

10 *Intergenerational transmission of behavior*

CHRISTOPHE CHAUVIN AND CAROL M. BERMAN

Introduction

The notion of a species-typical society implies a strong degree of continuity in social behavior and in social organization across generations. Although the players change with each generation, patterns of subsistence and social interaction in a given group tend to remain constant or to vary within certain limits. Some cases of behavioral continuity have been traced to heritable behavioral tendencies that place considerable constraints on behavioral flexibility of, for example, herding behavior in hamadryas baboons (e.g., Sugawara, 1988), or the vocal repertoire of macaques (e.g., Owren *et al.*, 1992). In other cases, intergenerational continuity appears to be at least partly the result of social processes operating primarily, but not exclusively, during ontogeny. Although a variety of social influences may theoretically lead to behavioral continuity (Whiten & Ham, 1992; Avital & Jablonka, 2000), most research has focused on social transmission, in which one individual learns to perform a behavior as a result of interaction with a model of that behavior (Imanishi, 1952). This focus has grown out of a longstanding interest in the nature and origins of culture. Although biologically-oriented researchers vary widely on definitional criteria, virtually all agree that in order for a behavior to be considered cultural, there must be, at least, clear evidence that its acquisition depends on social transmission. In this chapter, we examine the extent to which macaques may acquire and transmit behavior from one generation to another through social transmission.

Research in social transmission in macaques has focused on two main areas. The first has concerned the transmission of social patterns from mothers to offspring, including dominance status, maternal style and affiliative networks. The second area concerns the transmission of specific techniques or behavioral variants. For each area we ask: what behaviors may be transmitted? Who are the

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demonstrators and how does their identity influence transmission (see Coussi-Korbel & Fragaszy, 1995)? What specific learning mechanisms may be involved (see Galef, 1992)?

Definitions of terms and processes

Galef (1988) defines social transmission as instances of social learning or enhancement in which social interaction results in increased homogeneity of the behavior of the interactants that endures beyond the period of interaction between the transmitter and the recipient. This definition excludes both response facilitation (also called social facilitation or contagion) in which the presence of individual A performing an act in individual B's repertoire temporarily increases the probability of its performance by B, and matched dependent learning, in which B learns to use A's act as a discriminant stimulus (see Whiten & Ham, 1992).

Intergenerational social transmission (or more simply, intergenerational transmission) might thus be defined as instances of social transmission between members of different generations. Given our interest in the processes that lead to species-typical societies, we are most interested here in examples in which behavior is transmitted from older generations to younger generations and in which the behavior endures after the models in the older generation are no longer present or displaying the behavior. When shown by a substantial proportion of a social group or population, such examples may also be referred to as traditions (Nishida, 1987; Fragaszy & Perry, 2003).

Operationally, behavioral homogeneity may relate to specific behavioral variants (e.g., qualitatively different food processing or grooming techniques), social preferences or consistent styles of interaction (e.g., quantitative or contextual differences in interactional patterns). Thus, social transmission may involve learning a novel behavior, or it may simply involve modifying where, when, how much, or toward what (whom) an extant behavior is performed (Galef & Giraldeau, 2001). To qualify as a style or variant, different forms of behavior should be displayed consistently by different subsets of group members or by conspecific members of different social groups.

The earliest mechanism proposed to explain the intergenerational transmission of behavior in primates was identification. Imanishi (1957) derived his concept of identification from psychoanalysis, and hypothesized that some individual attributes among macaques might be socially inherited from parents because young and other group members identify the young with their mothers – that is, they “assume” the offspring possesses certain characteristics of the mother. For example, both offspring and other group members behave as

if the offspring carries the mother's dominance status even when the offspring's own ability to fight is poor. Although Imanishi's specific hypotheses were never thoroughly tested and were clearly oversimplifications (e.g., Chapais, 1988a; Chapais & Gauthier, 1993), his focus on the intergenerational transmission of behavior was pioneering.

Currently, our concept of social transmission is not restricted to a specific social learning mechanism. A possible mechanism is exposure learning in which B learns a new act or preference because its association with A places it in an environment conducive to individual learning. This mechanism could encompass the effects of familiarity on social preferences, in which a mother's preferences are transmitted to dependent offspring as a result of their close association with both their mother and her preferred partners. Other possible mechanisms include: social control by conspecifics either in the form of encouragement or discouragement to behave in particular ways or with other particular conspecifics; and various forms of observational learning.

The tendency for individuals to form preferences for familiar conspecifics, frequent interactants, and even familiar inanimate objects is well documented in a variety of taxa (Hinde, 1974). In addition, there is evidence that social control by the model may lead to social transmission either when the model actively encourages the recipient to behave as it does or discourages it from doing otherwise. Social control by mothers has been implicated in the transmission of affiliative preferences (e.g., Timme, 1995; Berman & Kapsalis, 1999) and in the avoidance of particular foods or objects (e.g., Hikami *et al.*, 1990). In addition, aggressive intervention by mothers and close kin on behalf of young is thought to be an important means by which infants initially learn whom to challenge (e.g., Chapais & Gauthier, 1993) and by which older females acquire ranks in the adult female hierarchy (Chapais, 1988a).

Finally, although there is no definitive evidence for true imitation in macaques (Whiten & Ham, 1992), infants may acquire new behaviors through other forms of observational learning, including observational conditioning, response or stimulus enhancement, and/or emulation. In observational conditioning, the emotional responses of A are transmitted to B when B observes that A responds to an object, individual, or context. In response or stimulus enhancement, B's attention is drawn to an object or location by the performance of A. In emulation learning, B learns to associate an object, part of the environment or an aspect of an action (but not a particular technique) used by A with a particular goal (Tomasello & Call, 1997). Empirical examples of emulation learning are usually related to tool use rather than social behavior (e.g., Tomasello & Call, 1997), although there is as yet no theoretical reason why social behavior should be excluded. Studies of emulation learning in monkeys are just beginning to appear in the literature. Although there is evidence that some species are capable of

emulation, definitive conclusions about macaques are not yet possible (e.g., Custance *et al.*, 1999; D. Custance, personal communication). Mothers are thought to be particularly salient models for observational learning (e.g., Avital & Jablonka, 2000) at least partly because of their high tolerance for offspring, although other kin and conspecifics may also serve this purpose.

Once an individual is exposed to or has its attention drawn to particular objects, conspecifics, goals or actions, it is more likely to attempt to perform the behavior or interact with the object or individual. In so doing, the recipient learns directly from the consequences of its own actions (and interactions) and is likely to achieve increased behavioral homogeneity with the model. Thus, in addition to interaction with a model, social transmission may involve both independent learning mechanisms and other social influences. In reality, it is often difficult to distinguish behavioral homogeneity arising from various social and nonsocial processes, including social learning, other social influences, independent learning, and unlearned genetically-influenced propensities, because they are likely to interact with one another in complex ways (Galef, 1995). This is particularly true of behavior observed in natural situations.

It is noteworthy that the processes guiding the maintenance of a socially transmitted behavior may differ from the processes guiding its acquisition. Galef (1995) theorizes that behavior acquired socially may be subsequently reinforced, modified, or replaced as a result of the consequences of its performance by the learner. He refers to behavior that is acquired socially but subsequently altered through independent learning as socially-biased independent learning. To be maintained in a given individual or across generations (Galef & Whiskin, 1997), the socially transmitted behavior should provide equal or greater rewards than available alternatives (see Boyd & Richerson, 1985). Other researchers maintain, however, that neither the acquisition nor the maintenance of a behavior necessarily depends on concrete rewards (e.g., Laland *et al.*, 1996; Matsuzawa *et al.*, 2001). Matsuzawa and collaborators (2001) and de Waal (2001), for example, hypothesize that motivation to perform socially-transmitted behavior may derive from a desire for social conformity with socially-bonded or otherwise salient performers.

Transmission of mothers' social styles

Close, persistent, and tolerant mother–daughter relationships, typical of female-bonded macaques, potentially provide rich contexts for the intergenerational transmission of behavior. Below we examine three hypothesized examples of maternal transmission of social style in macaques: dominance status (see Chapais, Chapter 9), maternal style, and affiliative networks. Each example is

considered a candidate for maternal transmission, based on observations that: (1) individual females vary consistently in behavior; and (2) daughters show variations similar to those of their mothers.

Social inheritance of maternal dominance status

Numerous studies of cercopithecine monkeys, including macaques, document strong tendencies for females to maintain stable dominance ranks over their lifetimes (e.g., *M. fuscata*: Koyama, 1967; *M. mulatta*: Sade, 1972a; yellow baboons: Hausfater *et al.*, 1982). Described first in Japanese macaques (Kawamura, 1958; Koyama, 1967), adult daughters in many species acquire ranks within the female hierarchy (1) just below their mothers and (2) above their older sisters (e.g., *M. mulatta*: Datta, 1983a; *M. fascicularis*: de Waal, 1977), patterns that occur so consistently they are called "Kawamura's principles" (Chapais, Chapter 9). Longitudinal observations of adopted infants who eventually acquire their foster mothers' ranks, suggest that the status a female attains is not highly dependent on genetic influences, but rather on social influences during ontogeny (Itani, 1959; Bernstein, 1969).

Rank acquisition appears to follow distinct stages, thoroughly described in rhesus and Japanese macaques (e.g., Datta, 1983a; Chapais & Gauthier, 1993). In brief, youngsters first acquire their mothers' ranks vis-à-vis peers, often during the second half of the first year of life. They then begin both to direct more aggression to older lower-born females (and their offspring) than their mothers outrank than to those their mothers cannot outrank (higher-born) and to selectively join coalitions against them. Thus they develop alliances with powerful females, particularly mothers and other older female kin. As they develop into juveniles and adolescents, they increasingly target older lower-born females, including their own older sisters, with the aid of higher-ranking allies. Gradually they establish dominance over these females, and consequently, each eventually achieves a rank immediately below her mother and above her older sisters. Careful experimental studies have confirmed the critical importance of alliance support in this later stage of rank acquisition (e.g., Chapais, 1988a, Chapter 8).

Observational studies of macaque infants suggest that they may learn to select appropriate targets for aggression in numerous ways, some of which involve social transmission (e.g., Berman, 1980; Chapais & Gauthier, 1993). Before infants can be assigned ranks among themselves, mothers and close kin actively and effectively intervene on their behalf against lower-born females and immatures. Thus high-ranking mothers actively control the outcome of their infants' early agonistic interactions with lower-ranking individuals. Hence,

infants develop “dependent ranks” that correlate with those of their mothers (Kawai, 1958), but depend on her support. In addition, mothers direct aggression toward lower-born infants both in and out of their own infant’s presence. High-born infants may thus learn whom they can threaten with impunity through observation of the mother, and lower-born infants to whom they must defer independently by associating the higher-born infant with its mother. Finally, low-born infants may be subject to observational conditioning when they observe their mothers avoid higher-born females and their offspring. However, at this point, the relative importance of each proposed early learning mechanism is still unclear.

A striking aspect of rank acquisition among rhesus and Japanese macaques is the apparent assertiveness that mothers show both in threatening lower-born infants of other females and in intervening on behalf of their own infants during interactions with lower-born peers. This assertiveness appears to trigger assertiveness by offspring, as indicated by their active and persistent challenging of lower-born females until they rise in rank over them (Datta, 1983a). Given that high rank among females in many species brings increased access to limited resources and ultimately increased reproductive success (e.g., Silk, 1987), it is reasonable to hypothesize that propensities toward assertiveness in such situations may be in part a product of natural selection. However, it is unclear how a system of maternal rank transmission per se could have been selected. Recent research suggests that the fidelity of transmission is likely to be affected by the availability of allies, the benefits of alliances and other factors affecting aggression between females (e.g., Chapais, Chapter 9). Where aggression tends to be mild, mothers and close kin may have less need to intervene on behalf of young relatives, and as a consequence, youngsters are more likely to attain ranks based on their own competitive abilities rather than on birth order and mother’s rank. Thus, it is reasonable to propose that maternal rank transmission is the product of adaptive tendencies to strive for high rank interacting with another functional system designed to protect immatures from harassment and injury.

Intergenerational transmission of rejection style

For decades, researchers have casually described tendencies for mothers to display similar maternal styles with successive infants and for adult daughters to display maternal styles similar to their own mothers (Altmann, 1980; Goodall, 1986). These phenomena were first demonstrated quantitatively when Berman (1990a) showed that free-ranging rhesus mothers that raised three or more infants on Cayo Santiago varied consistently from one another on several

measures of mother–infant interaction, including relative rejection rates. Conversely, each mother was reasonably consistent with each of her infants. Finally, this consistency was evident even when variations in group size (Berman *et al.*, 1997) and numbers of older siblings (Berman, 1992), known to influence maternal behavior, were controlled.

Berman (1990b) compared relative rejection rates of mothers with those of their adult daughters for three 6-week infant age periods (13–18, 19–24 and 25–30 weeks). Mean rejection rates for mothers were moderately but significantly correlated with those of their adult daughters in all three age periods. Although this result raised the possibility that rejection styles may be socially transmitted by mothers to daughters, it did not establish whether or not daughters acquired rejection styles specifically from mothers or from other sources to which the mother was also exposed. For example, in two out of three age periods, rejection scores differed significantly between mothers who belonged to different lineages, raising the possibility that mothers and daughters acquired their rejection styles through their membership in a common lineage. Thus, mothers and daughters may have acquired similar rejection rates through observation or interaction with common close associates (i.e., primarily lineage mates) or as a result of immediate social and environmental circumstances affecting all lineage females similarly (e.g., lineage rank). To tease apart the independent effects of mothers and lineages, the relationship between mother's and daughter's rejection scores was re-analyzed using analysis of covariance methods. The results supported the notion of transmission through the mother over transmission through the lineage: (1) daughters' scores were associated specifically with those of their mothers' scores independently of lineage effects; and (2) differences between lineages (and conversely similarities within lineages) could be explained entirely by the association between the scores of mothers and their adult daughters. No specific common attributes nor external social factors were founded to explain the similarity of mothers' and daughters' rejection scores (e.g., similarity in size of kin support networks, dominance ranks, amounts of maternal experience, sexes of offspring, or numbers of older immatures), thus lending further support to the notion of mother–daughter transmission.

To narrow possible mechanisms of transmission, Berman (1990b) correlated adult daughters' scores separately with: (1) the rejection rates the daughters experienced as infants; (2) the rates they observed their mothers apply to their younger siblings; and (3) the rates their mothers applied to their older siblings. The only significant positive correlations were for rates mothers applied to the daughter's younger siblings. These results both suggest that daughters had been influenced by observing their mothers raise their younger siblings and argue against genetic hypotheses, because they would have predicted correlations of equal strength in the three analyses.

Berman (1996) further refined this analysis by separating rejection rates daughters may have witnessed as juveniles and as adults raising their infants alongside their own mothers. The rejection styles of mothers and daughters were similar only when mothers and daughters gave birth in the same years. This surprising result leaves open several possibilities. It may be that mothers transmit rejection styles to daughters, but that the process is highly biased toward current rather than early experience. If this is the case, the similarity of rejection styles may represent an example of social learning but not social transmission, since the behavioral similarity does not necessarily endure after the model is no longer available. It is also possible that mothers and their adult daughters exert a mutual, equalizing influence over one another. Finally, mothers and daughters may display similar rejection styles not because one learns from the other but rather because they share common attributes or social circumstances not yet examined by researchers.

The scarcity of studies on the continuity of maternal style across generations makes it difficult to generalize across species and situations. What evidence is available suggests caution. First, not all studies have been able to demonstrate consistent maternal styles, even at the level of individual mother–infant pairs (Silk, 1991). Second, probable mechanisms may vary with species and/or with the particular measure of interaction. For example, Fairbanks (1989) found positive correlations between vervet monkey mothers and adult daughters in levels of contact with infants, but her data pointed to the daughter's own experience as an infant as the most likely route for transmission between the generations. Third, even where a strong argument for similarity by social learning can be made, other factors may increase or decrease the extent to which mothers and daughters actually display similar maternal styles. Indeed, the Cayo Santiago data suggested that resemblance in rejection styles between mothers and daughters do not depend on similarities in dominance ranks, sexes of infants, number of older immature, or support networks. However, when these factors happen to coincide, as they tend to do for rank and support networks (but not for infant sex or immature siblings), they are likely to lead to greater degrees of similarity between mother and daughters than when they do not.

Similarly, even where adult daughters learn aspects of maternal style from mothers, the extent to which they resemble one another might depend on the extent to which they respond similarly to changeable environmental conditions. Some measures of maternal behavior (not rejection rates) track year to year changes in group size and density (Berman *et al.*, 1997; see also Maestripieri, 2001). In large/high density groups, infants are at more risk of harassment and injury from others, and mothers respond by spending less time at a distance from them. Since proximity-seeking is sensitive to variations in rank and aspects of the mother's support network, and since these factors tend to be similar for

rhesus mothers and daughters, we might expect both to respond to changes in group size and density in similar manners each year. However, in macaque species that are less despotic than rhesus macaques, daughters are less likely to have similar ranks and support networks than their mothers (Butovskaya, Box 9; Maestripereri, Box 10; Thierry, Chapter 12). Nor are their infants as vulnerable to harassment and injury from conspecific group members (Maestripereri, 1994a,b). Thus we would not necessarily predict that they would adjust their maternal behavior similarly to changes in group size/density. Furthermore, in relaxed species, mothers and daughters spend less time together and more time interacting with a broad range of adult females. Hence, they may be less likely to learn maternal styles specifically from one another.

Although variation in maternal care patterns is likely to have important consequences for mothers' and infants' future reproductive success, evidence that the intergenerational transmission of maternal style is adaptive or that it has been specifically selected is still lacking. In some cases, it may be clearly maladaptive. For example, it has been suggested that captive macaque mothers transmit abusive care patterns that lead to infant injury or death (e.g., Maestripereri *et al.*, 1997). Cases of abuse tend to cluster within families, but as yet, the mode of transmission (genetic and/or social) is unclear. Nevertheless, the transmission of maternal style, and particularly rejection style, is likely to have important consequences on life-history variables. High levels of rejection have been associated with high infant mortality and morbidity (Altmann, 1980), whereas low levels have been associated with long interbirth intervals for mothers (e.g., Gomendio, 1989b; Berman *et al.*, 1993). The degree to which a particular level of rejection is adaptive is likely to depend on several factors related to the nutritional conditions of the mother and infant (Hauser & Fairbanks, 1988). Nevertheless, an implication of the consistency of rejection behavior from infant to infant is that the long-term consequences of particular rejection styles may accumulate over a lifetime and have profound effects on life-history variables. To the extent that daughters carry on their mothers' rejection styles it seems that the consequences will also affect grandoffspring.

Intergenerational transmission of the maternal social network

Early mirroring of social networks

Close mother–infant relationships epitomize the early development of macaques and many other cercopithecines. Macaque mothers and infants maintain nearly constant contact with one another during the first weeks of life, after which infants gradually begin to spend time away from the mother. Within this context, infants have their first experiences with other group members and begin

to interact with them. When they do, their interaction patterns closely resemble those of their mothers; they associate primarily with the same individuals the mother associates with (e.g., de Waal, 1996b; Berman & Kapsalis, 1999). In some macaque species, these are primarily, but not exclusively, close female kin and their immature offspring (e.g., Berman, 1982a). In other macaques kin bias may be more moderate or absent (Rosenblum *et al.*, 1975; Maestripieri, Box 10; Thierry, Chapter 12). This early mirroring of maternal networks is due at first to two tendencies. First, infants are exposed primarily to the mothers' close associates and their offspring because they maintain close proximity to one another. Second, in species where mothers exert a large degree of control over their infants' social interactions, mothers are typically more tolerant of their close associates and their associates' offspring than of others (e.g., Spencer-Booth, 1968). In addition, other individuals may be more likely to initiate interaction with the infants of close associates than with others (e.g., Berman, 1982a; de Waal, 1996b). In any case, it is important to note that such mirroring can be observed even before infants are able to take an active role in initiating and sustaining their own relationships. Thus, de Waal (1996b) used the term "dependent affiliation" to describe early relationships, highlighting parallels with the notion of dependent rank (Kawai, 1958).

To what extent do early maternal patterns endure as the infant develops an independent social network? Berman (1982a) followed the development of social relationships in free-ranging rhesus macaques from birth to 30 weeks of age. This age span included both the initial period of close maternal proximity plus control and a period of gradual emancipation in which the infant spent progressively more time distant from its mother and in which the mother's control relaxed considerably. Moreover, by 30 weeks, the infant's relationships acquire some degree of independence from those of the mother with the same partners; approaching peers and older immature partners appeared to be attracted specifically to the infant rather than to its mother (Berman, 1982b). The results showed a remarkable degree of stability over infant age periods. Infants' networks still appeared to resemble those of their mothers at 30 weeks of age (Berman & Kapsalis, 1999) even though many of their interactions took place far from her and were less likely to be prevented (or encouraged) by her.

The enduring similarity of mothers' and infants' social networks, brought about initially through close mother–infant interaction and control, suggests a process of maternal transmission in rhesus macaques. Furthermore, the intensity of kin bias among infants parallels that of their mothers and is related to the amounts of time the infants spend near their mothers. This is also linked with the mother's relative role in maintaining proximity to her infant, highlighting the importance of the mother in bringing about this resemblance (Berman *et al.*, 1997; Berman & Kapsalis, 1999). Additional studies illustrate the gradual nature

of the development of kin bias when infants are not under the full control of the mother (de Waal, 1996b; Berman, 2004) and suggest that the similarity between mothers' and daughters' social networks endures throughout juvenile development and into adulthood in both rhesus and Japanese macaques (de Waal, 1996b; Nakamichi, 1996).

Our understanding of the mechanisms that lead to the maternal transmission of affiliative networks is still fragmentary. It is possible that several hypothesized mechanisms play a role. They include familiarity based on differential amounts of exposure to and interaction with the mother's frequent and infrequent associates, observational learning with the mother as model as well as active and selective maternal intervention (see review in Berman, 2004). The tendency for individuals to form active preferences for familiar conspecifics has been studied intensively, primarily in the context of parental attachment (e.g., Rajecki *et al.*, 1978; Suomi, 1995). Studies of infants describe initial periods of broad social openness when attachments are formed easily and there is little fear of strangers, followed by a period when unfamiliar conspecifics are more likely to be avoided. The advent of "stranger anxiety" may serve to translate early patterns of exposure while under the direct control of the mother into longer-term social preferences (Hinde, 1974).

In a hypothesis based on observational conditioning, Altmann (1980) suggests that infant baboons may be specially prepared to learn about their mothers' relationships with other females through her differential display of fear or distress in their presence. Alternatively, mothers could serve as foci for directing infants' attention to preferred conspecifics, in a process of stimulus enhancement similar to that by which they learn the mother's preferred foods (Hikami *et al.*, 1990). Finally, mothers may influence their infants' development of social preferences by disrupting interaction with infrequent associates (Hrdy, 1976) or by actively encouraging infants to interact with close associates and their offspring (e.g., Timme, 1995).

Factors that may influence maternal transmission of social networks

Tendencies for mothers to seek proximity with infants and to regulate their early interactions with other group members can be seen as a manifestation of a functional system by which mothers protect infants from injury and harassment (Berman, 2004). Given that these tendencies also appear to lead to the transmission of maternal social networks, we may also view this transmission as an outgrowth of the same functional system (see Berman, 2004).

In situations in which mothers seek less proximity and are less protective, infants tend to associate with and receive handling from a wider range of group members than in situations in which mothers are more protective. As a result, we might expect infants with less protective mothers to develop social networks that



Fig. 10.1. Maternal protectiveness in rhesus macaques (Strasbourg Primate Center, France). (Photograph by B. Thierry.)

do not closely resemble those of their mothers in comparison to infants with highly protective mothers. This prediction might be particularly relevant for understanding differences in the way social networks arise in macaque species that differ in dominance style. For example, mild resemblance between mothers' and offsprings' social networks might be expected in relaxed or tolerant species that exhibit a high degree of social tolerance such as stumptailed and Sulawesi macaques. Several comparative studies have found higher levels of maternal protectiveness and more highly constrained social networks among infants of despotic than among infants of tolerant macaque species (Rosenblum *et al.*, 1975; Thierry, 1985b; Maestripieri, 1994a,b, Box 10; Mason *et al.*, 1993). However, no data are yet available to support or refute the prediction that infant social networks among despotic species resemble those of their mothers more than do those of tolerant species.

Berman and Kapsalis (1999) investigated the relationship between maternal protectiveness (Fig. 10.1) and resemblance of social networks within species by testing the prediction that free-ranging infant rhesus macaques who spent relatively more time near their mothers would come to resemble them more than other infants in terms of intensity of kin bias. However, the prediction was

not supported. Whether or not similar predictions would be supported for other aspects of social networks, settings, or species needs testing.

Although the evidence implicating maternal transmission in the development of daughters' social networks is strong for macaques, recent evidence from free-ranging rhesus macaques suggests that other processes may also contribute (Berman & Kapsalis, 1999; Berman, 2004). First, by 25 to 30 weeks, individual infants display degrees of kin bias that are only moderately correlated with those of their mothers. Thus by this age, infants tend to modify rather than duplicate their mothers' patterns. Second, as described above, the degree to which individual infants display patterns similar to those of their mothers is not related to the amount of time they spend together. Berman and Kapsalis (1999) hypothesize that infant kin networks at this age represent maternally transmitted behavior patterns that have been subsequently modified by the consequences of their performance by the infant (socially biased independent learning, *sensu* Galef, 1995). Under this hypothesis, infants learn to prefer kin partly through the quality (as opposed to quantity) of their direct experiences with kin and nonkin. Through direct experience with kin and nonkin, infants could either reinforce or moderate patterns of affiliation acquired initially through maternal transmission.

In addition, over time, offspring take increasingly more initiative in their interactions with group members (Fairbanks & Pereira, 1993). Who they choose to pursue is likely to be influenced by individual, sex-specific and species-typical temperamental characteristics (Clarke & Boinski, 1995). Such temperamentally-based attractions may be inherited to some extent from mothers and interact with maternal care patterns, but may also be influenced by other kinds of experience during infancy. Finally, Widdig and collaborators (2001) speculate that paternal siblings may be attracted to one another based on similar inherited personality profiles, thus further modifying maternal patterns of association.

Transmission of material techniques

New behaviors or new variants of pre-existing behaviors may appear spontaneously in some individuals. These innovations usually remain idiosyncratic. In a limited number of cases, however, such behaviors appear to be transmitted to other group members, including members of different generations. The establishment of apparent local traditions has been described in several provisioned troops of Japanese macaques (e.g., Nishida, 1987; Tanaka, 1998). Three modes of social transmission have been hypothesized: (1) vertical (parent to offspring); (2) horizontal (among members of the same generation); and/or

(3) oblique (from nonparents in the mother's generation to offspring) (Cavall-Sforza *et al.*, 1982).

Transmission of food-associated techniques

Kawai (1965) described two food-processing techniques in the provisioned troop of Japanese macaques on the Koshima Islet. The first technique, sweet-potato washing, consists of holding a sweet potato in one hand, dipping and/or scrubbing it in the water with the other hand. These actions remove the sand before the potato is eaten. Kawai (1965) also reported variants of this technique that consist of using salt water instead of fresh water and of dipping the potato into the water after taking one or two bites. The newly developed variants, first seen in 1953, have been maintained over six generations and nearly 50 years (e.g., Kawai *et al.*, 1992; Hirata *et al.*, 2001). In recent years, however, few individuals display rubbing behavior, presumably because only clean potatoes are available for provisioning. The mode of transmission before 1959 was primarily horizontal, that is, from one individual to peers or playmates, often from younger to older immatures. However, two mothers also apparently learned from their immature offspring.

After 1959, sweet-potato washing was observed among a variety of age–sex classes, although it was rare among adults over the age of 11 years. Infants and juveniles appeared to learn from their mothers, but in fact vertical and horizontal (and then oblique) modes of transmission were difficult to distinguish with certainty. There were no sex differences in acquisition rates among immatures, but adult males were less likely to learn than adult females, probably because of their more peripheral social positions within the group. Several additional variants appeared during this period, including digging a little pool to collect water before sweet-potato washing (Kawai *et al.*, 1992), but particular variants were not disproportionately associated with particular lineages (Hirata *et al.*, 2001). Sweet-potato washing also appeared in other provisioned populations of Japanese macaques, but failed to spread beyond a few individuals in each group. K. Watanabe (personal communication) suggests that this was due to the manner of provisioning; potatoes were distributed closer to water sources on Koshima than elsewhere.

The second technique described in the Koshima troop was called wheat washing or placer mining. It consisted of taking a fistful of sandy wheat from the ground and placing it in water (Kawai, 1965). Because the wheat floats, it is then easy to collect it without the sand. The spreading of this technique was slower than that of sweet-potato washing and fewer individuals finally displayed it. As for sweet-potato washing, there were sex differences in acquisition rates among

adults but not among immatures (Hirata *et al.*, 2001). In addition, this behavior appeared to disappear when the rate of provisioning was greatly reduced in 1972. With less provisioned food available, monkeys that washed wheat were likely to lose their bounty to higher-ranking or stealthy individuals. Interestingly, at this point a number of scrounging and counter-scrounging variants for this technique appeared and became common (Kawai *et al.*, 1992), suggesting that social factors can both discourage the maintenance of some variants and encourage the acquisition and spread of new ones.

Similar food washing techniques, accompanied by the spontaneous appearance of new variants have also been described in captive settings (Scheurer & Thierry, 1985). The patterns of diffusion in captive Japanese macaques were similar to those described on Koshima for sweet-potato washing and wheat washing: initiation by a young individual, spreading among kin, especially peers, but no acquisition by adults aged more than 11 years (Scheurer & Thierry, 1985).

Interestingly, on Koshima, acceptance of two foods that required little or no processing was spread markedly differently from those for sweet-potato washing and wheat washing. Both raw fish eating and candy eating were acquired first by older adult males, then by adult females and finally by youngsters. Rates of spread were very slow for fish eating but were rapid for candy eating (e.g., Watanabe, 1989).

Transmission of grooming techniques

Technical traditions may also concern activities not associated with food. Using video tape recording, Tanaka (1995), documented the consistency of lineage-based grooming techniques in Japanese macaques. He observed variations in techniques used to remove lice eggs from fur. Three out of five matriline displayed single variants almost exclusively. In the fourth matriline, most members used a single variant, but some individuals used one of two minor variations. In the fifth matriline, two variants were common, but some individuals used quite different variants (Tanaka, 1995).

In a further investigation, Tanaka (1998) described the social diffusion of a newly acquired variant within one of the matriline previously mentioned. A 22-year-old female member initiated the process. Within six months, her 20-year-old sister, two daughters (11 and 5 years old) and one 5-year-old granddaughter adopted this variant. All members of this matriline subsequently abandoned the new variant in favor of a second new variant. Tanaka actually witnessed the transition for two out of five focal individuals and described the acquisition of the second variant as a result of serendipitous movements

during the performance of the previous variant. Interestingly, a third variant that involved skin pinching failed to spread or even to be sustained for long, apparently because of the painful reactions it produced in groomees. Hence, this case serves as an example in which social feedback discouraged rather than encouraged the propagation of a variant. In any case, the spreading pattern of the “successful” variants appeared to differ oddly from that described for food-washing techniques in that the initiator was an older individual and the technique spread quickly among relatives as old as 20 years. To our knowledge, innovation and acquisition of a complex technique has never been described elsewhere in individuals more than 20 years old.

Transmission of non-utilitarian techniques

Some hypothesized examples of social transmission in Japanese macaques involve apparently non-adaptive behavior. The best studied one concerns stone handling techniques (Huffman, 1984, 1996). Huffman (1984) recognized eight basic stone handling variants including gathering, picking up and hand rolling (Fig. 10.2). As in Koshima washing techniques, the initiator was a young female. Within 4 years after their first appearance, the stone handling techniques were exhibited by more than 75% of the 115 group members. However, only three were older than the initiator, and each of the three was a female only 1 or 2 years older than the initiator. Moreover, two out of the three belonged to the initiator’s matriline. Although the rate of transmission was high among playmates and kin, no individuals who were adult at the time of initiation acquired the technique perhaps because of its playful nature. This horizontal spreading pattern recalls that of sweet-potato washing and wheat washing techniques, but the rate was faster. The ease and attractiveness of the behavior for youngsters, coupled with free time supplied by provisioning may have contributed to the high acquisition speed (Huffman, 1996). At the same time, the extent to which stone handling was transmitted via the vertical mode was uncertain. By 1985, all offspring of stone handling mothers and most (72%) offspring of nonhandling mothers also handled stones (Huffman, 1996), suggesting that maternal transmission may have contributed to its spread, but that youngsters were not dependent on learning from their mothers.

In other examples, Machida (1990) reported the spontaneous standing of poles against a smooth wall and subsequent climbing up on them in a captive group of Japanese macaques. The behavior had never been observed before, despite the constant availability of poles. The initiator was a juvenile female. Two years later, two other juvenile females performed “standing and climbing a pole.” As they grew older, these three individuals stopped displaying the



Fig. 10.2. Stone handling as a form of socially transmitted play in young Japanese macaques (Arashiyama, Japan). (Photograph by B. Thierry.)

behavior and there was no evidence of transmission to any other individuals. Similar behavior with poles and its limited spread was also observed in captive Tonkean macaques (Ducoing & Thierry, 2004). This behavior had never been observed during the 15 years preceding this first occurrence. Contrary to other examples, the initiator was a subadult male. Within 3 months, three other males acquired the technique. Again there was no sign of further spreading or of intergenerational transmission.

Another reported case of apparently transmitted behavior concerns vocalizations. Differences in the vocalizations uttered at the initiation of provisioning were found between different study sites in Japanese macaques (Green, 1975). The author suggested that such locale-specific “dialects” were displayed by both sexes but were confined to young individuals. Older individuals uttered a same general tonal pattern but never included the locale-specific modification (Green, 1975). At present, it is not known whether these vocal variations were socially acquired and/or resulted from genetic differences between populations.

Proposed mechanisms and processes

Definitive data on social mechanisms that may have been involved in the spread of techniques among provisioned natural groups are not available. Although

many researchers originally accepted that the spread of techniques involved imitation or at least some form of social learning, Galef (1992) argued that they may not have. Galef suggested that the rate of spreading of sweet-potato washing and wheat washing among Koshima monkeys were too slow to implicate social learning. Moreover, rates of transmission did not accelerate over time, as one might expect as the number of potential models of the behaviors within the groups increased (Boyd & Richerson, 1985). Rather than learning new techniques from observation, Galef suggested that the monkeys independently learned to reorganize existing behaviors (e.g., food rubbing) when confronted with provisioned food near water (see also Visalberghi & Frigaszy, 1990), although stimulus enhancement may have initially drawn their attention to the potatoes and water. Finally, Galef suggested that human provisioners may have inadvertently shaped monkeys to use the new variants by directing food to monkeys whose behavior approximated sweet-potato washing or wheat washing (see also Green, 1975), a practice denied by at least some of the provisioners (de Waal, 2001).

In other studies, new techniques have spread much more quickly (e.g., Huffman, 1984; Visalberghi & Frigaszy, 1990; see also Hauser, 1988) and at accelerating rates (Lefebvre, 1995). And in any case, researchers dispute the importance of speed and acceleration as criteria for social learning (e.g., de Waal, 2001), especially when evaluated in a natural setting (Laland *et al.*, 1996). Stone handling among juvenile Japanese macaques (Huffman, 1996) offers an example not only of fast spreading but also of behaviors involving objects not specifically provided by humans (although human provisioning may have provided the monkeys with sufficient time and energy to pursue an apparently nonproductive activity). Beyond this, the specific mechanism responsible for the spread of stone handling is still unclear, but the example suggests that tangible rewards are not always necessary.

When authors speculate on specific social learning mechanisms, if any, that may be involved in the spreading of techniques among free-ranging macaques, most cite a form of stimulus enhancement, at least partly because definitive evidence is lacking that macaques are able to learn by emulation or imitation (Whiten & Ham, 1992; Tomasello & Call, 1997; D. Custance, personal communication). An exception is Tanaka (1998) who described lice-egg removal techniques as consisting of hierarchically organized subroutines. He speculated that the monkeys learned the specific structure of subroutines through observation, and did not merely have their attention drawn to relations between hand and hair through stimulus enhancement. Thus Tanaka suggests a form of imitation learning. Clearly the questions of emulation and imitation in macaques need further work, especially in view of recent findings of emulation and/or imitation in tufted capuchin monkeys (Custance *et al.*, 1999), and other animals

(e.g., Galef, 1998). Finally, Matsuzawa and collaborators (2001) and de Waal (2001), citing examples of social transmission with no tangible reward, propose socioemotional (as opposed to cognitive) mechanisms based on social bonding, identification and a desire to act like the model to explain nut cracking in chimpanzees and stone handling in Japanese macaques.

Experimental evidence for social transmission

Although observational studies, particularly those in free-ranging populations, have been useful in describing spreading patterns in naturally-organized groups, experimental studies on captive groups are potentially better able to confirm the role of social influences in behavioral continuity and to address questions of mechanism. The number and rigor of such experimental studies has blossomed in recent years (e.g., Frigaszy & Perry, 2003), although only a few studies have focused on macaques. Below we describe some of them.

Quantitative similarity

In an experiment dealing with the transmission of behavioral style, de Waal and Johanowicz (1993) asked whether juvenile rhesus macaques might increase their rates of reconciliation as a result of co-housing with juvenile stumptailed macaques. Stumptailed macaques normally display substantially higher reconciliation rates than rhesus. After 5 months of co-housing, the rhesus macaques were returned to their original groups consisting of only conspecifics. After co-housing, the rhesus juveniles showed marked increases in their reconciliation rates compared with both their rates before co-housing and rates of a control group of rhesus juveniles. Since the groups were observed for only 6 weeks after the period of co-housing, it is unclear how long increased reconciliation rates would have been maintained. Hence we cannot be sure whether this apparent example of horizontal social transmission had the potential to be carried on over generations. Interestingly, the rhesus and stumptailed macaques used different specific behaviors during reconciliation, suggesting that propensities to reconcile may have transmitted, but not specific behaviors used to reconcile.

Qualitative similarity

Studies of fear responses to snakes have demonstrated the potential for social transmission through observational conditioning. When confronted with

various kinds of snakes (real, toy or model), naïve laboratory-reared rhesus macaques typically show no strong emotional reactions and do not appear to either avoid or prefer them to neutral objects. In contrast, wild-reared individuals display an almost complete avoidance of snakes (Mineka *et al.*, 1984). To investigate the basis of this difference, these authors compared the responses of naïve laboratory-reared offspring rhesus macaques before and after the youngsters observed older wild-born monkeys confront a snake. After a single trial, the subjects themselves reacted with intense fear to snakes. In nature, models are likely to be parents or other older group members, and in this sense, the observational conditioning of snake fear appears to represent a *sensu stricto* case of intergenerational transmission of behavior. In reality, genetically influenced factors also play a role in that observational conditioning of fear specifically for snakes appears to be more easily achieved than for other objects. To show this, Cook and Mineka (1990) used videotape to compare the responses of naïve laboratory-reared monkeys to images of monkeys behaving fearfully to snakes and without fear to flowers, and vice versa. Interestingly, the naïve offspring, afraid of neither snakes nor flowers before the tests, acquired a fear of snakes, but not of flowers, suggesting that they were inherently prepared to respond with fear to such experiences with snakes but not with flowers. The extent to which observational conditioning in macaques occurs for other risky objects, individuals or situations is unknown. Nor is it clear whether macaques actively look for the emotional responses of mothers or others upon encountering novel objects, individuals or situations, as do human infants (Feinman, 1982).

Examining social transmission of feeding techniques in Tonkean macaques, Drapier and Thierry (2002) provided five mothers with four kinds of fruit they had never encountered. The technical variants used by each mother were recorded as their offspring were allowed to observe only their own mother's consumption of the fruits. In subsequent trials, isolated offspring were provided with the same fruit types, but they used different techniques to process them than did their mothers. In a second experiment, the authors recorded different variants used during the consumption of familiar fruits in the two maternal lineages of the group (Drapier & Thierry, 2002). They found some significant differences in variant usage between the two maternal lineages. The technical variants appeared arbitrary in that no variant was more efficient than another. The authors suggested that the differences between the two sets of results may have been due to differences in the number of opportunities the youngsters had to observe the techniques used by others. The probability of social transmission may also have been affected by the constraints of the experimental design. In this case, the youngsters had very limited opportunities to interact freely with both the demonstrators and the new foods. Social transmission of feeding

techniques may not necessarily involve one-trial learning like the observational conditioning of snake fear. Rather it may require several exposures and opportunities for refinement via trial and error to be integrated in the individual repertoire.

In an attempt to throw light on the mechanisms that may have led to the propagation of food-washing techniques at Koshima, Visalberghi and Frigaszy (1990) documented the acquisition of a similar technique in captive longtailed macaques. They gave four naïve hand-reared juveniles access to a water-filled basin with toys floating on the surface. After four hours of habituation to the apparatus, they provided the monkeys with sandy fruits, a novelty for them. Three of the four subjects acquired a food-washing technique within three 30-min sessions. The fourth subject was frequently threatened when attempting to gain access to the basin, but nonetheless played with the food in the water and retrieved food from the water as early as the first session. The authors concluded the three individuals learned to wash fruit through independent learning mechanisms, but that response facilitation might have aided their acquisition of the new behaviors.

Conclusion

While each example we have reviewed offers some evidence for the influence of social learning on behavioral continuity across generations, in all cases the evidence is incomplete. In many cases, we are able to describe patterns of propagation in the field (e.g., sweet-potato washing), but we have little or no understanding of specific learning mechanisms that may be involved. In others, we have identified a specific learning mechanism (e.g., observational conditioning of snake fear), but lack a clear idea about the range of objects or situations to which it may apply in a natural situation. And in most examples we have only a fragmentary appreciation of the various social and environmental factors that affect the fidelity and duration of transmission and the likely ultimate effects of transmission on the evolution of the species. Clearly much more research needs to be done, particularly with ontogenetic and experimental approaches.

In recent years, theoretical modelers have explored the possibility of complex evolutionary interaction between socially and genetically transmitted information in the form of dual-inheritance models (e.g., Boyd & Richerson, 1985; Laland *et al.*, 1996). In general these models have suggested that a mixture of intergenerational social transmission and individual learning is likely to have advantages over both purely genetic modes of transmission and purely individual learning under a wide range of ecological circumstances, especially when environmental change occurs at intermediate rates relative to the frequency of

transmission. As such, we might expect the widespread occurrence of intergenerational transmission among macaques.

In our examples of maternal transmission of social style, however, there is little evidence that transmission per se has been specifically selected. Rather they appear to be outcomes of selection for other behavioral propensities and motivations (e.g., to strive for high rank, to protect infants from harassment and injury, to tolerate close associates) within particular social and demographic contexts. In this sense, the maternal transmission of social behavior may be considered the end product of the interaction of a number of flexible behavioral propensities channeled through the constraints and opportunities presented by a particular social organization.

Nevertheless, where transmission has reproductive consequences for individuals, a potential for natural selection to enhance or moderate intergenerational transmission is present, producing genetically biased social transmission systems (e.g., Richerson & Boyd, 1989). The specificity and efficiency with which naïve monkeys learn to fear snakes through observational conditioning suggests that such a process may have occurred at least once. However, so far no such mechanisms have been linked to other examples of intergenerational transmission in macaques.

Finally, one aspect of transmission that has received increased attention recently is niche construction – i.e., the potential for the introduction and transmission of technical variants to open up new adaptive niches for exploration and exploitation (Avital & Jablonka, 2000; Laland *et al.*, 2000; Perry, 2003). For example, Hirata and collaborators (2001) suggest that the introduction of provisioned foods near and in the water led not only to sweet-potato washing and wheat washing, but also ultimately to the exploitation of new food sources (e.g., fish) and new ways to play and escape the heat (e.g., sea bathing, swimming, and diving). However, at present, the extent to which socially transmitted behavior in nonhuman primates leads to niche construction independently of human encouragement, and the extent to which it creates new selective pressures for the next generation is still unknown (Thierry, 1994b; Russon, 2003).

Box 10 Maternal behavior, infant handling, and socialization

Dario Maestriperi

Macaque females typically produce a single offspring after a period of gestation of about 5.5 months and care for their infant with little or no help from other individuals. Feeding, transport and protection represent the main

forms of maternal care prior to weaning, which usually occurs within one year. Mothers continue to provide grooming and agonistic support to their offspring throughout their lives, or in the case of males, until they emigrate from the group. Adult males typically avoid young infants but often affiliate with male juveniles and adolescents. In Barbary macaques and to a lesser extent in some closely related species (e.g., stumptailed, Assamese, bonnet, toque and Tibetan macaques), adult males hold and carry unrelated young infants as a buffer against aggression from other males (see Fig. 15.1) (Maestriperieri, 1998). The taxonomic distribution of agonistic buffering with infants suggests that this behavioral phenomenon emerged quite early in the evolutionary history of the tribe Papionini and subsequently disappeared in some of most recently evolved macaque species (Maestriperieri, 1998).

Sex differences in interest in infants emerge early on and persist throughout the lifetime, with females being far more involved in infant handling than males (e.g., *M. arctoides*: Bruce *et al.*, 1988; *M. fuscata*: Glick *et al.*, 1986a,b; *M. mulatta*: Lindburg, 1971; *M. nemestrina*: Wheeler, 1986; *M. radiata*: Silk, 1999; *M. silenus*: Kumar & Kurup, 1981; *M. sinica*: Baker-Dittus, 1985; *M. sylvanus*: Small, 1990b). Most female interactions with other females' infants are brief and do not carry any obvious benefits to infants or their mothers (Maestriperieri, 1994c). Infant handling by female juveniles may be a way to acquire mothering skills that will subsequently improve offspring survival (Lancaster, 1971). Infant handling by older and experienced females, however, requires a different explanation. One possibility is that infant handling is a by-product of female responsiveness to infant stimuli (Paul & Kuester, 1996b; Silk, 1999). Another possibility is that infant handling reflects a form of reproductive competition among females (Silk, 1980; Maestriperieri, 1994c).

Different explanations for infant handling need not be mutually exclusive and may apply to different types of interactions or age classes of individuals. For example, the reproductive competition hypothesis may only apply to a subset of infant handling interactions in which reproductively experienced females harass or kidnap other females' infants (Maestriperieri, 1999).

The quality of female infant handling in macaques tends to covary across species in relation to maternal protectiveness or permissiveness as well as to the quality of adult female relationships (Maestriperieri, 1994c; Thierry, 2000, Chapter 12). Infant harassment and kidnapping have been best documented in rhesus macaques and, in this species, mothers are generally described as very protective and intolerant (e.g., Hinde & Spencer-Booth, 1967). Rhesus macaques are also often described as the most despotic and nepotistic macaque species, in that their social interactions are strongly affected by dominance rank and kin support (de Waal, 1989b). Japanese and longtailed



Fig. 10.3. In Tonkean macaques, high levels of maternal tolerance allow juvenile females to handle infants and carry them for extended periods of time (Strasbourg Primate Center, France). (Photograph by B. Thierry.)

macaques are closely related to rhesus macaques and share with them some similarities in adult social relationships, the quality of infant handling, and the degree of maternal protectiveness (Hiraiwa, 1981; Eaton *et al.*, 1985; Thierry, 1985b).

Rhesus macaques are similar to pigtailed macaques in terms of the risks associated with infant handling and these two species also exhibit similarities in maternal protectiveness and intolerance (Rowell *et al.*, 1964; Wheeler, 1986; Maestriperi, 1994a,b). Pigtailed macaques, in turn, appear to resemble a closely related species, the liontailed macaque, for patterns of infant handling and maternal protectiveness (e.g., Kumar & Kurup, 1981), although direct comparisons between these two species have not been made. The Sulawesi macaques (e.g., *M. nigra* and *M. tonkeana*), which are also closely related to pigtailed and liontailed macaques, exhibit relatively benign infant handling and high maternal tolerance (Fig. 10.3) (Thierry, 1985b). Their adult female relationships also tend to be affiliative and egalitarian (Thierry *et al.*, 1994). Bonnet, stumptailed and Barbary macaques are another cluster of closely related species in which infant handling is mostly benign, mothers are permissive, and female social relationships are generally affiliative and egalitarian (Rosenblum & Kaufman, 1967; Blurton-Jones & Trollope, 1968;

Caine & Mitchell, 1980; Small, 1990b; Maestripieri, 1994a,b; but see Paul, 1999 for Barbary macaques, and Simonds, 1965, and Silk, 1980, for bonnet macaques).

Taken together, these observations suggest that the evolution of infant handling and maternal styles in macaques can be viewed, in part, as an adaptation to evolutionary changes in adult social relationships and social organization, and in part as the result of phylogenetic inertia (e.g., Thierry *et al.*, 2000). Although differences among species are often striking, there is also a great deal of variation between groups and populations of the same species. The relation between social environment, quality of infant handling, and mothering style, however, seems to hold also at the intraspecific level. For example, rhesus macaques living under conditions of high social density exhibit higher risk of infant kidnapping and harassment and higher maternal protectiveness than rhesus macaques living in less crowded environments (Maestripieri, 2001).

Both infant handling and parenting styles are likely to have multiple determinants and be subject to multiple selective pressures and constraints. Variation in other dimensions of parenting style such as frequency and timing of maternal rejection seems to be better accounted for by ecological and reproductive factors than by social factors. For example, in seasonally breeding species, maternal rejections begin earlier and are more frequent than in non-seasonal species (e.g., Worlein *et al.*, 1988; Maestripieri, 1994a). This is because among seasonal breeders mothers are under pressure to wean their infants early to be able to conceive again during the mating season (Simpson *et al.*, 1981). Differences in maternal rejection also occur between seasonal breeders such as rhesus and Japanese macaques, in part as a result of differences in climate (and hence infant thermoregulatory needs) or in seasonal availability of food (Hiraiwa, 1981).

Intra- and interspecific differences in interactions between infants and other individuals, including their mothers, are likely to have important consequences for social development. Unfortunately, aside from the information provided by social deprivation studies, little is known about the influence of early social experiences on behavioral development in macaques. Macaque infants typically spend their first years of life in close interaction with their mothers, other matrilineal kin, and peers. Sex differences in grooming, play, and in the extent to which infant behavior is biased toward kin, infants, or adult males emerge predictably during development and across different environments (e.g., Eaton *et al.*, 1985; Glick *et al.*, 1986a,b). Such early sex differences are a prelude to the different life histories of males and females, with males preparing for emigration from the natal group and females preparing for integration into their matrilineal social network. It is likely that the

developmental trajectories taken by macaque infants are, in part, genetically determined and, in part, the result of social and learning processes. Although macaque mothers initially play an active role in encouraging infant independence (Maestriperi, 1995, 1996a), infants are not actively encouraged or instructed by adults to acquire skills that will prepare them for their adult social roles. Instead, the development of macaque behavior is probably shaped by individual learning processes that occur in the context of interactions between the infants, their mothers and peers, and other group members (e.g., Berman & Kapsalis, 1999; Chauvin & Berman, this Chapter). Comparative studies of macaque social development are rare (e.g., Thierry, 1985b) and the evolutionary relationship between social organization and infant socialization remains poorly understood.