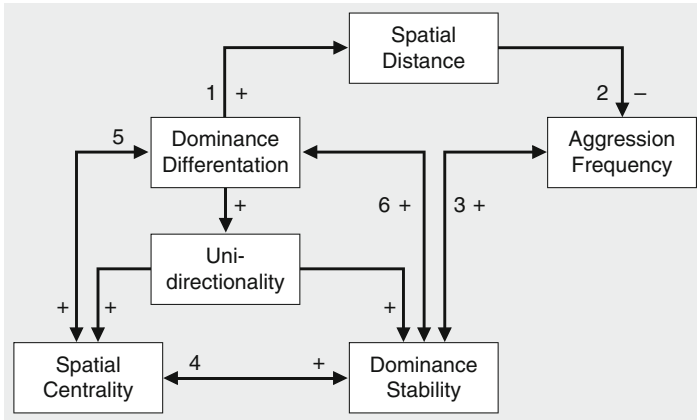
central dominants were observed, although no centre-oriented locomotion appeared (Krause and Tegeder 1994). Furthermore, this spatial structure has been described in hammerhead sharks in spite of the absence of any predatory threat (Klimley 1985). Thus, the model provides a new way of understanding spatial structure.

### 22.3.3 *Dominance Style: Egalitarian and Despotic Societies*

High dominance ranking is supposed to be associated with benefits such as priority of access to mates, food and safe locations. If benefits are strongly biased towards higher-ranking individuals, the society is called ‘despotic’, whereas if access to resources is more equally distributed, it is called ‘egalitarian’. These terms have been used to classify social systems of many animal species (such as insects, birds and primates). Egalitarian and despotic species of primates, such as macaques, appear to differ in many other traits too, such as in group density, their intensity and frequency of aggression and in their frequency and patterns of affiliation (grooming). Usually these differences are explained from the perspective of optimisation of single traits by natural selection. However, Thierry (1990b) suggests that in macaques the many behavioural differences can be traced back to two inherited differences, namely degree of nepotism (i.e. cooperation among kin) and intensity of aggression. Note that despotic macaques display aggression of a higher intensity, i.e. they bite more often, whereas egalitarian macaques display aggression that is milder, they only threaten and slap.

The model *DomWorld* presents an even simpler hypothesis (Hemelrijk 1999b), namely that a mere difference in intensity of aggression produces both types of societies. By increasing the value of one parameter, namely that of intensity of aggression, the artificial society switches from a typically egalitarian society to a despotic one. For instance, compared to egalitarian artificial societies, despotic ones are more loosely grouped, showing a higher frequency of attack, their behaviour is more rank-related, aggression is more asymmetric, spatial centrality of dominants is clearer and female dominance over males is greater. All these differences between despotic and egalitarian societies arise via feedback between the development of the hierarchy and spatial structure and this happens only at a high intensity of aggression. The steep hierarchy develops as a consequence of the high aggression intensity, because each outcome has a stronger impact than at a low intensity and it is strengthened further via a mutual feedback between the hierarchy and the spatial structure with dominants in the center and subordinates at the periphery (Hemelrijk 1999b, 2000).

Pronounced rank-development causes low-ranking individuals to be continuously chased away by others and thus the group spreads out (1 in Fig. 22.6). Consequently, the frequency of attack diminishes among the individuals (2 in Fig. 22.6) and therefore the hierarchy stabilizes (3 in Fig. 22.6). While low-ranking individuals flee from everyone, this automatically leaves dominants in the center, and thus a spatial-social structure develops (Fig. 22.5). Since individuals of similar



**Fig. 22.6** Interconnection between variables causing spatial-social structuring at a high aggression intensity

dominance are treated by others in more or less the same way, similar individuals remain close together; therefore, they interact mainly with others of similar rank; thus, if a rank reversal between two opponents occurs, it is only a minor one because opponents are often similar in dominance. In this way the spatial structure stabilizes the hierarchy and it maintains the hierarchical differentiation (4 and 5 in Fig. 22.6). Also, the hierarchical differentiation and the hierarchical stability mutually strengthen each other (6 in Fig. 22.6).

In short, the model (Hemelrijk 1999b) makes it clear that changing a single parameter representing the intensity of aggression, may cause a switch from an egalitarian to a despotic society. Since all the differences resemble those found between egalitarian and despotic societies of macaques, this implies that in real macaques these differences may also be entirely due to a single trait, intensity of aggression. Apart from intense aggression, such as biting, however, a high frequency of aggression can also cause this switch (Hemelrijk 1999a). A higher frequency of aggression also leads to a steeper hierarchy. This in turn, results in a clearer spatial structure which again strengthens the development of the hierarchy and this has the cascade of consequences as described for aggression intensity.

One of the shortcomings of the model may be considered as the lack of individual recognition among group members. In a subsequent model, this was corrected by having each individual keep a record of the dominance value of each group member. This value was updated depending on its experiences gained with other group members (Hemelrijk 1996, 2000). With regard to the development of spatial structure, hierarchy and dominance style remained similar, but patterns were weaker than in the case of a direct perception of dominance without individual recognition. Weaker patterns arise due to the contradictory experiences that different individuals have with specific others. This will impede a hierarchical development and thus weaken the accompanying consequences. Even though this may be



more realistic for certain modelling purposes, it is more useful to have clearer patterns in a simpler model. Such a caricature is more helpful for building upon understanding and developing new ideas.

Dominance style is usually considered to be species specific, but Preuschoft and colleagues (Preuschoft et al. 1998) raised the question whether competitive regimes (egalitarian versus despotic) should not rather be considered as sex specific. In their study of the competitive regime of both sexes of Barbary macaques, they found an unexpected sex difference: males behave in an egalitarian way whereas females are despotic. It is unexpected that the sex with the larger body size and fiercer aggression evolved a more egalitarian dominance style. Therefore, it seems to be a separate adaptation. However, the same difference in dominance style between the sexes was also found in DomWorld: males appear to be more egalitarian than females. The unexpectedly stronger egalitarianism of males in the model is due to yet another difference between the sexes, the higher initial dominance of males compared to females (which relates to differences in body size). Consequently, single events of victory and defeat have less impact on their overall power or dominance. Therefore, they lead to less hierarchical differentiation than among females, who are much smaller and weaker and on whom each victory and defeat therefore has more impact. The greater the sexual difference in initial dominance between the sexes, the more egalitarian the males behave among themselves compared to the behaviour of the females among themselves. The conclusion of this study is that the degree of sexual dimorphism may influence the competitive regime of each sex, in the model and in real primates. Further empirical studies are needed to investigate whether the degree of sexual dimorphism is directly proportional to the steepness of the gradient of the hierarchy of females compared to males.

With regard to its evolution, dominance style is supposed to be a consequence of different degrees of competition within and between groups (van Schaik 1989). According to this theory, when competition within groups is high and that between groups is low, despotic societies evolve and if it is reversed, and competition between groups is high, egalitarian groups emerge. In line with this, DomWorld already shows that high competition within a group leads to a despotic society (Hemelrijk 1999b). However, in a subsequent study, competition between groups appears to favour despotic rather than egalitarian groups (Wantia 2007). To study effects of competition between groups, the DomWorld model was extended to several groups (i.e. GroupWorld, Wantia 2007). Here, as in real primates, usually individuals of high rank participate in encounters between groups (e.g. see, Cooper 2004).

The model generates a number of unexpected results. Firstly, among groups of the same dominance style, competition between groups does not affect dominance style, since it happens at a very low frequency compared to competition within groups. However, in competition between groups of different dominance style, remarkable results came to light. Unexpectedly, under most conditions groups with a more despotic dominance style were victorious over others with a more egalitarian style. This arose due to the greater power of individuals of the highest rank of the despotic group compared to that of the egalitarian group. In the model, this is a consequence of the steeper hierarchy in despotic groups compared to that in

egalitarian groups. In reality this effect may be even stronger, because higher-ranking individuals may also obtain relatively more resources in a despotic group than in an egalitarian one. The outcome of fights between groups depends, however, on the details of the fights between groups and the composition of the group. When participants of inter-group fights fought in dyads or in coalitions of equal size, the despotic group out-competed the egalitarian one. If, however, individuals of egalitarian groups, for one reason or another, fought in coalitions of a larger size or if their coalitions included more males than those of the despotic groups, the egalitarian group had a chance to win. Thus, the main conclusion of the study is that it depends on a number of factors simultaneously, which dominance style will be favoured. Therefore, this model suggests that group composition and details of what happens in fights between groups should be studied in order to increase our understanding of the origination of dominance style.

### ***22.3.4 Distribution of Affiliation, Grooming***

Grooming (to clean the pelage of dirt and parasites) is supposed to be altruistic and therefore it should be rewarded in return (Trivers 1971). Using the theory of social exchange, Seyfarth (1977) argues that female primates try to exchange grooming for receipt of support in fights. For this, they direct the supposedly altruistic grooming behaviour more towards higher- than towards lower-ranking partners. As a consequence of this supposed competition for grooming partners of high rank, and by being defeated by dominant competitors, females will end up grooming close-ranking partners most frequently and are groomed themselves most often by females ranking just below them. According to him, this explains the following grooming patterns that are apparent among female primates: (a) high ranking individuals receive more grooming than others and (b) most grooming takes place between individuals that are adjacent in rank.

DomWorld presents a simpler alternative for the explanation by Seyfarth (Hemelrijk 2002b) in which a mental mechanism of social exchange for future social benefits is absent, for newer updates see Puga-Gonzalez et al. (2009), Hemelrijk and Puga-Gonzalez (2012). This is important, because it is doubtful whether grooming involves any real costs at all (see Wilkinson 1988).

The core of the argument is that individuals more often groom those whom they encounter more frequently. In the case of spatial structure with dominants in the centre and individuals in closer proximity to those that are closer in dominance (as described for primates (e.g. see Itani 1954)), these patterns will follow automatically. Individuals more often groom those that are nearby in rank (as found by Seyfarth 1977). Further, because dominants are more often in the centre, they are frequently surrounded on all sides by others. Subordinates, however, are at the edge of the group, and therefore have nobody on one side. Consequently, dominants simply meet others more frequently than subordinates do (as is shown in

DomWorld Hemelrijk 2000). Therefore, dominants are more often involved in grooming than subordinates (as found by Seyfarth).

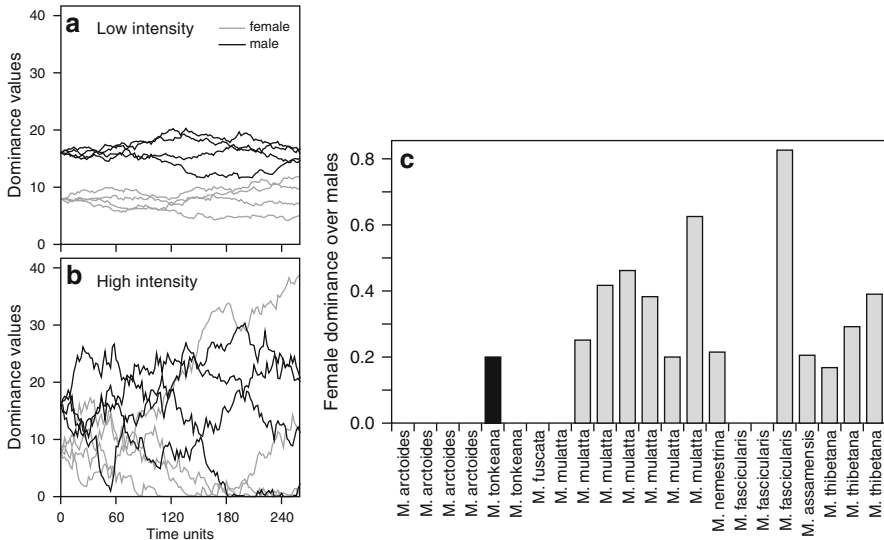
In support of the model, grooming patterns in despotic macaques appear to be more dominance oriented, and in egalitarian species grooming is more often directed at anyone (Thierry et al. 1990). To establish the relevance of this model-based hypothesis for real primates, it should be tested further in more species and groups, whether or not the patterns of grooming among individuals of similar rank and of the receipt of grooming by individuals of higher rank occur especially in groups with centrally located dominants, and less so in those with a weak spatial structure.

### 22.3.5 *Dominance Relationships Between the Sexes*

Most primate species live in bi-sexual groups. Apart from the order of Lemuriformes, males are usually dominant. However, variation occurs and even if males are larger than females, females are sometimes dominant over a number of them (Smuts 1987). To study whether this may arise through chance and the self-reinforcing effects of dominance interactions, the sexes are modelled in DomWorld. When, for the sake of simplicity, the sexes in DomWorld are distinguished only in terms of an inferior fighting capacity of females as compared to that of males, then, surprisingly, males appear to become less dominant over females at a high intensity of aggression than at a low intensity (Hemelrijk 1999b; Hemelrijk et al. 2003). This is due to the stronger hierarchical differentiation, which causes the hierarchy to develop in a more pronounced way. This implies that the hierarchy is also more strongly developed for each sex separately. Since this differentiation increases the overlap in dominance between the sexes, it causes more females to be dominant over males than in the case of a hierarchy that has been less developed (Fig. 22.7a, b).

Similarly to females, adolescent males of despotic macaques have more ease than those of egalitarian species in outranking adult females (Thierry 1990a). Thierry explains this as a consequence of the stronger cooperation to suppress males among related females of despotic macaques than of egalitarian ones, and van Schaik (1989) emphasizes the greater benefits associated with coalitions for females of despotic species than egalitarian ones. However, DomWorld explains greater female dominance, as we have seen, simply as a side-effect of more pronounced hierarchical differentiation.

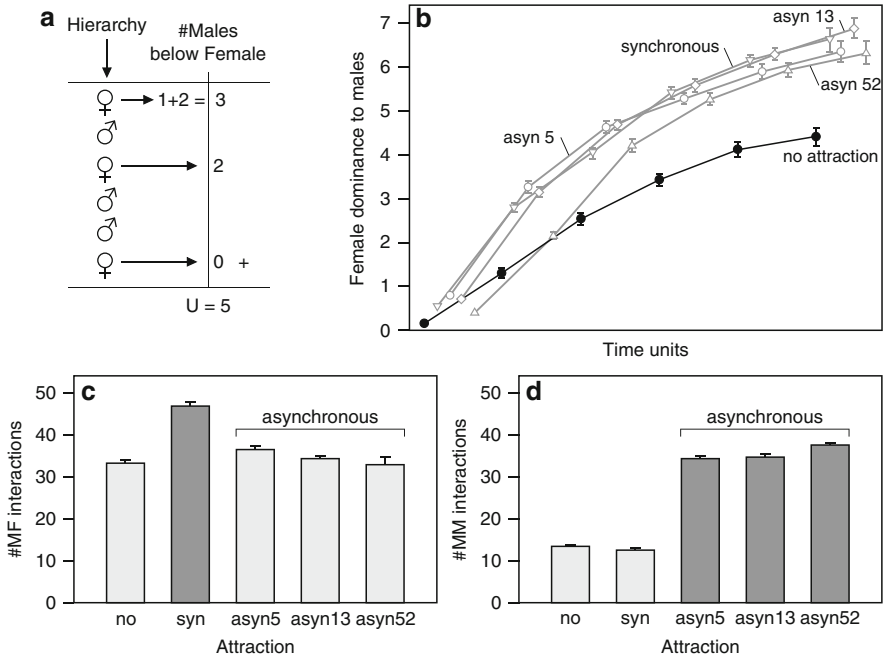
Differences in overlap of ranks between the sexes may affect sexual behavior. Males of certain species, such as Bonnet macaques, have difficulty in mating with females to which they are subordinate (Rosenblum and Nadler 1971). Therefore, following the model, we expect that despotic females (because they outrank more males) have fewer males to mate with than egalitarian ones. In line with this, in macaques despotic females are observed to mate with fewer partners and almost exclusively with males of the highest ranks (Caldecott 1986); this observation is



**Fig. 22.7** Female dominance over males or degree of rank overlap: (a, b) female dominance over males over time and aggression intensity (Hemelrijk 1999b), (c) degree of rank overlap of females with males (i.e. female dominance over males) in groups of egalitarian macaques (in black) and in groups of despotic macaques (in grey) (Hemelrijk et al. 2008)

attributed to the evolution of a more pronounced female preference in despotic than in egalitarian species of macaques. The explanation derived from the model, however, is simpler. In a subsequent study, in support of this hypothesis, the relative dominance position of both sexes in egalitarian and despotic macaque species indeed appeared to differ in macaques as expected: females of despotic species were dominant over a significantly higher percentage of the males in their group than females of egalitarian species (Fig. 22.7c).

In a similar way as high aggression intensity, a high frequency of aggression in the model also results in more female dominance. A higher frequency of aggression in the model can be obtained by increasing the SearchAngle over which individuals search for others (Fig. 22.4). Due to a greater SearchAngle they return to the others sooner, the group becomes denser and thus the frequency of aggression is higher. A difference in group density may be of relevance to the difference in female dominance observed between common chimpanzees and bonobos (also known as pygmy chimpanzees (Stanford 1998)). Despite their similar sexual dimorphism, female dominance in pygmy chimpanzees is higher than in common chimpanzees. This is usually attributed to more intensive coalition formation among pygmy females against males. However, in line with DomWorld, we may also explain it as a side-effect of the difference in density between both species (Hemelrijk 2002a, 2003). Density is high in groups of pygmy chimpanzees. Due to the higher density there is a higher frequency of aggression and according to DomWorld this may result in more female dominance over males. This hypothesis should be tested by



**Fig. 22.8** Female dominance over males and sexual attraction. (a) Measurement of female dominance; (b) female dominance over males over time without attraction (control) and when attracted to females that cycle synchronously and asynchronously; (c) number of interactions between sexes with(out) attraction during (a) synchronously cycling; (d) number of interactions among males with(out) attraction during (a) synchronously cycling. *Asyn* asynchronous cycles; 5, 13, 52 are duration of estrus period

comparing different groups of bonobos and by studying the relationship between female dominance and frequency of aggression.

Sexual attraction in real animals is usually thought to be accompanied by strategies of exchange. For instance, chimpanzee males are described as exchanging sex for food with females (Goodall 1986; Stanford 1996; Tutin 1980). Yet, in spite of detailed statistical studies, we have found no evidence that males obtain more copulations with, or more offspring from those females with whom they share their food more often (Hemelrijk et al. 1992, 1999, 2001; Meier et al. 2000). Male tolerance of females seems to increase during the females’ period of estrus even without noticeable benefits. Thus, we need another explanation for male tolerance of females. DomWorld provides us with such an alternative hypothesis. ‘Sexual attraction’ of males to females is implemented in such a way that males have a greater inclination to approach females than individuals of their own sex. In the model (and in the preceding models and empirical studies of Fig. 22.7), we measure the relative dominance position of females compared to males by counting the number of males ranking below each female and calculating this figure (Mann–Whitney U-value, Fig. 22.8a). It appears that this value of relative female

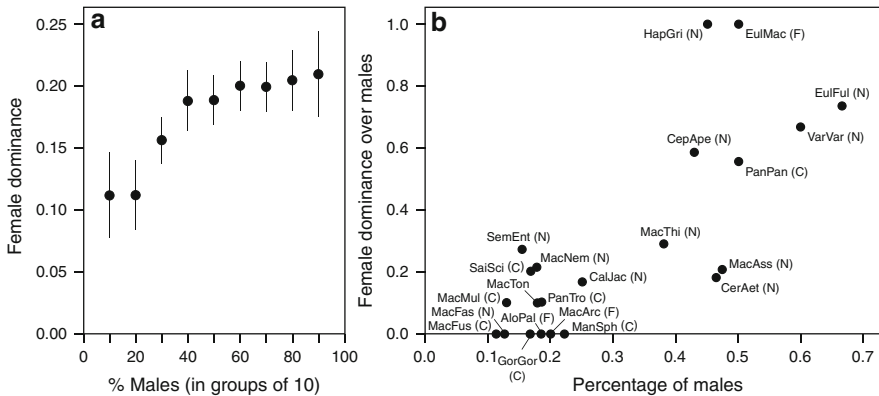
dominance to males increases with sexual attraction as an automatic consequence of the more frequent encounters between the sexes (Fig. 22.8b, synchronous). This result is in line with the observation that female dominance in chimpanzees increases when males are sexually attracted to the females (Yerkes 1940). The question of whether female dominance over males also increases during sexual attraction in other species should be studied in the future.

Whereas the examples mentioned above concern species in which females are synchronously sexually attractive (tumescent), in other species they cycle asynchronously. In the model, however, female dominance over males is relatively similar regardless of whether they are attractive synchronously or asynchronously (Fig. 22.8b, synchronous, asyn). The process leading to increased female dominance differs, however, for the two conditions. If single females are attractive in turn, many males cluster close to a single female. Consequently, in contrast to synchronous tumescence, the frequency of interaction between the sexes remains similar to that when females are not attractive to males, but the frequency of male-male interactions is increased markedly (Fig. 22.8c, d). Due to the higher frequency of interactions among males, the differentiation of the male hierarchy is stronger than without attraction and this causes certain males to become subordinate to some females (Fig. 22.8b, asyn).

Furthermore, the adult sex ratio (or percentage of males) in the group influences the relative dominance of females compared to that of males (Hemelrijk et al. 2008). Female dominance appears to be higher when there are more males in the group (Fig. 22.9a). This arises from a shift in the relative number of intra- and inter-sexual interactions. A higher proportion of males causes both sexes to interact more often with males. Due to the males' higher intensity of aggression, this causes a greater differentiation of the dominance values of both females and males. Consequently, at a high intensity of aggression, the hierarchy of females overlaps more with that of males and thus, the dominance position of females is higher in relation to males than if there are fewer males in the group. Subsequent analysis of these patterns in real primates has confirmed that female dominance increases with a higher percentage of males in the group (Fig. 22.9b). It appeared that in line with the preceding modelling results, in groups of a despotic species (rhesus macaques) a higher percentage of males appeared to be correlated with greater female dominance over them, whereas such a correlation was absent among groups of an egalitarian species (stump-tailed macaques).

### 22.3.6 *Strategies of Attack*

When real animals are brought together for the first time, they perform dominance interactions only during a limited period. This has been empirically established in several animal species, e.g. chickens (Guhl 1968) and primates (Kummer 1974). The interpretation is that individuals fight to reduce the ambiguity of their relationships (Pagel and Dawkins 1997); once these are clear, energy should be saved. On the other hand, it has also been suggested that individuals should



**Fig. 22.9** Percentage of males in the group and female dominance over males. (a) Model (average and SE), (b) real data of primates. 6-letter codes indicate species. Environmental conditions: *N* natural, *F* free-ranging, *C* captive condition

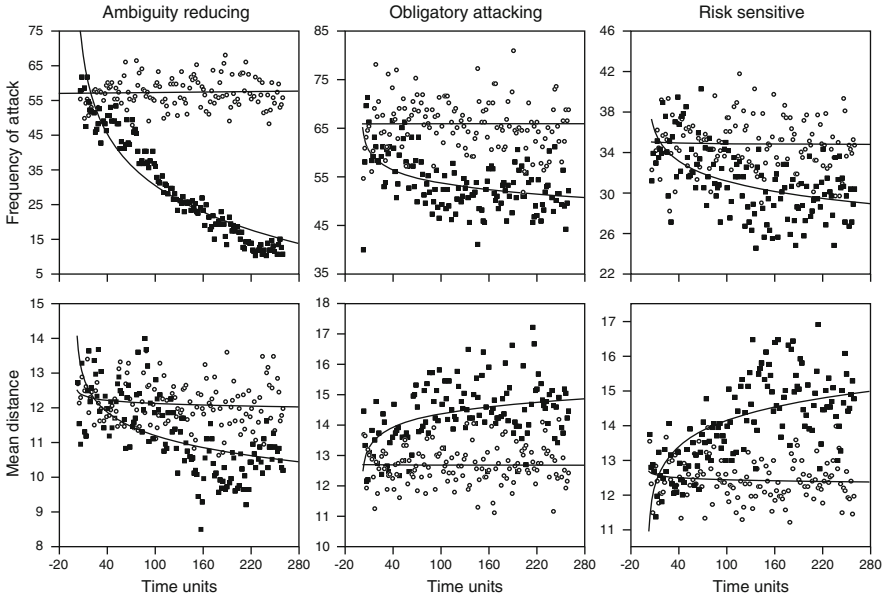
continuously strive for a higher ranking and therefore always attack, unless an opponent is clearly believed to be superior (e.g. see Datta and Beauchamp 1991).

In the DomWorld model, we compare these popular ethological views with each other and a control strategy, in which individuals invariably attack others upon meeting them (this is called the ‘Obligate’ attack strategy). Here, the ‘Ambiguity-Reducing’ strategy is a symmetrical rule in which individuals are more likely to attack opponents that are closer in rank to themselves. In the so-called ‘Risk Sensitive’ strategy, the probability of an attack is higher when the opponent is of a lower rank (Hemelrijk 1998). Remarkably, it appears that, with time, the frequency of aggression decreases in all three attack strategies, at least when groups are cohesive and the intensity of aggression is sufficiently high (Fig. 22.10).

This decrease of aggression is a direct consequence of the ‘Ambiguity-Reducing’ strategy, but unexpectedly it also develops in the other two. Because of the high intensity of aggression each interaction has a strong impact on the rank of both partners, and thus, a steep hierarchy develops. This automatically implies that some individuals become permanent losers and that, by fleeing repeatedly, they move further and further away from others (bottom row in Fig. 22.10). The increased distance among individuals in turn results in a decrease of the frequency of encounters and hence aggression. This provides a test for the real world: it has to be examined whether the development of the dominance hierarchy is accompanied not only by a reduction of aggression but also by an increase in inter-individual distances.

### 22.3.7 Personality Types

Two of these attack strategies, i.e. ‘risk-sensitive’ and ‘obligate’ attack (Hemelrijk 2000) resemble the attack strategies of individuals of different personality types,

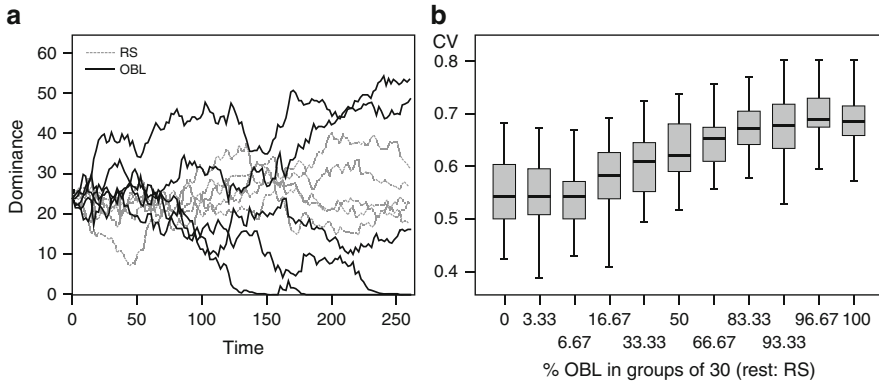


**Fig. 22.10** Development of frequency of aggressive interactions (*top half*) and mean distance (*lower half*) among individuals for different attack strategies and intensities of aggression (logarithmic line fitting). *Open circles* represent StepDom of 0.1, *closed blocks* of 1.0

namely those of the cautious and the bold personality, respectively (Koolhaas 2001). When groups in the model consist of both types (mixed groups), the differentiation of dominance values appears to be greater among individuals that are attacking obligatorily than risk-sensitively due to their higher frequency of attack (Hemelrijk 2000). Consequently, obligate attackers rise very high and descend very low in the hierarchy (resulting in a bimodal distribution of dominance values, fat lines in Fig. 22.11a), whereas risk-sensitive attack leads to less variation, a unimodal distribution of values (fat lines in Fig. 22.11a), and therefore to more intermediate dominance positions. Further, among risk-sensitive individuals, the average dominance is slightly higher than among those that always attack (obligatorily). This is due to higher ‘intelligence’ of the risk-sensitive attack-strategy, because these individuals will attack, especially when the risk of losing the fight is minimal.

This resembles the distribution of dominance in mixed groups of a bird species, the great tits (Verbeek et al. 1999). Here, bold individuals become very high up in the dominance hierarchy or descend very low, whereas cautious individuals have intermediate ranks that on average are above those of bold individuals. Differences in high and low rank were explained by different stages in which the individuals were. With regard to the moulting of their feathers and to a difference in tendency to attack from a familiar territory or an unfamiliar one and to a difference in speed of recovery from defeats. DomWorld shows that there is no need to add causes based on different stages of moulting, or on familiarity to a territory or to different speed of recovery. Thus, the model produces a far simpler explanation for the distribution of dominance





**Fig. 22.11** Dominance distribution and personality types: (a) example of hierarchical development of mixed group (*fat lines*: obligate attackers, *dotted lines*: risk-sensitive individuals).  $N = 10$ , 5 of each type. (b) hierarchical differentiation in mixed groups with different ratios of obligately attacking (OBL) and risk-sensitive (RS) individuals. CV Mean coefficient of variation of DomValues. *Box* = S.E., *whiskers* = S.D

values in these groups of great tits. To verify these results empirically, differences in risk sensitivity of both types of personality need to be confirmed empirically.

Secondly, the model provides us with an alternative explanation for the associations between dominance behavior and personality style in great tits found by Dingemanse and de Goede (2004). This association appears to differ among individuals that own a territory and those that do not; whereas among territory owners bolds were dominant over cautious ones, the reverse held for those without a territory. To explain this the authors use a context-specific argument in which they need an additional trait, namely speed of recovery from defeat (Carere et al. 2001). They argue that particularly among those individuals without a territory, bolds have more difficulty in recovering from defeat than cautious ones and that therefore, they become low in rank, whereas territory-owners do not suffer this setback and, therefore, they become higher in rank.

Alternatively, a simpler explanation, in line with our model, may apply. Here, we start from existing dominance relationships and suppose that these exert a decisive influence on the question who will obtain a territory (instead of the other way around). We assume that, because territories are limited in numbers, the higher-ranking individuals (say the top half of them) will acquire them, whereas individuals in the lower part of the hierarchy are unable to get one. Due to the bimodal distribution of dominance values among the bold birds, and the uni-modal distribution of the cautious ones, the most extreme dominance positions in the colony will be occupied by bold-ones, and the cautious are located in the middle of the hierarchy. Thus, among individuals in the top half of the hierarchy (the territory-owners) the bolds will rank above the cautious, whereas in the bottom half of the hierarchy, namely among the individuals without a territory, the reverse is true (Fig. 22.11a). For this explanation to be proven correct, we must verify whether territory owners belong to the upper half of the dominance hierarchy or not.

Thus, DomWorld produces new explanations for dominance relationships of these 'personality styles' in great tits.

An important question regarding personality is how different types, bold and cautious may co-exist, and why one type did not take over. Although there are a number of explanations for various species, none of them applies to primates. Since in primates group survival and individual survival depend on competition within and between groups, Wantia and Hemelrijk (Wantia 2007) have studied the two personality types in these contexts. They have found that risk-sensitive individuals out-competed obligate-attackers in fights within groups, but that in fights between groups the obligate attackers did better: the higher the percentage of individuals that attacked obligatorily in fights between groups, the greater the chance of the group winning (Fig. 22.11b). The better performance within groups of risk-sensitive individuals was due to their more cautious and deliberate strategy: to attack when the chance of winning was high. Greater success by obligate attackers in fights between groups was a consequence of the higher dominance value of the highest ranking individuals in groups with more obligate attackers. This is due to the steeper hierarchy as a consequence of the higher frequency of aggression in groups with more individuals that carry out obligatory attacks. Thus, whereas risk-sensitive individuals out-compete obligate-attackers in conflicts within groups, the reverse happens in conflicts between groups. Since competition within and between groups is essential for primate societies (van Schaik and van Hooff 1983), and the success of both attack strategies depends on these contexts, we may imagine that a similar differential performance may contribute to the co-existence of bold and cautious primates.

### 22.3.8 *Distribution of Tasks*

It seems a miracle that a colony of social insects consisting of tens of thousands of individuals is able to cope with the huge socio-economic demands of foraging, building, cleaning nests and nursing the brood. It appears that group-members are somehow able to divide the work efficiently among them. Such a division of labour is flexible, i.e. the ratio of workers performing different tasks varies according to changes in the needs and circumstances of the colony. There are several ways in which this task-division may arise. Different mechanisms may operate in different species (for a review, see Beshers and Fewell 2001). Task-division may be based on a genetic difference in predisposition (e.g. Moritz et al. 1996; Robinson 1998; Robinson and Page 1988), or a response-threshold to perform certain tasks (Bonabeau et al. 1996b). Such a threshold may be combined with a self-reinforcing learning process (Gautrais et al. 2002; Theraulaz et al. 1998). Thus, after performing, the threshold is lessened (by learning) and after a long period of no involvement in the task, it increases by forgetting.

The execution of tasks may also be a consequence of dominance values, as is shown in a model of bumblebees (*Bombus terrestris*) developed by Hogeweg and

Hesper (1983, 1985). This was based on an earlier experimental study (van Honk and Hogeweg 1981) that showed that during the growth of the colony, workers develop into two types, the low-ranking, so-called 'common', and the high-ranking, so-called 'elite', workers. The activities carried out by the two types differ noticeably: Whereas the 'common' workers mainly forage and take rest, the 'elite' workers are more active, feed the brood, interact with each other and with the queen, and sometimes lay eggs. In their study of the minimal conditions needed for the formation of the two types of workers (on the assumption that all workers are identical when hatching), Hogeweg and Hesper (1983, 1985) used an individual-based model based on biological data concerning the time of the development of eggs, larvae, pupae, etc. Space in the model is divided into two parts, peripheral (where inactive common workers doze for part of the time) and central (where the brood is, and all interactions take place). The rules of the artificial, adult bumblebees operate 'locally' in so far as their behaviour is triggered by what they encounter. What they encounter in the model is chosen randomly from what is available in the space in which the bumblebee finds itself. For instance, if an adult bumblebee meets a larva, it feeds it, if it meets a pupa of the proper age, it starts building a cell in which a new egg can be laid, etc. All workers start with the same dominance value after hatching, with only the queen gifted with a much higher dominance rank. When an adult meets another, a dominance interaction takes place, the outcome of which (victory or defeat) is self-reinforcing. Dominance values of the artificial bumblebees influence almost all their behavioural activities (for instance, individuals of low rank are more likely to forage).

This model automatically, and unexpectedly, generates two stable classes, those of 'commons' (low-ranking) and 'elites' (high-ranking) with their typical conduct. This differentiation only occurs if the nest is divided into a centre and a periphery (as in real nests).

The flexibility of the distribution of tasks among individuals manifests when we take half the work force out of the model. In line with observations in similar experiments with real bumblebees, this reduction in work force causes the remaining ones to take over the work. In the model this arises because the decreased number of workers reduces the frequency of encounters among them and increases encounters between them and the brood (which has not been reduced in number). An increased rate of encounters with brood induces workers to collect food more frequently. Therefore, workers are absent from the nest more often and, consequently, they meet other workers less frequently.

In real bumblebees the queen switches from producing sterile female offspring to fertile offspring (males and females) at the end of the season. Note that whereas females are produced by fertilised eggs, males are produced from unfertilised eggs. Usually females will develop into sterile workers, but if they are fed extra 'queenfood' during larval development, they will develop into queens. The switch seems to take place at an optimal moment, because it occurs at the time when the colony is at its largest and can take care of the largest number of offspring. Oster and Wilson (1978) point out that it is difficult to think of a possible external signal that could trigger such a switch, because it takes 3 weeks to raise fertile offspring and during these 3 weeks there must still be enough food.

Hogeweg and Hesper (1983) discovered that no such external signal is needed in their bumble bee model, but that the switch originates automatically as if scheduled by a socially regulated ‘clock’; it arises from the interaction between colony growth and stress development of the queen as follows. During the development of the colony, the queen produces a certain pheromone that inhibits the extra feeding behaviour of larvae by ‘elite’ workers (that lead to queens) and worker-ovipositions (i.e. unfertilised male eggs). Just before she is killed, she can no longer suppress the ‘elite’ workers from feeding larvae to become queens and from laying drone-eggs, because the colony has grown too large. Consequently, individual workers meet the queen less often and are less subjected to the dominance of the queen, so they start to lay unfertilised (drone) eggs. Furthermore, the stress on the queen increases whenever she has to perform dominance interactions with workers during her egg laying. When the stress on the queen has reached a certain threshold value she switches to producing male eggs (drones).

Because generative offspring are also sometimes found in small nests, van der Blom (1986) challenges the notion that dominance interactions induce stress in the queen and thus lead to this switch. However, in the model, it is not the number of workers that causes the switch: Hogeweg and Hesper (1985) have shown that in small nests the switch also appears to occur at the same time in the season as in large nests. For this they studied the bumblebee model for a reduced speed of growth. They found that the switch occurs at a similar moment due to the following complicated feedback process. If the colony grows faster, the heavy duties of caring for the brood leave the workers little time to interact with each other and the queen. Consequently, the dominance hierarchy among workers only develops weakly. Therefore, if workers interact with the queen they do not pose much of a threat to her and as a result, the queen is not severely stressed and the colony can grow very large. In contrast, in a slowly growing colony, the small number of brood gives the workers little work and leaves them time to interact with each other. Consequently, their dominance relationships are clearly differentiated. Furthermore, by often interacting with the queen, they become on average higher-ranking themselves. In the end, the queen receives as much stress from frequent interactions with a few high-ranking workers in a slowly growing nest as from few interactions with very many low-ranking workers in a fast growing nest. Consequently, the switch to reproductive offspring takes place at about the same moment in both nests in the model.

## 22.4 Evaluation

The power of these kinds of models is the generation of phenomena that are emergent. These emergent phenomena lead to explanations that are more parsimonious than usual, because the patterns emerge from the interaction among individuals and their environment rather than from the cognition of an individual. These explanations can be tested empirically.

Considering the kind of questions posed in the models discussed above, it becomes clear that most of them can only be studied using certain kinds of agent-based models. Other kinds of models, such as partial differential equations based on density functions or even individual-based models of fluids and gases cannot incorporate the complexity of the rules and/or emergent effects.

The behavioural rules of the agents in the agent-based models that were treated here were in all cases biologically inspired. In some cases, behavioural rules were based on precise experimental results specific to a certain species, such as in the case of group formation (Camazine et al. 2001; Jeanson et al. 2005). Usually, however, parameters were tuned only loosely to the real system (e.g. the angle of vision in fish is set at about  $270^\circ$  and that of mammals at  $120^\circ$ ). Sometimes, mathematical equations were used that were developed for a different species, such as in the case of dominance interactions. Here, the equations were initially derived for the self-reinforcing effects in bumblebees (van Honk and Hogeweg 1981) and subsequently extended and applied to explain social systems in primates (Hemelrijk 1999b). In all cases the behavioural rules are supposed to capture the essentials of those of real animals.

If, however, macro patterns are obtained that resemble patterns observed in the real system, this is still no proof of the correctness of the rules in reflecting behavioural rules of real animals, because different sets of rules may lead to the same macro-pattern. The relevance of the rules and other aspects of the model could be studied further by investigating additional hypotheses and comparing further results of the model to natural systems.

Agent-based models appear to be particularly useful in showing the consequences of interactions among individuals for social structure and the reverse, i.e. from social structure to social interactions. In this way, they teach us about the integration of traits. This is particularly apparent when the models include a representation of space (time is always represented). The representation of time and space is of general importance, because all real individuals live in time and space and thus it is unrealistic to ignore these aspects. It appears that by representing the interaction of individuals with their social and physical environment in time and space, patterns result in such a way that explanations become unusually parsimonious in terms of their specific adaptive traits and the cognition needed (in line with findings of situated cognition Pfeifer and Scheier 1999).

These explanations give a new insight into the phenomenon of social complexity that may either be very general (e.g. conceptual model) or specific to the type of animal and the kind of behaviour under investigation. Usually, it leads to hypotheses that are easily tested in the real system. These hypotheses make unexpected connections between variables, such as between the production of sterile and reproductively-active offspring with colony dynamics in bumblebees. Testing can be done by natural observation, for example, by studying the effects of different group sizes on group shape in case of fish. Furthermore, testing can be done by experimental interventions, such as by putting together individuals of both sexes in different group compositions to study effects on relative dominance of females to males.

While ignoring models of certain topic areas where no emergent effects appeared (so-called output-oriented models), we have here surveyed a large number of the most important models of social complexity. Of course, it is impossible to discuss them all. Note that we have not treated models concerning biological evolution since only a few are related to social systems (such as Kunz et al. 2006; Oboshi et al. 2003; Ulbrich et al. 1996). This is due to the fact that evolution usually happens on a far larger time scale than phenomena of social complexity. However, see Chap. 18 in this handbook (Chattoe-Brown and Edmonds 2013) on how concepts from biological evolution have influenced recent approaches in programming simulation models.

Furthermore, we have not treated a number of other complex phenomena, such as synchronisation of lighting behaviour of insects, temperature regulation of nests and the building of nests, because in these cases no agent-based models have been used, or the behaviour is insufficiently social. These topics are, however, covered by Camazine and co-authors (Camazine et al. 2001).

## 22.5 Future Work

With regard to areas that may be important for future work, I suggest (1) models of self-organisation that help us understand specific social systems better by being closely tuned to empirical systems, such as fish schools, insect colonies or primate groups, (2) models that present social behaviour and its ontogenetical development in greater detail and (3) evolutionary models that include also spatial effects.

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## Further Reading

For further reading I recommend the book on self-organisation in biological systems by Camazine and co-authors (Camazine et al. 2001). This forms an extensive introduction to almost all topics treated above and more (with the exception of task division and social systems of primates). Furthermore, new extensions of a number of the models are treated by Sumpter (2006). For teaching I suggest the well-written book by Resnick (1994). This book has been used in secondary schools and teaches to think in terms of complexity and self-organisation in general. For more advanced readers, I recommend “Self-organisation and Evolution of Social Systems” (Hemelrijk 2005). This is an edited book and contains recent articles on modelling of social systems, including those of humans.

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