13 *The use of artificial-life models for the study of social organization*

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Introduction

When observing differences between species, scientists tend to invoke a separate adaptive explanation for each difference. In this way, they explain the complexity that is observed at a higher level (such as the level of the relationship, the group, or the species) as if it resides in the individuals (Deneubourg & Goss, 1989; see Mason, Box 13). Accounting for each aspect of behavior separately, scientists have to invent theories to integrate these separate aspects. Now, however, a new method to arrive directly at integrative hypotheses has been introduced. This is the so-called "synthetic" or "bottom–up" approach, in which artificial individuals (robots and computer models) are designed that exclusively react to the information they receive from their nearby (local) environment (Braitenberg, 1984; Pfeifer & Scheier, 1999); the behavior of these virtual individuals is studied in detail. It then appears that many more behavioral patterns emerge than we expect to result from their simple behavioral rules. These patterns arise by self-organization from the interaction among these simple individuals as a consequence of the changes that take place in the agents and in their environment. Because we have complete knowledge of their behavioral rules, we can fully explain these patterns as arising from their integration, without resorting to additional and separate genetic or cognitive mechanisms. The aim of the present study is to show how this "bottom–up" method may be used to generate hypotheses that are simple in terms of the cognitive assumptions that are made and that can be tested in the study of macaques in the real world.

Group-life, in real animals, is supposed to serve the protection of group-members against predators (van Schaik, 1983); its main disadvantage is the competition for food it generates. Individual group-members vary in their competitive abilities and can be arranged in hierarchical order as regards their degree

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of dominance over others. How they acquire dominance is a point of discussion. While some argue for the importance of (genetic) inheritance of dominance (Ellis, 1991), others reject this for the following reasons: dominance is a relational phenomenon instead of an individual characteristic (Barette, 1993). Experimental results show that dominance depends on the order of introduction in a group (Bernstein & Gordon, 1980b). 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. The effect has been established empirically in many animal species and is accompanied by psychological and physiological changes, such as hormonal fluctuations (Mazur, 1985; Chase *et al.*, 1994; Bonabeau *et al.*, 1996; Hemelrijk, 2000a). Macaques species differ in their competitive behavior, and in respect of this, Thierry (2000, Chapter 12) classifies them into different categories: among other things, a weak hierarchy classifies a group as an egalitarian society and a steep hierarchy as a despotic one. Clearly-despotic macaques display aggression of an intenser kind (e.g., biting) than egalitarian ones (which limit themselves to threatening) and are more nepotistic in their behavior than egalitarian ones (Thierry, 1985a,b). Despotic species differ also in other aspects from egalitarian ones, such as the degree to which they become reconciled after a fight and the degree of infant protection by mothers (Thierry, 1985a,b, 1990; de Waal & Luttrell, 1989). Instead of presenting a separate adaptive explanation for each single difference, Thierry believes that all differences in dominance style are brought about by only two internal differences: a higher intensity of aggression and a higher tendency to support related individuals (nepotism) among despotic macaques as compared to macaques that are egalitarian. In this chapter, I will use a model called "DomWorld" to explain how one of these internal differences at the individual level (intensity of aggression) may suffice to explain many of the differences observed at the level of social organization.

DomWorld is a so-called individual-based or multi-agent model. Such a model differs from models in which the "average" individual or strategy is studied (such as "hawks" versus "doves," Maynard Smith, 1983), because different individual agents are represented separately and each individual is supplied with rules to react to what it perceives locally. Therefore, it is possible to study social behavior in a more "natural" situation involving parts of the context of behavior. Representation of context is increased greatly in multi-agent models by the representation of space. In DomWorld, for instance, spatial proximity determines who meets whom (in contrast to a random draw of potential candidates for interaction). By means of the representation of the spatial distribution of food, Deneubourg and co-authors have shown that in artificial ants, even when only a single set of behavioral rules is implemented, different environments may lead to extremely different behavioral patterns (Deneubourg & Goss, 1989). These kinds of models display a high potential for self-organization, which may or may not be accompanied by structural changes in the agents (Pfeifer & Scheier, 1999: 475). Whereas in most models structural changes are lacking (e.g., the fish-model of Huth & Wissel, 1992; for insects, see Deneubourg & Goss, 1989), in DomWorld individuals change their fighting capacity, as reflected in their changing dominance values.

The model DomWorld encompasses two aspects that are relevant for most animal societies: grouping behavior and competition. Although it reproduces grouping, the cause why agents group (e.g., to avoid predators or because of resources being clumped) is not specified and irrelevant to the model and all ecological characteristics are ignored. As regards competition in DomWorld, any "genetic" differences among individuals of one sex are absent, all are completely identical at the start. They even have the same capacity to win a fight. The hierarchy develops exclusively as a consequence of chance and the abovementioned winner–loser effect because of its general occurrence (see above). In this way the model makes the working of self-organization clearly visible: despite its minimal rules and limited environmental properties, it leads to behavioral patterns in DomWorld that closely resemble certain behavioral phenomena found in macaque societies. Because of this correspondence, DomWorld can be used to infer a statistical method for measuring the gradient of the hierarchy. As it produces hypotheses for the interconnection of behavioral traits, we ought to ascertain whether such interconnections may also be found among real macaques. In order to establish this, these traits must be studied simultaneously in several groups of different species. Since DomWorld also produces other patterns that have not yet been studied in macaques, these should also be included (e.g., spatial structure and female dominance). In short, DomWorld generates simple explanations for social behavior and its evolution.

The model: Dominance World (DomWorld)

The model represents an artificial world that consists of a homogenous space inhabited by artificial agents that exclusively group and compete, but do nothing else (Fig. 13.1). Grouping arises as follows: as long as individuals are nearby (in NearView), "they are group-members" and therefore, continue to move straight ahead. However, in periods of sexual attraction, male behavior changes in that a male moves one step toward a female upon encountering her in his NearView.

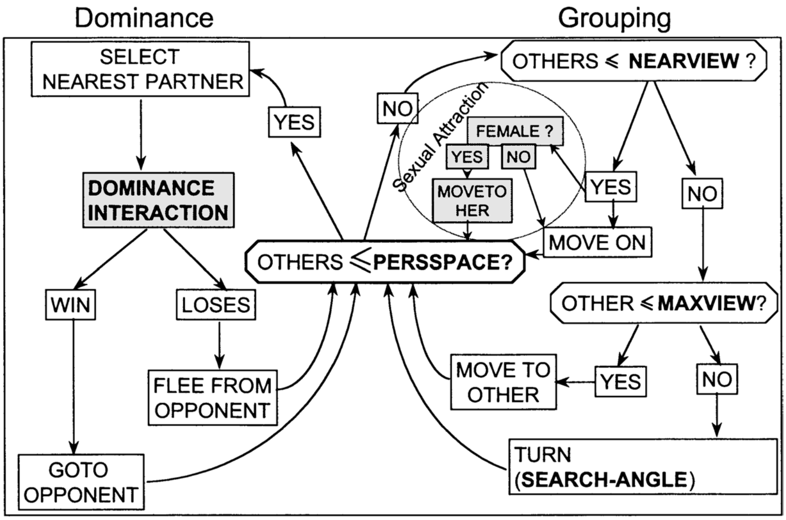

Fig. 13.1. Outline of behavioral rules. Grey shaded areas indicate behavioral interaction types that are experimented with. The encircled part of the diagram, labeled as sexual attraction, is activated for males in certain runs only. (See text for explanation.)

If individuals (of either sex) see no one close by, "group-members are too far away." If they notice an individual further off (in maxView), they move one step toward the other "in order to join a group;" but when they see no one, they turn over a specific angle in order to spot others (SearchAngle).

If, however, another agent is very near, in the personal space of "ego" (PersSpace), a competitive or dominance interaction may take place, though it is not specified what the cause of this competition is (food or the wish to mate). Therefore, encounters among agents are not random, but depend on their spatial proximity. After a fight, the winner chases the opponent (one unit) and the defeated agent flees (2 units).

The likelihood that an artificial individual undertakes an aggressive interaction (instead of remaining nonaggressively close by) increases with its chance to defeat its opponent (Hemelrijk, 2000a). The agent's capacity to be victorious is represented in its dominance value (i.e., body posture). This dominance value is displayed and observed among agents upon meeting each other. Initially, it is the same for all agents of one sex. Thus, during the first encounter, chance decides who wins. Subsequently, the higher-ranking agent has a greater chance to win. Changes in dominance values reflect the self-reinforcing effects of the victories and defeats in conflicts. In the model, this is implemented by an increase of the dominance value of the victorious agent after its victory (thus increasing the probability of victory the next time) and decreasing that of the defeated one (thus increasing the probability of defeat the next time) by the same amount. When, unexpectedly for us, an agent defeats a higher-ranking opponent, this outcome has a greater impact than when, as we would expect, the same agent conquers a lower-ranking opponent, and the dominance values of both opponents are changed by a greater amount (in accordance with detailed behavioral studies on bumble bees by Honk & Hogeweg, 1981). Thus, the impact of a conflict or the change in dominance values varies according to the expectation whether an outcome is likely or not. In this way we allow for rank reversals.

Besides, intensity of aggression is determined by a fixed scaling factor, called StepDom. This factor, StepDom, is multiplied with the degree of change in dominance value per fight. A high value of StepDom (of 1.0) implies that the impact of a single interaction may be high (such as in biting), a low value (of 0.1) allows only for low impact (such as threats and staring).

The sexes differ only in their attraction to the opposite sex and in their fighting capacity: “male” agents start with a higher initial dominance value (twice as high as that of females) and are characterized by a higher intensity of attack than “female” agents. To show the effects of winning and losing as clearly as possible, all agents of the same sex are identical at the start. Groups consist usually of four (or five) males and four (or five) females. Further, in those runs in which sexual attraction is operative, males have a greater inclination to approach females than individuals of their own sex, whereas females ignore the sexual identity of others.

Parameters are set so that the grouping of agents on the computer screen “looks like” a macaque group; the number of agents (8 or 10) is chosen so as to reflect the number of adults in groups of macaques; the high and low values of StepDom are chosen so as to create a large difference between both settings.

The behavior of the agents is analyzed by means of behavioral units and statistical methods similar to those used for observing real animals. For a more complete description, see Hemelrijk (1999a, 2000a).

Results of DomWorld

Hierarchical stability and the gradient of the hierarchy

At the beginning of each run, the dominance of all individuals of one sex is the same; in the course of time hierarchy develops and the dominance stabilizes

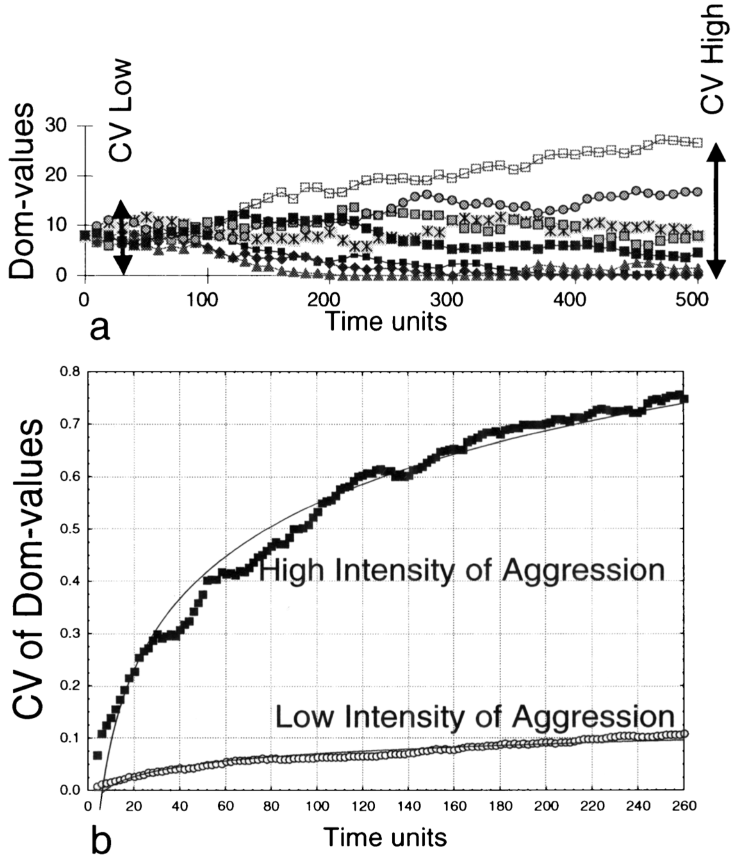

Fig. 13.2. Development of the dominance hierarchy. (a) Hierarchical development and the coefficient of variance (CV) of dominance values for one sex at a low and at a highly differentiated hierarchy; (b) average coefficient of variance of dominance values over time at a high and at a low intensity of aggression.

(Fig. 13.2a,b). The degree of hierarchical development is measured by the coefficient of variance of dominance values (Fig. 13.2a): at the beginning, during the weak development of hierarchy, the coefficient of variance is low, but later on, the coefficient of variance reaches a high value (reflecting a steep hierarchy). (From here on, the measurements of this chapter have been taken only during periods of clear hierarchical development.) Further, Figure 13.2b shows that the hierarchy develops more strongly at a high intensity of aggression than at a low one. Figure 13.3c shows that a steeper hierarchy is accompanied by more asymmetrical aggression. (Asymmetry of aggression is used as an indication of the gradient of the hierarchy in real animals.)

Positive feedback between spatial structure and dominance hierarchy

Figure 13.2b shows how, at a high intensity of aggression, a steep hierarchy develops. This comes about via a mutual feedback between the hierarchy and the spatial structure (with dominants in the center and subordinates at the periphery) (Fig. 13.3a) (Hemelrijk, 1999a,b, 2000a). In this process, pronounced rank-development causes low-ranking agents to be chased away by others continuously and thus the group spreads (1 in Fig. 13.3d and Distance in Fig. 13.3b). Consequently, the frequency of attack diminishes among the individuals (2 in Fig. 13.3d and Attack in Fig. 13.3b). Because of this reduction in the frequency of aggression, the hierarchy stabilizes (3 in Fig. 13.3d). While low-ranking individuals flee from everyone, this automatically leaves dominants in the center, and thus a spatial-social structure develops (Fig. 13.3a). Since individuals of adjacent dominance are treated by others in more or less the same way, similar agents remain close together; therefore, they interact mainly with others of adjacent rank. Further, if a rank reversal between two opponents occurs, it is only a minor one because opponents are often adjacent in dominance. In this way the spatial structure stabilizes the hierarchy and it maintains the hierarchical differentiation (4 and 5 in Fig. 13.3d). Also, the hierarchical differentiation and the hierarchical stability mutually increase each other (6 in Fig. 13.3d).

When at a high intensity of aggression a steep hierarchy develops (Fig. 13.2b), it is accompanied by aggression that is more asymmetrical (as measured by a negative τ_{Kr} – correlation for bidirectionality between aggression initiated with and received from other group-members, see Fig. 13.3c). This asymmetry is due to the great rank-distances, which inhibit low-ranking agents from initiating a dominance interaction with high-ranking ones. It also explains why at a low intensity, when a weaker hierarchy develops, aggression is more bidirectional. Further, increased unidirectionality (= decreased bidirectionality) strengthens the stability of the hierarchy, its differentiation and the spatial configuration (Fig. 13.3a,d).

Female dominance and the lowest-ranking male

How does the gradient of the hierarchy influence inter-sexual dominance relations? Unexpectedly, female dominance over males is greater at a high intensity of aggression than at a low one (Fig. 13.4a). This is a direct consequence of the stronger hierarchical development found at a high intensity, which automatically causes certain females to become very high- and some males very low-ranking. Consequently, certain females dominate some males and the dominance of the

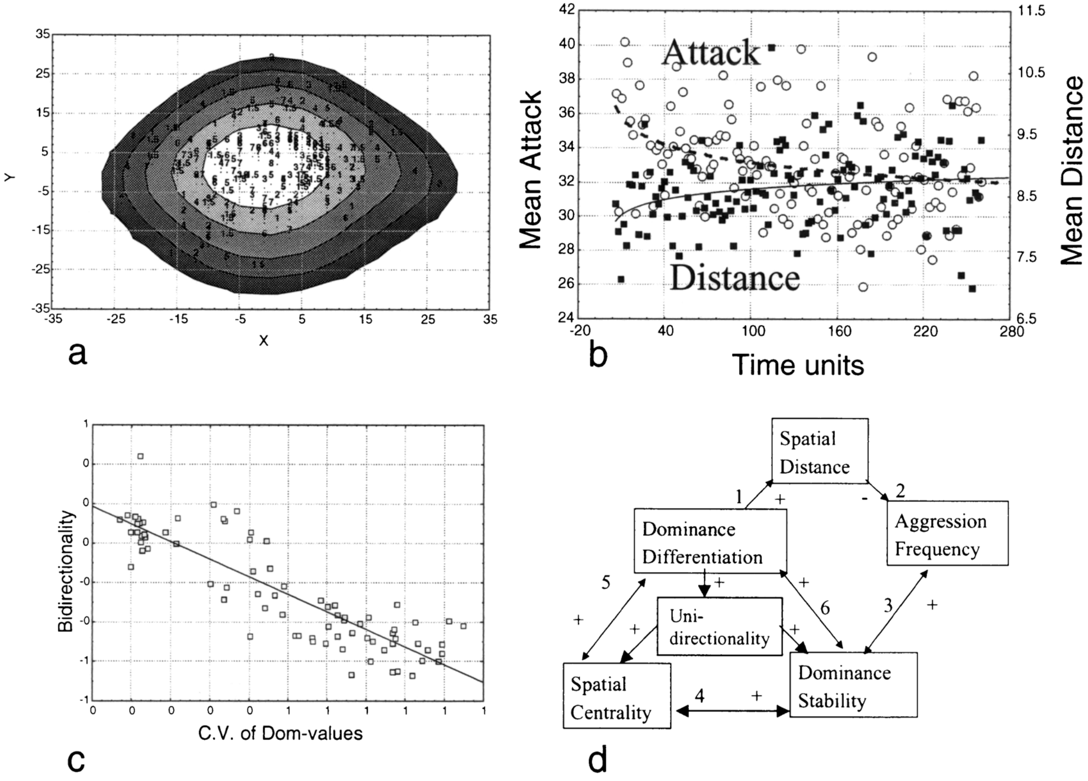

Fig. 13.3. Spatial–social structuring among agents at a high intensity of attack. (a) Spatial structure: different shades indicate areas occupied by individuals of different dominance; (b) decrease of aggression (open circles) and increase in average distance (closed blocks) over time; (c) bidirectionality (= symmetry) of dominance interactions measured by the τ_{Kr} – statistic of the matrix-correlation between aggression initiated and received (Hemelrijk, 1990a,b) versus coefficient of variance (CV) of dominance values; (d) summary of interconnection between behavioral traits.

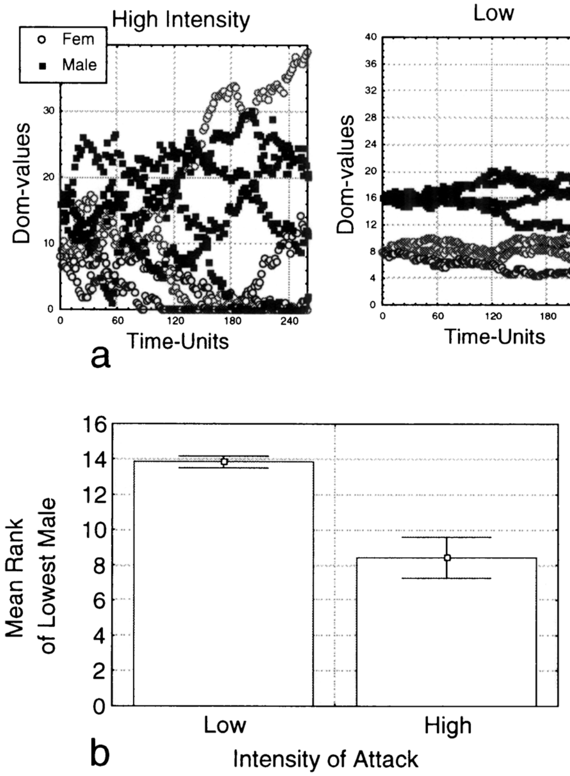

Fig. 13.4. Hierarchical development at a high and a low intensity of aggression. (a) A typical case for both sexes. Females, open circles. Males, closed blocks. (b) Average and standard error of dominance of the lowest-ranking males.

lowest-ranking male is lower than at a low intensity (Fig. 13.4b). In contrast, at a low intensity, nothing much happens to the hierarchy, and if females start out being lower than males, they remain so.

Sexual attraction

If we add social attraction of males to females to the model (as a preferential male orientation toward females rather than toward males), female dominance over males increases (Fig. 13.5a), but only if the intensity of aggression is high (Hemelrijk, 2000c), not if it is low (Hemelrijk, 2002)! Such an increase is due to the higher frequency of interactions between the sexes during sexual attraction in combination with the inbuilt mechanism that unexpected victories and defeats

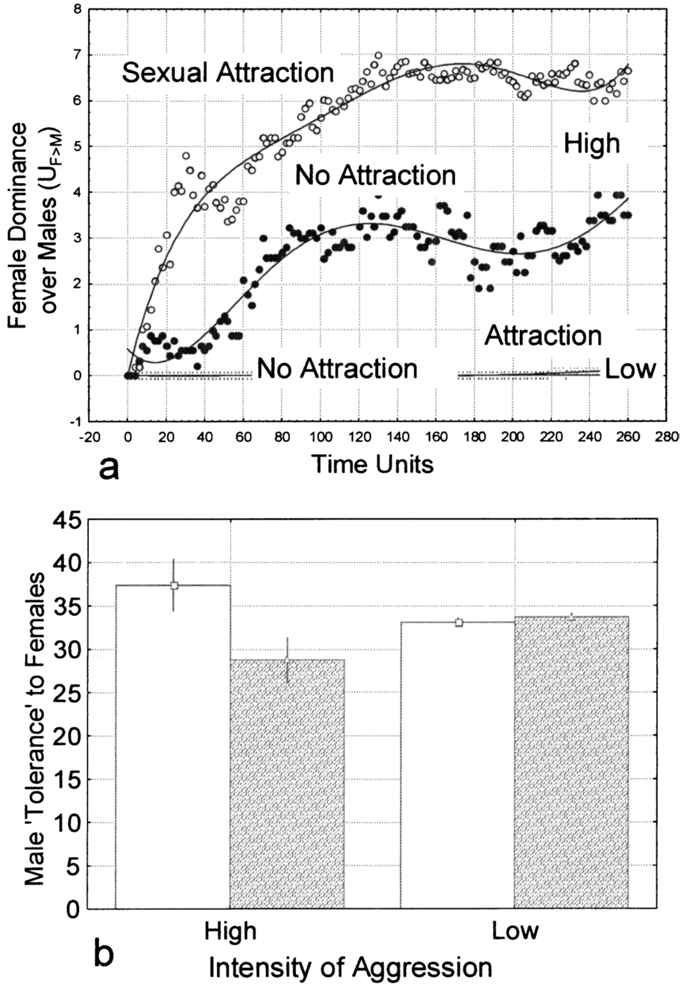

Fig. 13.5. Consequences of sexual attraction at a high and a low intensity of aggression. (a) Average female dominance over males (measured by the Mann–Whitney *U* statistic indicating the degree with which females rank above males); (b) average male “tolerance” (= non-aggressive proximity) towards females during sexual attraction (white bars) and without it (shaded bars).

cause a greater change in the dominance values of both opponents than expected outcomes do. Such an increase is absent at a low intensity, because their female dominance is very low anyway (Fig. 13.4a), and thus, even if the sexes interact more often during sexual attraction, there is almost no possibility for females to defeat males at all.

When during sexual attraction female dominance increases, at a high intensity of aggression, females run less risk if they attack males and thus, they display more frequent aggression against males. Males, in contrast, run a greater risk when they attack females and therefore, they approach females more often nonaggressively (Fig. 13.5b). It therefore seems as if males become more "tolerant" to females during sexual attraction, though, in fact, they become more "respectfully timid." Nothing of this happens at a low intensity, because there female dominance does not increase during sexual attraction.

Similarity of societies in DomWorld to real macaques

As shown above, in DomWorld, aggression declines more strongly over time when unfamiliar individuals are put together at a high intensity of aggression than at a low one. Further, at a high intensity, aggression is less frequent and less symmetrical, and the hierarchy is steeper. Also, approach- and attack-behavior are more clearly correlated with dominance. Besides, grouping is looser and spatial structure with dominants in the center and subordinates at the periphery is clearer. Compared to a low intensity of aggression, the dominance of the lowest male is lower, female dominance over males is higher and during sexual attraction the increase of female dominance over males is greater (Hemelrijk, 1999a, 2000a,c, 2002). As far as these patterns have been studied, the same is found when despotic societies of macaques are compared with egalitarian ones (Thierry, 1985a,b; de Waal & Luttrell, 1989). Thus, the result is an even simpler hypothesis than that of Thierry, namely that differences between both types of societies may be due to a difference in intensity of aggression only, ignoring all nepotistic tendencies.

Since in the model all differences are interconnected (Fig. 13.3d) and are due to a change in only one trait (intensity of aggression), this may also be true for real monkeys. Therefore, it is important to study in real monkeys the interconnection between all these variables: intensity of aggression, symmetry of aggression, cohesion, stability of the hierarchy, spatial structure, and female dominance (Hypothesis 1, Table 13.1). In addition, these results lead to several hypotheses for grooming and sexual behavior in real monkeys, as explained below.

Hypotheses for the study of real macaques

Grooming behavior

In DomWorld, spatial centrality of dominants is clearer at a high intensity of aggression than at a low one and, although spatial structure has not been studied systematically in macaques (or in any other primates), spatial centrality of

Table 13.1. *Hypotheses to be tested in macaques*

Hypothesis	Model-based hypotheses	That can be tested for macaques
1	Interconnection of variables	Spatial centrality, gradient and stability of the hierarchy, cohesion and unidirectionality are associated as in Fig. 13.3d
2	Spatial structure with dominants in center	Occurs more often in despotic groups of macaques than egalitarian ones
3	Spatial structure with dominants in center	Is mirrored in grooming distribution of despotic groups of macaques, but not of egalitarian ones
4	Female dominance over males	Is greater in despotic societies
5	Female dominance over males	Is greater if hierarchy is steeper (= more unidirectional, measured by τ_{Kr})
6	“	Leads to fewer mating partners for females
7	“	Leads to increased migration of subordinate males
8	“	Increases during periods of sexual attraction in species with some female dominance and seemingly leads to “male tolerance”
9	“	Increases female aggression toward males, particularly during male attraction to females

dominants has, so far, been mentioned only for species that are despotic (e.g., Itani, 1954). If we assume that spatial structure influences the distribution of grooming, then we may expect that the distribution of grooming differs between egalitarian and despotic primate societies (Hypothesis 2 and 3, Table 13.1). If individuals groom others in proportion to their encounter rate, then spatial arrangement determines – through proximity – the grooming pattern at a group level. Then, at a high intensity of aggression, dominants should be groomed more often than subordinates: because they are more often in the center, and thus, meet others more frequently. Furthermore, individuals should groom more often those that are similar in dominance, because they are close to each other. Note that exactly the same patterns of grooming have been found by Seyfarth (1977) among female monkeys (but he does not distinguish between egalitarian and despotic species and does not expect a difference in the distribution of grooming between them): (1) high-ranking individuals receive more grooming than others; and (2) most grooming takes place between individuals that are adjacent in rank. Seyfarth gives, however, an explanation that is far more complex than those we derive from DomWorld. He assumes that two principles underlie these phenomena: (1) higher-ranking females are more attractive to groom, because potentially more benefits (such as more efficient support in fights) can be gained from them than from lower-ranking individuals; and (2) access to preferred

(= higher-ranking) grooming partners is restricted by competition. Consequently, in the end each female grooms most frequently close-ranking partners and is groomed herself most often by the female ranking just below her.

The hypothesis derived from DomWorld is simpler than Seyfarth's, in that it requires neither the occurrence of competition for grooming partners nor assumptions about exchanges for future social benefits, nor do individuals discern the relative rank of group members in order to groom higher-ranking partners more often than others (in contrast to assumptions by Seyfarth, 1981).

Another common hypothesis states that attraction among related individuals (which often are of similar rank) explains the high frequency of grooming among individuals of similar dominance. Note that the explanation presented by DomWorld holds without invoking kin-relations.

To establish the relevance of this explanation for real primates, it should be tested whether the patterns of grooming as described by Seyfarth occur particularly in groups with a spatial structure with individuals of adjacent rank close together and dominants in the center, and not in those with a weak spatial structure (Hypothesis 2 and 3, Table 13.1) and whether it occurs even in the absence of kin relations. This hypothesis is supported by the egalitarian society of Tonkean macaques where grooming is neither dominance- nor kin-oriented (Thierry *et al.*, 1990) and by several species of despotic macaques where grooming appears clearly dominance- and kin-oriented (rhesus macaques: Sade, 1972b; de Waal & Luttrell, 1986; Japanese macaques: Mehlman & Chapais, 1988).

Inter-sexual dominance, sexual behavior and migration

The close agreement of the results of DomWorld with the dominance styles of macaques inspires confidence for its further use for developing hypotheses regarding male–female dominance relationships among these monkeys.

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, at a high intensity of aggression, males appear to be less dominant over females than at a low intensity. This is due to the stronger hierarchical differentiation, which causes both sexes to develop their hierarchies in a more pronounced way and, thus, causes females to dominate over males to a higher degree. A similar thing is seen in monkeys. Circumstantial evidence shows that in despotic species of macaques, adolescent males have greater difficulty in outranking adult females than in egalitarian species (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 female dominance, as we have seen, simply as a side effect of the more pronounced hierarchical differentiation (Hypothesis 4 and 5, Table 13.1).

Differences in rank-overlap between the sexes may affect sexual behavior. In their study of male bonnet macaques, Rosenblum and Nadler (1971) discovered an ontogenetical effect: adult males ejaculate after a single mount, whereas young males need several mounts. These authors (and others, see Abernethy, 1974) suggest that males have difficulty in mating with females that outrank them. When we combine these observations with the patterns of female dominance over males found in DomWorld we come to the conclusion that at a high intensity of aggression, females have fewer males with which to mate than at a low intensity of aggression. In fact, observations of this kind have been reported for macaques. According to Caldecott (1986a) despotic females are observed to mate with fewer partners and almost exclusively with males of the highest ranks. He attributes this 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: the differences in sexual behavior between egalitarian and despotic macaques may directly arise from the difference in female dominance over males, which in turn arises from a difference in hierarchical development due to a different intensity of aggression. Therefore, we would expect in real animals, that in those groups in which females are dominant over some males, higher-ranking females have fewer mating partners than lower-ranking females (Hypothesis 6, Table 13.1).

Further, in real macaques, after a certain period of living in a group, males migrate to new groups whereas females usually remain in the same group for life (Gachot-Neveu & Ménard, Chapter 6). Males that emigrate are more often of low-rank. In the model, the bottom-ranking males are particularly low in dominance when the intensity of aggression is high (due to the stronger hierarchical differentiation). Thus, if emigration were possible in the model, we would expect that at a high intensity of aggression more males migrate than at a low one. Exactly this is described by Caldecott (1986a) for the rate of emigration of males of despotic primate species versus egalitarian ones. The explanation suggested by DomWorld is that the lower dominance of the bottom-ranking males implies that these males have mating problems with females and suffer competition for food from them and therefore benefit more from migration than those males that are dominant over females (Hypothesis 7, Table 13.1). Thus, it is not only competition with males (as is usually assumed), but also with females that may drive males from the group.

In the model, female dominance increases with sexual attraction as an automatic consequence of the more frequent encounters between the sexes. The explanation that more frequent interaction between individuals of two dominance classes makes them more alike may be a general process that holds for all natural species. This phenomenon is also observed in detailed behavioral studies of dominance interactions among bumblebees (Honk & Hogeweg, 1981): at the beginning there are two dominance classes of bumblebees, the high-ranking queen and the low-ranking "common"-workers. In due time, a third dominance class of high-ranking "elite"-workers develops. These elite-workers interact more often with the queen than do the common ones. Consequently, they come to resemble her.

However, instead of being associated with increased female dominance (as in Yerkes, 1939, 1940), sexual attraction in real animals is usually thought to be accompanied by reproductive strategies of exchange. For instance, chimpanzee males are described as exchanging sex for food with females (Tutin, 1980; Goodall, 1986; Stanford, 1996). Yet, in spite of detailed statistical studies, we have found no evidence that males obtain more copulations with, or more offspring from, those females who they allow more often to share their food (Hemelrijk *et al.*, 1992, 1999, 2001; Meier *et al.*, 2000). Thus, male tolerance seems to increase even without noticeable benefits. DomWorld provides us with the useful alternative hypothesis that males seem more tolerant at food sources to females when males are sexually attracted to them, because female dominance over males has increased. Whether the increase of female dominance is in fact greater in groups where there is already some female dominance, and whether the increase is greater among despotic macaques than among egalitarian ones, should be studied in real animals (Hypothesis 8, Table 13.1).

Further, DomWorld shows that artificial females become more aggressive when artificial males are attracted to them. Similarly, primate females are described as being more aggressive during their tumescent period (e.g., macaques: Michael & Zumpe, 1970; chimpanzees: Goodall, 1986). Though this may be due to their special hormonal state (as is traditionally supposed), the model suggests a more simple mechanism that may be operative: an increase of encounter-frequency with males and, consequently, an increase of female dominance over males (Hypothesis 9, Table 13.1).

Conclusion

DomWorld shows how many behavioral characteristics arise as side effects of other characteristics of individuals and of their interactions, and demonstrates how a number of behavioral aspects are interconnected. These are the gradient of the dominance hierarchy, bidirectionality, spatial centrality, rank-correlated behavior, the rank of the lowest male, and female dominance over males. The interconnection between, or the integration of, these traits causes many behavioral patterns to emerge and forms the basis of the alternative explanations generated by the model.

One of the emergent effects of a steeper hierarchy is the spatial structure with dominants in the center and subordinates at the periphery; another is the degree of female dominance over males. As regards spatial structure, DomWorld presents a hypothesis as to why it should be different in egalitarian and despotic societies and how it should be reflected in sociopositive behavior such as grooming. As regards female dominance over males, it may be pointed out that, so far, its variation in anthropoid primates has not been studied systematically. As a matter of course male dominance is regarded as the rule despite the frequent occasions on which females have been observed to be dominant over males (e.g., in talapoins, vervets and macaques, see Smuts, 1987: 407). Perhaps the lack of studies of this problem is due to the lack of a relevant theory. This gap may now be filled, as DomWorld presents us with the following hypotheses. Female dominance over males increases with the gradient of the hierarchy, and the gradient of the hierarchy in turn may increase from three causes: an increase in the intensity of aggression; in the frequency of interaction between the sexes; and in the degree of cohesion (as has been shown by Hemelrijk, 1999b). Cohesion increases female dominance by two processes (namely via the gradient of the hierarchy and via the frequency of inter-sexual encounters). First, as regards the hierarchical gradient, cohesion increases the frequency of interactions, and the degree of spatial limitation. Both combined cause a spatial structure to develop, which in turn strengthens the hierarchy and, thus, contributes to female dominance. Second, cohesion also increases the frequency of interaction between the sexes compared to what happens in loose groups and, thus, the opportunities for incidental victories of the weaker sex. Consequently, it increases female dominance too. Both effects may in part explain why female dominance is often reported to be stronger in bonobos than in common chimpanzees, in spite of their similar sexual dimorphism: groups of bonobos are more cohesive and groups include both sexes more often than groups of common chimpanzees (Hemelrijk, 2002).

Although individuals in the model represent certain key elements of real animals and their environment, they come, of course, nowhere near their real complexity. Therefore, as future additions to DomWorld, we intend to add offspring, youngsters, social positive behavior, and ecological conditions (see te Boekhorst & Hogeweg, 1994), and allow for immigration and emigration. This will permit us to study additional aspects that are often studied in primates, such as dominance acquisition by youngsters, post-conflict affiliation, etc., and how they are affected by the ecological environment (for preliminary studies on coalitions in DomWorld, see Hemelrijk, 1996, 1997). The remarkable resemblance of DomWorld (in its present form) with the behavior of real macaques, such as is typical of egalitarian and of despotic macaques, suggests that DomWorld sheds light on the processes that are essential to macaque societies. Since such resemblance occurs despite the omission in the model of ecological conditions, it may be suggested that social effects are probably also of crucial importance in macaques, overruling effects due to local ecological variation.

In distinguishing egalitarian macaques from despotic ones, it is difficult to decide which are their most important characteristics. Usually, the gradient of the hierarchy is taken as the key factor, because it is supposed to reflect the competitive regime and to cause variation in reproductive possibilities among group-members. The gradient of the hierarchy (the statistical variance of dominance values) cannot be measured in real animals, but in DomWorld it can be measured by the coefficient of variance of dominance values, and this coefficient of variance appears to be closely associated with the degree of bidirectionality (as measured by the τ_{Kr}-correlation between the frequency of aggression which each individual directs to, and receives from, each group-member) (see Hemelrijk, 2000a,b). Bidirectionality is a variable that is central in the interconnection of the behavioral traits (Fig. 13.3d); it is easily measurable in the real world (it can, for instance, be directly obtained from published matrices of aggression). In a comparative study of real primates, we have applied this measurement and we have shown that, as was to be expected, the degree of bidirectionality is greater during periods in which the hierarchy is unstable, and greater for typical egalitarian species than for despotic ones (Hemelrijk & Dübendorfer, unpublished data). Therefore, we regard it as a useful measure to grade the hierarchy. Yet, to scale species in regard of their degree of despotism is complicated by the fact that in real data the degree of bidirectionality varies greatly within groups over time and between groups of the same species. This implies that sometimes a group of typical egalitarian species may behave despotically and vice versa; for example, a group of typical egalitarian species may behave relatively despotically when its frequency of aggression has become very high because it is confined to a small space. In formulating hypotheses for real macaques it therefore seems appropriate to measure the degree of bidirectionality (as an indication of the gradient of the hierarchy) for each group separately and to determine per group whether it should be classified as despotic or egalitarian.

Cognitive and genetic traits

DomWorld provides us with general ideas regarding the minimum number of genetic and cognitive traits. As we have seen, changing only one trait (namely intensity of aggression) in the model leads to a great number of phenotypic differences at the level of the individual and of the group. Thus, the connection between the behavioral rules and the observed behavior (which respectively correspond loosely to the genotype and the phenotype) becomes nonlinear by self-organization. The results mentioned here not only bear a strong resemblance to primate societies (particularly of egalitarian and despotic macaques), but also to the behavior of fish as described in a selection experiment by Ruzzante and Doyle (1991, 1993). In this experiment, a decrease in aggression was accompanied by an increase in density of schooling and in social tolerance. This the authors explain by a so-called "threshold-hypothesis" for intensity of aggression, in which they assume that the selection they introduce results in a high genetic threshold for aggression (i.e., a reduced frequency of aggression) and that it genetically influences the other two aspects of social behavior, namely cohesion and social tolerance. To produce similar results in DomWorld, however, only the intensity of aggression has to be changed "genetically," and then the other changes of social behavior follow as side effects.

Further, DomWorld also produces hypotheses in which there is little need for assumptions of cognitive capabilities, because what may look like an exchange between the sexes (such as of female sex for male tolerance) appears to be a side effect of changes in female dominance and male timidity (Hemelrijk, 2000c). Further, the supposed exchange among females of grooming for something else (such as support), which is thought to underlie certain grooming patterns (see Seyfarth, 1977) and which should involve keeping track of the number of acts given and received, is according to DomWorld a superfluous supposition. There is no need for such cognitive book-keeping, nor for any genetic tendencies to exchange services, if such grooming patterns, as in our model, arise directly from a spatial configuration with dominants in the center and subordinates at the periphery.

It must be added, however, that on the other hand, DomWorld does not preclude the presence of such higher cognitive abilities in real animals. For instance, dominance perception of others and risk assessment may be based on direct perception, such as perceiving the body posture and size of an opponent (as reported here), but it may also be based on more complex cognitive processes, such as that agents recognize others individually and remember interactions they had with them in the past. Such memory-based dominance perception I have represented in the so-called "estimators" (Hemelrijk, 2000a). Whereas this leads to similar spatial-social structuring as in the case of direct perception, patterns were generally weaker, because the experiences each individual had with every other differed, and since different experiences by different individuals with the same partner cancel each other out, the dominance hierarchy becomes weaker.

Evolutionary adaptations

As we have seen in respect of certain behavioral patterns, DomWorld generates hypotheses that require fewer adaptations by natural selection than are usually assumed. DomWorld makes clear how by changing the value of a single trait (that which represents the intensity of aggression), one may switch from an egalitarian to a despotic society. Because of the resemblance with societies of real macaques, natural selection may in the real world also have operated simply on intensity of aggression. One may imagine that in the distant past certain populations of the common ancestor of macaques (which was supposedly egalitarian, see Matsumura, 1999; Thierry *et al.*, 2000) may have lived under conditions of limited resources and that, therefore, a higher intensity of aggression developed as it was profitable to them. In such a case, individual selection would operate on only one trait (intensity of aggression) and this may have led, via self-organization, to a switch from the characteristics of an egalitarian society to those of a despotic one. Thus, we need not invoke a separate adaptation by natural selection for each single difference in social organization between an egalitarian and a despotic species. In this context, it may be mentioned that in a phylogenetic study of macaques by Thierry and collaborators (2000), greater male migration and female dominance over males (phenomena that are associated with despotism) display phylogenetic inertia. DomWorld makes this understandable, because both traits arise as side effects of the gradient of the hierarchy.

Box 13 Proximate behaviors and natural selection

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An evolutionary interpretation of the proximate behaviors contributing to macaque social organization requires a multi-level perspective that posits at least two major modes of natural selection. I call these modes *particulate selection* and *system selection*. The major contrasts between them are presented in Fig. 13.6. The heading: *phenotypic qualities* in Fig. 13.6 refers to differences in potentially observable attributes resulting from particulate selection versus system selection: *tempo of evolutionary change* (gradual versus punctuated), *units of behavioral change* (specific stimulus-response elements versus suites of behavior), *organization* of behavior (tight versus loose), behavioral *variability* (constrained versus permissive), behavioral *adaptability* (limited versus broad), and behavioral susceptibility to *environmental influences* (weak versus strong). Figure 13.6 also shows

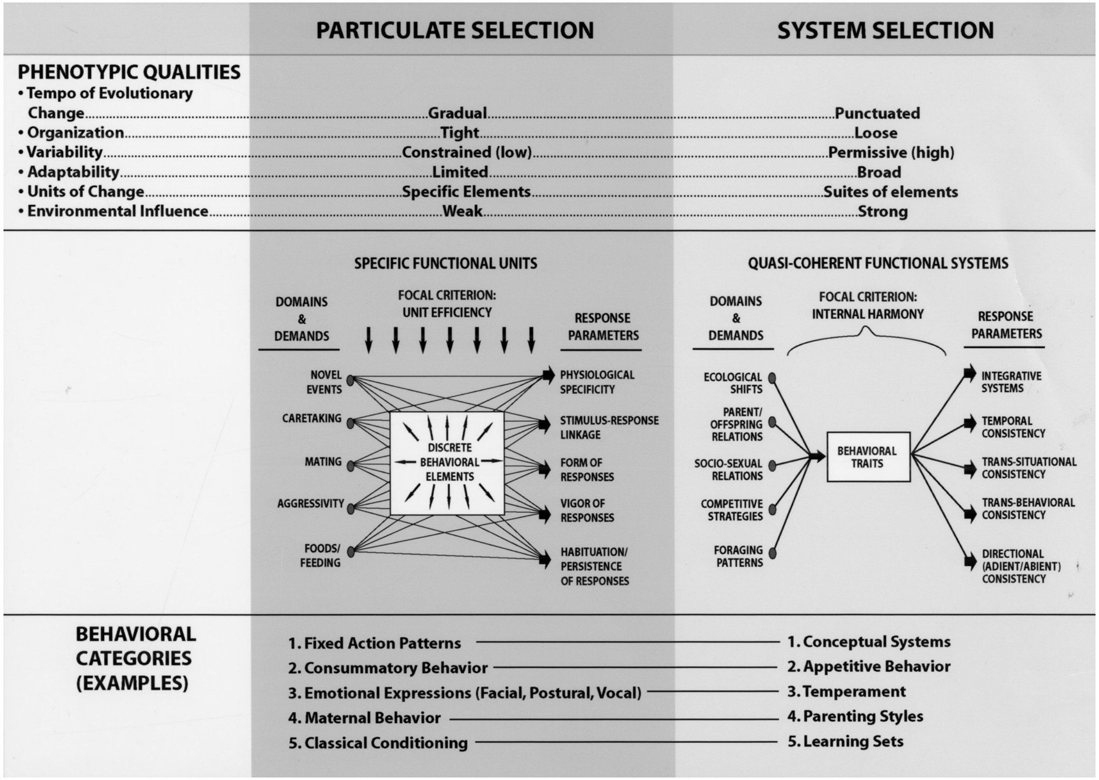

Fig. 13.6. Modes of natural selection.

how the two modes are reflected in the relations between the environment (*domains-and-demands*) and behavior (*response parameters*), and provides examples of *behavioral categories* that are characteristic of each mode. The properties of each mode are discussed separately below.

Particulate selection

Results of particulate selection are most evident in a highly predictable relation between a stimulus and a specific response, as in the classic paradigms of the conditioned response and the fixed action pattern. A *focal selective criterion* in this mode is the reliability of the association between a "stimulus" and a "response." A general term for such stimulus-response units is *schema* (Piaget, 1971; Lorenz, 1981). Schemas cannot be dichotomized as "learned" or "innate," although they vary in the degree to which they are open to modification during ontogeny (Mason, 1984). Openness is generally greater on the stimulus (input) side than on the response (output) side of schemas. The adaptive value of schemas is as sources of organized behaviors that, with little or no practice, can become effective skills (knowing how).

Schemas are distinguished by the species-typical *form* of the response – a relatively stereotyped and coordinated pattern of motor elements. Schemas are abundant at all stages of development and serve many specific functions. Some of the more conspicuous and recurrent schemas in social interaction (social schemas) include grooming, facial expressions (e.g., threat, lipsmacking, fear, silent bared-teeth display), postures (e.g., sexual present, mounting, crouching, clasping, present-for-grooming), gait (e.g., brisk striding), and certain sounds (e.g., bark, coo, scream) (Hinde & Rowell, 1962; Rowell & Hinde, 1962; Altmann, 1963; Andrew, 1963; Kaufman & Rosenblum, 1966; van Hooff, 1967; Redican, 1975).

The forms of social schemas are fundamentally similar across individuals and species and they are also relatively impervious to environmental influences (Mason, 1985), suggesting they have been conserved in macaque evolution as *discrete behavioral elements* (Fig. 13.6), probably in a process of *mosaic evolution*. In addition, social schemas are readily observable categories, easily accommodated within the common 'who-does-what-to-whom' formula, and serve communicative functions, features that may seem to qualify them as primary causes of social organization. More likely, however, they are surface manifestations of dynamic motivational and cognitive processes organized at a more fundamental level – the biobehavioral system (Mason, 1978b; Mendoza & Mason, 1989; Mendoza *et al.*, 2002; Capitanio, Chapter 2; Hemelrijk, this Chapter).

System selection

Selection at the level of the biobehavioral system operates on suites of behaviors within broad domains that constitute the basic functional dimensions of macaque social organization (Fig. 13.6). A suite consists of schemas that have been individually shaped by particulate selection and differ from other schemas within the domain in their forms and specific functions. Although they share an abiding affinity with the larger functions of the domain (e.g., sexual relations) and are often regarded as expressions of a unitary *behavioral trait*, they are not causally connected, but associated probabilistically in a *quasi-coherent functional system*. An important selective criterion in the evolution of these systems is *internal harmony* among constituent schemas.

A major adaptive value of quasi-coherent functional systems derives from the feature of openness within the configuration of schemas. In contrast to the functional emphasis of particulate selection on skill (knowing how), the emphasis of system selection is on knowledge (knowing that). This emphasis is supported by the evolved potential of macaques to form higher-order categories, concepts, rules, strategies, and the like. Such achievements are thoroughly documented and their development is known to depend on an individual's experience. Socialization influences are likely to be particularly influential and to contribute to reported variations within and between macaque species in social organization.

Evidence for the concept of quasi-coherent functional systems is abundant. Reliable differences exist between as well as within macaque species in such domains as foraging and feeding patterns, predator identification, relationships among kin, socio-sexual patterns, tolerance between and within the sexes, dispersal tendencies, characteristic stance toward the environment, and care of offspring.

A good illustration of the organization of a quasi-coherent functional system in macaques is maternal behavior (Mason, 2002). The principal schemas shown by a competent mother during the first few weeks following birth are clasping the infant to her ventral surface, carrying it as she goes about her normal routines, restraining it if it attempts to leave against her wishes, and retrieving it if she perceives it in danger or distress. These schemas appear in immature animals of both sexes and they are accessible throughout life (Breuggeman, 1973). To a casual observer the elements may appear as different expressions of a fully integrated unitary system of maternal care.

Contrary to this impression, the quality of maternal behavior is influenced by such factors as the mother's experience of being mothered and the quality of care she received, opportunities during development to interact with infants, to observe others caring for infants, and the experience of giving birth itself (see Chauvin & Berman, Chapter 10). Even when these opportunities are available, however, associations among the participating schemas may be tenuous. The same mother may show high levels of some positive aspects of maternal behavior (approach, making contact, restraining, grooming), while also displaying a strong tendency to reject, break contact, and leave the infant (Fairbanks, 1996). A mother may also be extremely abusive (dragging, stepping on, biting, hitting her infant), but also show high levels of proximity and protectiveness. Such contradictory behaviors have been noted in mothers raised in social groups and living in seemingly optimal conditions. Some effects may be modified by experience, whereas others apparently cannot (Maestripieri & Carroll, 1998).

The behavior of most mothers falls within the species-typical norm and the benefits to their infants of the inherent plasticity of the quasi-coherent maternal system are not noticed. There are cases, however, in which infants with serious developmental defects receive extensive compensatory maternal care that goes well beyond the normal pattern (Berkson, 1973; Fedigan & Fedigan, 1977; Nakamichi *et al.*, 1997).