From "The Cultural Nature of Attachment: Contextualizing Relationships and Development,"
Heidi Keller and Kim A. Bard, eds. 2017. Strüngmann Forum Reports, vol. 22,
series ed. J. Lupp. Cambridge, MA: MIT Press. ISBN 978-0-262-03690-0.

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Primate Infancies

Causes and Consequences of Varying Care

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Abstract

Bowlby recognized that studying other primates could help identify the needs of human infants; his evolutionary perspective has had a wide impact on understanding of human development. Much more is now known about evolutionary processes and variation, within and between species. This chapter reviews aspects of evolutionary theory and primatology relevant to Bowlby's theory of attachment. Beginning with primate phylogeny, ecological and social forces that contribute to the varieties of primate sociality are considered and some reasons canvassed that explain why primatologists do not all agree on the choice of words to describe the relationships between animals, including use of the term "attachment." To appreciate primate variation, interactions between infants, mothers, and others are characterized in a range of species. Variations and commonalities are identified and used to explore how development in human infants can be understood in terms of social relationships and maturational state at birth and weaning compared to other primates. Infant experience has long-term effects in primates other than humans. Some of that evidence is summarized and special attention is given to interactions between particular chimpanzee mothers and infants in an unusual setting, where trusting relationships between mothers and human researchers reveal variations in mothering style that appear to result from early life events, recent experience, and social context.

Group photos (top left to bottom right) James Chisholm, Katja Liebal, Kristen Hawkes, Lynn Fairbanks, Johannes Johow, Masako Myowa, Barbara Finlay, Elfriede Kalcher-Sommersguter, Bernard Thierry, James Chisholm, Lynn Fairbanks, Kristen Hawkes, Johannes Johow, Volker Sommer, Katja Liebal, Bernard Thierry, Barbara Finlay, Masako Myowa, Kristen Hawkes and Katja Liebal, Elfriede Kalcher-Sommersguter, Volker Sommer

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An Evolutionary Perspective

Since the theory of natural selection is about "descent with modification," phylogeny (descent) and fitness-related effects (modification) are both paramount. The language of evolutionary biology draws attention to theory missing in descriptions of human attachment, bonding, and welfare, as natural selection does not maximize kindness, happiness, health, or serenity—only inclusive fitness. More of one thing usually means less of something else. Allocation problems are everywhere for all living things. Interactions among individuals are complicated by pervasive conflicts of interest, situated in varying ecologies. For our topic here, the necessary conflicts of interest that pervade the most intimate relationships (i.e., between mothers and fathers, among closest kin, even between mothers and their developing fetuses) constitute the central features of biological theory about the evolution of physiology, morphology, and behavior. Evolutionary expectations about tradeoffs and conflicts of interest distinguish our perspectives from those of attachment specialists, who are concerned primarily with the well-being of mother and child, a difference we will not resolve but underline.

Because there is no starting over in evolution, phylogeny is crucial. Selection can only drive adjustments in the capacities and tendencies of individuals from features already there. Over time, that process has produced the astonishing variation in living things, from the diversity in primates to all of the organisms in our microbiome. For questions about our own species it matters that we are hominids (i.e., our closest living evolutionary cousins are the great apes), that hominids are primates, that primates are mammals, and that mammals are vertebrates. We share most of our physiology with them by descent from our recent common ancestors.

Our charge is to examine the diversity in primate infant-caregiver interactions, but the value of a wider taxonomic perspective should not be ignored. The dazzling variation in vertebrate social systems and parental behavior shows how features of socioecology alter selection. In fact, the diversity that we will describe in primates alone underlines how little close phylogenetic relatedness constrains key features of social organization and parental roles. Conversely, across vertebrates, an impressive degree of conservation of fundamental brain structure (Yopak et al. 2010), neurotransmitter, neuromodulator and hormonal systems (Hofmann et al. 2014), and basic physiological mechanisms (Gerhart and Kirschner 1997) often produces a startling similarity in the mechanistic solutions that adapt brains and behaviors to similar socioecological contexts, even when housed in bodies as diverse as a 30 g house sparrow compared to a 1000 kg bison.

Parental care has evolved independently, hundreds of times in nonmammalian vertebrates as well as in birds and mammals. The nature of care—from single parent to biparental to multiple alloparental systems—shows predictable transitions when viewed from both phylogenetic and ecological perspectives

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(Reynolds et al. 2002). This range of parental protection and provisioning illuminates the central requirements. Parental care is nested within a wide variety of social structures (from solitary, to familial, to flocks of millions) as well as within territorial preferences (from territory-independent, to transitorily defined, to multigenerational defense of a huge resource). Only in looking widely at taxonomic interactions of the variations of parental care, social structure, and territoriality can the dependence and independence of the mechanisms of affiliation and care be understood (Goodson et al. 2005). In mammals, the size of the brain, developmental duration, and the possibility of extended parental care covary to a remarkably high degree (Charvet and Finlay 2012). As large brains per se are associated with particular behavioral capacities (MacLean et al. 2014; Stevens 2014), the similarities we discern when comparing our caregiver-infant interactions with those of other large-brained mammals (e.g., dolphins and elephants) may be much more than anthropomorphic projections. When investigating mechanisms of attachment, the insight gained from examining the differences in the neural circuitry associated with the neuropeptide oxytocin in monogamous prairie voles (*Microtus orchrogaster*) versus promiscuous montane voles (*M. montanu*) (Young et al. 2001) not only overshadowed previous work in primates but initiated an explosion of research in new psychiatric treatments for human developmental and social disorders (Young 2002). A full review of diversity and conservation in social structures and their mechanisms across taxa is far beyond the scope of this report. These few examples should, however, demonstrate the benefits of a wide taxonomic perspective from which we return to our primate focus.

Primates and Primatology

Primates are specialized to be unspecialized; that is, monkeys and apes have the capacity to act in different ways depending on circumstances. Laypersons have historically believed that there is such a thing as a "monkey mother" (or "the chimpanzee," "the gorilla," "the macaque") who behaves in stereotypical, universal ways. Nothing could be further from the truth, because behavioral plasticity is the very hallmark of primates, including our own species (Strier 1994). Understanding the state of affairs is even more difficult, since scientists studying primates will often disagree about "the facts." Like any scientific discipline, primatology, apart from being loosely grounded in evolutionary theory, does not embody a unified method or philosophical approach, generating conflict by its very scientific nature.

In what follows, we introduce a basic portfolio of terms and models, including snags, caveats, and some of the disagreements within primatology. (General introductions and overviews to primate biology, ecology, sexuality, sociality, and cognition that track the discipline's development can be found in Altmann 1980; Smuts et al. 1987; Dunbar 1988; Martin 1990; Hrdy 1999;

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Laland and Brown 2011; Campbell et al. 2012; Dixson 2012; Mitani et al. 2012; Strier 2016.) This brief review prepares readers for the concrete examples of primate-infant socialization presented herein. This multiauthored paper includes observations by primatologists from various schools of thought. Thus, while all examples are informed by firsthand research expertise, information about "mother-infant attachment" in primates is colored by the context in which a primatologist learned the ropes. Some will say that "attachment" as a universal, unique, and unchangeable bond is pure fiction, while others find the term useful. We have not homogenized the language that different academics employ as contributors to this chapter. As semantics indicate implicit methodological assumptions (see section on "Intellectual Fault Lines in Primatology"), the attentive reader may take that as a challenge to identify schools of thought that underlie descriptions and assertions.

Primate Taxonomy

Humans, along with several hundred other species, belong to the mammalian order of primates (Boyd and Silk 2015). This taxonomic unit was originally classified *phenetically* (based on appearance; see Figure 4.1, left panels) or more currently *cladistically* (based on ancestry, principally genomic analyses; Figure 4.1 right panels). The phenetic classification divides the group into prosimians and anthropoids (or simians), with the position of the tarsiers constituting the major difference to the cladistic approach. Most primatologists prefer the latter, as it reflects the currently accepted phylogenetic tree, although the term prosimian is still widely used.

The cladistic approach also identifies two major branches of the primate tree. The first is strepsirrhines, the "wet-nosed" primates. These are mostly nocturnal and benefit from a good sense of smell enabled by a mucous membrane around the nostrils. They include the prosimian lemurs and lorises, now typically small creatures found in Africa and Asia. All other primates belong to a second branch: the haplorrhines or "dry-nosed" primates, which generally rely more on vision than olfaction. These include the small-bodied and nocturnal tarsiers of Southeast Asia as the remaining prosimians. Almost all other haplorrhines are diurnal, representing the "true" monkeys. These are again divided into two kinds. Species native to South and Central America are called New World monkeys (platyrrhines), encompassing the small callitrichids (marmosets, tamarins) as well as capuchin, howler, and spider monkeys. Species living in Africa and Asia are called Old World monkeys (catarrhines) consisting of two clades, the preferentially folivorous (leaf-eating) colobines (e.g., langurs, colobus, snub-nosed monkeys) and the more omnivorous cercopithecines (e.g., macaques, guenons including vervets, drills, baboons).

The ape radiation (hominoids) is divided into two branches. The *small apes* (hylobatids) are confined to South Asia and comprise the siamang and various gibbons. All hylobatids are specialized fruit eaters that swing through the

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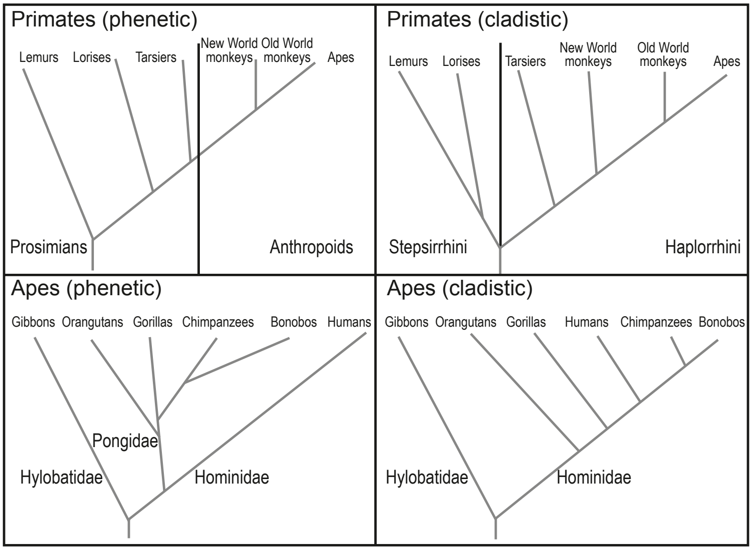

Figure 4.1 Primate taxonomy, with groupings according to appearance (phenetic, left panels) and ancestry (cladistic, right panels). Note that the graph separating the other great apes from humans (lower left panel) implies they are closer to each other, with our lineage at the far right supposedly progressing toward higher forms. This anthropocentrism is mitigated in the cladistic taxonomy (lower right panel) where actual ancestry nests humans among other great apes. Reproduced with permission from Volker Sommer.

canopy using brachiation as their characteristic mode of locomotion. The *great apes* (hominids) include orangutans (genus *Pongo*), the "red apes" of Sumatra and Borneo, as well as the African gorilla (genus *Gorilla*) and the two sister species, chimpanzee and bonobo (genus *Pan*). Humans (genus *Homo*) belong to this clade. We also originated in Africa, but have since populated the globe. Even though members of genus *Pan* and genus *Gorilla* are hairy knuckle-walkers with moderate to good climbing abilities that make them closer to each other than to humans on phenetic grounds (lower left panel), the cladistic approach takes genetic data and the fossil record into account (lower right panel). Those lines of evidence show that genus *Pan* shares a more recent common ancestor with humans than with gorillas, whereas gorillas share a more recent common ancestor with humans than with orangutans. Taxonomically, *Homo* and *Pan*, as well as extinct genera like *Australopithecus* (known only from fossils), are united in a tribus, the *hominini*.

Primate Sociality

Like many other animals, primates need to engage with conspecifics to survive and breed. John Bowlby's understanding of primate sociality was influenced by Robert Hinde (1976). According to this pioneering animal ethologist, individual acts of *behavior* can be distinguished: a behavior directed toward somebody is social, thus constituting an *interaction*; repeated interactions between the same individuals amount to a *relationship*. These technical terms circumvent questions about the actors' internal states (see below), while still allowing reconstruction of social dynamics.

A further set of terms distinguishes basic arrangements of sociality (cf. Sommer and Reichard 2000; Dixson 2012). In numerous species, males and females are more or less solitary and only meet occasionally. The cardinal types of *permanent male-female associations* are:

- one-male/one-female (*monogamy*),
- one-male/multifemale (*polygyny*),
- multimale/multifemale (*polygynandry*), and
- multimale/one-female (*polyandry*).

The neutral term "association" is consciously chosen because it may refer to patterns of grouping, mating, or breeding, and these different dimensions of social organization are not necessarily congruent (Kappeler and van Schaik 2002).

Thus, we can ask how individuals group ("Who resides with whom?"), mate ("Who has sex with whom?"), and reproduce ("Who generates offspring with whom?"). For example, female A may live with male A, the father of her first child (grouping monogamously) while engaging in occasional extra pair copulations with neighboring male B who lives with childless female B. The extra pair copulations lead to the conception of female A's second offspring. This means that female A is monogamously grouping but polyandrously mating and breeding; male A is monogamously grouping, mating, and breeding; and male B is monogamously grouping and breeding, but polygynously mating. Within the constraints and opportunities of these associations, females engaging in sexual encounters may be fertile (i.e., periovulatory) or infertile (i.e., in nonovulatory cycle stages, pregnant, in lactational amenorrhea, postmenopause). Although species tend to express typical grouping, mating, or breeding patterns, a great deal of intraspecific variability has been observed. For example, populations of gorillas or langur monkeys may live in polygyny or polygynandry, while hylobatids or callitrichids may live in monogamy, polyandry or polygyny. Moreover, in some species such as geladas, hamadryas, or Guinea baboons, and humans, social systems are modular or multilevel, with smaller monogamous, polygynous, or polygynandrous units clearly distinct within larger communities that travel, forage or sleep in proximity.

Another way to look at primate societies is in terms of natal *dispersal*; that is, to record who remains in their birth unit (philopatry) and who leaves to join another group. In many species, one sex may be philopatric whereas the other sex will emigrate. If females stay, *matrilineal* groups result (typical for, e.g., macaques, olive baboons, and at least some orangutan populations). With relationships among close female kin, such groups have been called *female bonded*, although some primatologists stick to the more neutral term

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female philopatry. *Patrilineal* groups result if males remain in the area where they were born. This is typical of chimpanzees and long thought typical of human hunter-gatherers, but careful appraisal has now falsified that assumption. Instead, among hunter-gatherers, either or both sexes may stay or leave, local group composition changes frequently, and bi- or multilocality is most common (Alvarez 2004; Marlowe 2004; Hill et al. 2011). Gorillas of both sexes disperse, with males going further in at least some populations (Roy et al. 2014). Both males and females also emigrate in some hylobatids and callitrichids as well as in many mercantile and industrial human societies.

Thus, the order of primates is characterized by a wide array of social features that differ not only between but also within species. With this considerable *interspecific* and *intraspecific* variability in which individuals are physically together, the frequency and modality of infant interactions with other group members, including its mother, must depend on numerous factors. These include social systems, kin relations, probability of paternity, parity of mothers, number and age of co-residing siblings, and dispersal pattern. We should not expect, therefore, to find a single pattern of "mother-infant attachment" (cf. Keller and Chaudhary, this volume).

Primate Socioecology

The sketch of primate sociality above was purely descriptive and did not address *why* these animals interact in particular ways and not in others. However, potential selection pressures were identified that may cause or at least influence different modes of gregariousness. The problem is complicated by the fact that while natural selection is expected to design the anatomical and psychological features of living things as adaptations to local environments, conditions change. This leaves organisms with phylogenetic legacies that do not indicate current selection pressures, but selection in the past (Grafen 1988; Chapman and Rothman 2006; Clutton-Brock and Janson 2012), producing misleading correlations, or lack thereof, that must be laboriously teased apart.

Multiple environmental pressures might affect social behavior. To illustrate, we present several examples and then describe one well-studied factor, food distribution, at greater length. One pressure that affects social behavior is *infectious disease* (Nunn and Altizer 2006). High frequency of infectious disease may favor smaller group sizes or, in the case of sexually transmitted diseases, may bias mating effort away from promiscuity and toward monogamy. In another scenario, increased *predation pressure* (Miller 2002) may select for groups where multiple males protect vulnerable females and offspring. Alternatively, females may benefit from mating with multiple males to distribute the possibility of paternity and reduce the risk of male-committed *infanticide* which may likewise create multimale/multifemale groups (van Schaik and Janson 2000). In yet another framework, trade-offs between cooperation and competition are proposed to select for *social intelligence* (Dunbar 1992),

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a cognitive capacity presumed to enable greater numbers of conspecifics to reside together.

Efforts to link the quality, quantity, and distribution of food to sociality have taken particular prominence (Wrangham 1980; van Schaik 1989). The starting point for this socioecological model is the different investment of the sexes in reproduction, beginning from the level of ova and sperm (Fisher 1930; Trivers 1972; Queller 1997; Kokko and Jennions 2003; Lehtonen et al. 2016). Moreover, the internal fertilization, gestation, and lactation of mammals further specializes primate sexes in reproduction. Whereas female reproductive success is limited by food and safety, reproductive success for males is limited by access to fertile females. These dynamics are encapsulated by the epigram that females go where the food is, while males go where the females are or, more technically, that males map themselves onto the distribution of females.

Other things equal, a female might avoid competition for food by living alone. Hence, the fact that females nevertheless are found in groups needs explanation. As in many other animals, females may reduce the risk of predation by staying together. Two other main reasons related to food distribution likely influence grouping. On one hand, costs of gregariousness can be low when females subsist on spatially dispersed, low-quality foodstuffs, such as grass or leaves, that no single individual can monopolize. On the other hand, when females depend on spatially clumped, high-quality food such as ripe fruit, competition with other group members may be high. Females in larger groups, however, may have greater success defending food patches against competing groups.

These conditions influence female social relationships via different competitive regimes. In this model, low-quality, dispersed food is correlated with mild *scramble competition*. Severe aggression is rare and dominance hierarchies are all but absent so the society is more or less egalitarian. By contrast, high-quality clumped food is correlated with *contest competition* where defending food gives winners greater shares. This behavior leads to steep and despotic dominance hierarchies. However, that steepness can be lessened if competition between groups results in benefits to higher ranked members while allowing subordinates enough access to resources to make staying in the group worthwhile.

The spatial distribution of females, whether they are dispersed or clumped, influences whether males are able to defend multiple females, as does the temporal distribution of female fertile periods. Hence, if fertile periods are synchronized, a single male, however strong, cannot monopolize the whole batch, because while copulating with one female, he cannot prevent competitors from mating with a second or third. Synchrony is expected in pronounced seasonal environments where pregnancy, lactation, and/or weaning are unlikely to be successful during certain months when food availability is insufficient. If groups are very large, even without seasonal breeding, multiple females will be

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fertile on any given day. As a result, multimale groups develop. Conversely, if female fertility is not synchronized and groups are not too large, single males may succeed in defending them.

Thus, we can relate the principal patterns of male-female associations described above to selective forces that are brought about by the spatiotemporal distribution of food and its consequences for the distribution of females:

- If females live solitarily, males cannot monopolize more than one of them (*monogamy*). A textbook example is found in gibbons.
- If females form groups, but their fertile periods are synchronized, multimale/multifemale societies will develop (*polygynandry*). Some macaque species provide a textbook example.
- If females form small groups, but their fertile periods are not synchronized, one-male/multifemale groups or "harems" can form (*polygyny*). Langurs are a textbook example.
- If females give birth to more than one infant at a time, multiple males may need to assist the female in carrying, grooming, and protecting the offspring to reduce mortality, thus resulting in one-female/multimale societies (*polyandry*). Tamarin species provide a textbook example.

Of course, real-life situations are far more complex, and this intentionally limited set of factors does not capture all possible variations. Notable exceptions and intraspecific variations exist, as we will describe. The socioecological model has its critics (e.g., Thierry 2008). Nevertheless, the model has produced valuable predictions about the willingness of females to let other females engage with their infants (Hrdy 1976; McKenna 1979). In fact, we can distinguish between permissive mothers who may spend considerable time away from their infant while it is carried around by troop mates, and restrictive mothers who will fiercely resist attempts by others to take hold of her youngster. As a rule, infant sharing characterizes societies with scramble competition (e.g., langurs). Here, a mother can easily retrieve her infant as the dominance hierarchy is more relaxed. Moreover, infants will not grow up to be future food competitors, and thus troop mates have little reason to be aggressive toward them. The situation is different under contest competition (e.g., some macaques, some baboons). Here a low-ranking mother, in particular, would be unable to retrieve her offspring if a high-ranking troop mate resisted her efforts. Numerous cases of infant "kidnapping" with subsequent "aunting to death" have been observed. Thus, in species with contest competitions, infant sharing is typically restricted to close kin (older sisters, grandmothers), who have an overlapping genetic interest with the mother and her newborn. Examples from nonhuman primates, like those from different cultural settings among humans, thus warrant "a radical change from a dyadic perspective to a network approach" (Keller and Chaudhary, this volume).

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Intellectual Fault Lines in Primatology

Primatology is conducted by human primates who have been educated as scholars and academics within an attachment network of mothers and others situated in a cultural context. As primatologists, therefore, we have our perspectives and senses of belonging. We identify with certain modes of "we"-ness and "other"-ness. In other words, we are not blank slates (Chisholm, this volume). Some of the more subtle factors that shape our research approaches follow. Being primates, we are, in fact, subject to intraspecific variation ourselves. Whether a primatologist prefers or detests certain phrases often reflects their school or academic circle.

Let us begin with what initially seems to be a semantic point regarding the relationships in which infants engage with others. Some primatologists will happily employ the term "infant caregiving." Others point out that such words render the infants as passive recipients whereas the infants might well manipulate others through signals of distress or "cuteness" into attending to them (Hrdy 1999). Similarly the term "allomothering" indicates that individuals other than mothers engage with the youngest group members (Hrdy 1977). This includes other females as well as juvenile or adult males who may show affiliative interest in babies or be rough or abusive. The relatively neutral expression "infant handling" can apply to mothers, fathers, siblings, aunts, uncles, nonrelatives or peers alike, whether they tend to the baby in a friendly mode or mistreat it.

Most primatologists agree that comparing wild populations with captive animals adds useful information to our understanding of the mechanisms and functions of primate sociality (Setchell and Curtis 2003). It is difficult to control the multitude of factors that influence behavior observed in the field, such as seasonality and food availability or pressures related to disease, predation, or intergroup competition. In the wild it is also more difficult (but not impossible) to obtain biological samples (urine, feces, blood, saliva, hairs) that can be analyzed to determine endocrine state, nutrition, pathogenesis, or genetics. Finally, it has been notoriously difficult (again not impossible) to conduct experiments in the wild that explore, for example, behavioral or cognitive suites. Without studies in captivity, we would not know that some orangutans can dive, that a nonhuman ape can operate a joystick to play the "Pac-Man" computer game, or that bonobos and gorillas readily use tools, because in their natural habitats, they have practically never been seen to do this. Thus, captive studies help us to understand a species' breadth of potential behavioral responses.

The community of primatologists also tends to be split between those who emphasize traits of human uniqueness (nicknamed "exceptionalists") and those who stress the evolutionary continuum ("gradualists") (cf. McGrew 2004; Finlay and Workman 2013). We might simply distinguish between those who are more interested in differences between humans and other primates

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and those who are more interested in similarities. Current research focus is on cognitive abilities (e.g., shared intentionality, mental time travel, language; Tomasello and Herrmann 2010; Hawkes 2014), which may or may not be specific to humans. Some primatologists identify the major cognitive rift not between humans and (other) animals, but rather between great apes and other primates (Russon et al. 1996). These opposing views generate lively debates, often to the puzzlement of a lay audience that expects clear answers, for example, as to whether chimpanzees have language abilities or not (Hurley and Nudds 2006).

The wider arena of cognition (Tomasello and Call 1997) brings us to the contentious topic of *internal* states, which has immediate relevance to the study of attachment (Bekoff 2007; Cheney and Seyfarth 2007; Stamp-Dawkins 2012). This time-honored conundrum is dominated by grand and often poorly defined vocabulary. Thus, we may ask if nonhuman animals possess "emotions," "feelings," "empathy," or "consciousness" (de Waal 2016), or if, in relation to our core question, they experience an inner "bond" of "attachment." Traditional Cartesian dualism denied that animals, which were seen as machines, can experience qualia (i.e., have an experience of internal states and sensations). One would be hard pressed to find current animal behaviorists who ascribe to this historical orthodoxy. Still, many students of behavior will avoid terms that imply private feelings, not because they deny that other animals can have emotions or feelings. On the contrary, modern-day ethologists and comparative psychologists tend to be at least moderate gradualists. Thus, they think it unlikely that internal experience emerged only in the more immediate ancestors of our own lineage (e.g., Panksepp 1998; Toda and Platt 2015): they prefer descriptive and less interpretative terms (e.g., "relationship" instead of "attachment"). Still this does not prevent others from reinterpreting their data in a language that implies internal states, only that the onus of justification would be on those who add such colorful layers to their portrayal of primates. In sum, gradualists recognize that we are not only justified, but obliged to employ a certain dose of *anthropomorphism* when looking at other animals (Daston and Mitman 2006; de Waal 2016). This is in line with Darwin's original idea that as with anatomy, likewise our psyche differs from that of other animals only in degree, not in kind (Darwin 1872/1965). A gradualist will therefore assume that mental experiences are more similar between humans and other hominids than between humans and small apes, and that the latter have more similarities than those between humans and monkeys. But similarity is not only a question of phylogeny. The socioecological model predicts that similar ecological pressures generate similar social responses; parallel evolution may likewise happen with corresponding neurological solutions. Thus, highly social nonprimate mammals, such as elephants and whales, and even nonprimates, such as birds (corvids perhaps, or parrots), may be most usefully viewed from an anthropomorphic perspective.

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Nevertheless many continue to avoid using emotive terms for heuristic reasons. We can simply not know if a macaque is enraged or anxious, if a chimpanzee feels guilty or ashamed, or if an orangutan mother that cradles her newborn feels happiness or love. To be precise, we are notoriously poor at introspection ourselves and cannot know for sure about the private feelings of fellow human beings. We just take their word for it as a convincing approximation. In addition, social anthropologists maintain that emotion-describing words are, even with respect to the human experience, susceptible to particular economic and political situations; that is, they are "socially constructed." The way a Nigerian baby feels when she is breastfed may differ from a Japanese infant.

Others, including hard-core Bowlbyists, might assume that such qualia are independent from the Zeitgeist and are therefore "universals." Still, prime examples of universal features have been disappearing at the same speed in which detailed knowledge about our fellow primates has been accumulating, leading us back to the elephant in the room: "attachment." Some primatologists use the word attachment, as it seems to embody how caregivers and infants engage that is otherwise hard to describe or define, while others prefer to avoid its use.

Whichever perspective one might hold, all agree about a basic flaw in Bowlby's attachment theory: a single species was recruited as the principal witness of the continuum in morphology and psyche to connect humans with other primates. Several decades of research in captivity and the wild have since made clear that one species cannot be seen as representative of another.

Some Primate Variation

The range of variation will be clear, even without a complete review of the primate order. Notably missing in our selection are prosimians, callitrichids, baboons, orangutans, gorillas, and bonobos. Comprehensive coverage is also out of the question because one population of any species might not be representative of another population of the same species, as we have learned that intraspecific variation can be extensive. In reference to humans, we speak of "cultural" variation (Keller and Chaudhary, this volume), and this term is now also commonly used to refer to behavioral diversity among nonhuman animals, in particular primates (McGrew 2004). Bowlby used one nonhuman primate as a stand-in for what happened during the course of human evolution: the rhesus macaque, not very aptly also called "the" monkey. Thus, it is there that we begin.

Rhesus Macaques

The attachment theory developed by Bowlby was directly influenced by the works of Harry Harlow, Robert Hinde, and their collaborators, who studied the effects of maternal separation in infant monkeys (Seay and Harlow 1965;

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series ed. J. Lupp. Cambridge, MA: MIT Press. ISBN 978-0-262-03690-0.

Spencer-Booth and Hinde 1967; Harlow and Suomi 1974). As all of them studied the same nonhuman primate, the rhesus macaque, characteristics of this species, like characteristics of the particular human subjects he studied, affected Bowlby's theoretical framework (see Vicedo as well as Keller and Chaudhary, this volume). We now know that the social system of rhesus macaques does not represent primates in general (Strier 1994) and is not even typical of the numerous species in their genus of Old World monkeys, *Macaca* (Matsumura 1999).

Rhesus macaques are often especially aggressive, with a temperament that drives them to threaten others at the slightest provocation; their strongly hierarchical social relations are marked by the paramount importance of dominance, submission, and kinship (Thierry 2007). Correspondingly, the rhesus macaque mother exerts close control over the social interactions of her infant, which leads to the development of an exclusive relationship between them (Figure 4.2). As a consequence, the experimental separation of mother and infant produces an intense response in the infant that typically follows two steps: (a) a "protest" stage characterized by an increase in locomotion and distress vocalizations and (b) a "despair" stage characterized by social withdrawal, inactivity, and a recognizable depressive posture (Spencer-Booth and Hinde 1967; Harlow and Suomi 1974). These stages mirror the anaclitic response reported for some human children in similar circumstances, which provided the foundation for Bowlby's views (1969).

Figure 4.2 Maternal protectiveness in rhesus macaques. A mother limits the moves of her infant. Photo used with permission from Bernard Thierry.

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Broader Variation in Macaques

Comparative study across the macaque radiation provides insights about the social factors affecting the degree of exclusivity of the mother-infant relationship and the development of infant caregiving. Macaques have a flexible diet that includes a major frugivorous component. This genus is characterized by similarity in basic patterns of association by sex, and great differences in the severity and importance of dominance hierarchies. On one hand, all macaque species live in multimale/multifemale groups with overlapping generations: females form kin-bonded subgroups within their natal group, while males transfer between groups at maturation. On the other hand, they present marked interspecific contrasts in levels of social inequality (Thierry 2004, 2007). Some species, like rhesus and Japanese macaques, display an intolerant social style: severe biting is not rare and conflicts are highly unidirectional, meaning that the target of aggression generally flees or submits, producing steep dominance hierarchies.

Other species, like crested and Tonkean macaques, have more tolerant relationships: weaker group members often protest or counterattack when threatened by higher-ranking individuals, biting is neither frequent nor injurious, and quarrels often end with mutual appeasement between previous opponents; dominance relationships are relaxed. The conditions of socialization covary with these patterns. In macaques with steep dominance hierarchies, most mothers are quite protective. Except for the highest-ranking females, mothers limit their infants' interactions mostly to close relatives. Consequently, the amount of alloparental care remains limited. By contrast, mothers from tolerant species are quite permissive, with mothers allowing most females in the group to handle and carry infants from an early age (Figure 4.3). Of particular importance for Bowlby's characterization of attachment, it has been shown that temporarily removing the mother from the group in tolerant macaque species does *not* induce the depressive state typically reported in rhesus infants because the relationship between mother and infant is less exclusive in tolerant species, and the care provided by other group members buffers maternal absence (Kaufman and Rosenblum 1969; Drago and Thierry 2000).

Several adaptive functions have been proposed to account for the occurrence of alloparental care: assistance to the mother, socialization for the infant, or a learning process for juvenile allomothers (Lancaster 1971; Hrdy 1976; Maestripieri 1994). These hypotheses do not explain why infant handling by individuals other than the mother is limited in some macaque species and frequent in others. Since female attraction to infants is vital in animals with extended periods of growth and development like primates (Quiatt 1979), selection must favor female tendencies to pay considerable attention to their own infant. For them to then show no interest in the offspring of other mothers, one would have to postulate that attachment processes only occur during brief sensitive periods, something incompatible with what we know about primate

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Figure 4.3 Alloparental care in Tonkean macaques. A juvenile female carries an unrelated infant. Photo used with permission from Bernard Thierry.

learning abilities. The covariation found between dominance style, maternal behavior, and patterns of infant caregiving may be best explained by the level of protection needed by infants in a given social environment (McKenna 1979; Thierry 2004). Mothers living in strict hierarchies have to be restrictive to secure their offspring. Females from more tolerant societies behave more confidently, allowing their offspring to move about unrestricted. Alloparental care could be a side effect of the expression of maternal behavior within a given social milieu and still provide advantages for nutrition and reproduction. Allomaternal care may allow the mother to devote more time to food searching (Stanford 1992) or decrease her interbirth interval by reducing the time spent with the infant at her nipple (Fairbanks 1990).

Several attempts have been made to correlate the contrasting social styles of macaques with the main ecological features of their habitats. The socioecological model, in particular, proposes that animals live in groups to reduce predator risk; that group living, in turn, induces feeding competition between individuals and groups, which varies with the character and distribution of resources (van Schaik 1989; Sterck et al. 1997). After decades of testing, however, it appears that this model fails to account for the interspecific variations observed in macaque social systems. We do not know of any ecological factor that can account for contrasts in macaque social styles (Ménard 2004; Thierry 2007; Clutton-Brock and Janson 2012). Instead of varying with the distribution of foods, social styles appear to vary predictably with phylogeny (Thierry 2007). The empirical finding that macaque social systems represent covariant sets of behavioral characteristics that travel together through evolutionary time means

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that no characteristic can be explained separately from others, and this includes the mother-infant bond and caregiving system.

Langurs

In contrast to the apparent lack of correlation between current ecology and dominance hierarchies in macaques, Indian langur monkeys, a species in which allomaternal care is common, fit the socioecological model outlined above (see section on "Primate Sociality"; also Hrdy 1977; McKenna 1979; Sommer 1989, 1996). In langur societies, infants interact from birth with a wide variety of group members. Typically, more than ten different nonmothers carry, groom, protect, and play with them. The only exclusive activity for mothers is nursing and closely embracing their infants through the night. Langur neonates are transferred the moment they are born, with the umbilical cord still attached (Figure 4.4).

Prospective caretakers will often quarrel among themselves as to who gets to hold an infant. As a result, during their first month of life, langurs spend on average one third (sometimes up to half) of their waking hours away from their mothers. All infants interact with multiple individuals, which sometimes includes juvenile males but is typically juvenile females and adult females of various reproductive stages (nulliparous, primiparous, multiparous), regardless of whether the female is pregnant, in menstrual cyclicity, or lactating. Limits to allomaternal investment appear in nursing: even if females are nursing their own offspring, they will not allow other infants to drink while tending to them. "Allo-nursing" is absent.

Unencumbered mothers will preferentially perform activities that are difficult with a baby on board, such as foraging in trees and interacting in friendly or agonistic ways with troop mates through mutual grooming and the occasional

Figure 4.4 Allomothering, where many females care for a newborn infant. On its second day of life, a newborn male infant (its umbilical cord still attached) is the subject of a tug-of-war between two unrelated juvenile females, while its half sister watches the event. Photo used with permission from Volker Sommer.

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squabble. Hence, infant sharing in Indian langurs is functionally quite precisely described as "babysitting" (Figure 4.5).

Socioecological theory links the high frequency of allo-handling to the langur-typical food: leaves, which they can depend on thanks to a ruminant-like sacculated stomach. Due to the abundance and low nutritional quality of leaves, there is little reason to engage in fierce competition over this resource, unlike females of other species that rely on ripe fruit. These basically folivorous females can thus afford to group, which in turn often allows a single strong male to monopolize a batch of females. Consequently, all infants sired by the resident adult male are at least paternal half-siblings, while some of them are also full-sibs. Thus, over generations, a close network of kin relations develops among the permanent female residents, as they remain for life in their natal troops.

Such complex and close kin relations among females are conducive to infant sharing as every individual babysitter, to a certain degree, helps copies of its own genes carried by the infants to be transported into the next generation. Alternatively, instead of invoking kin selection, some researchers have linked babysitting to potential benefits of "learning to mother." It is the nulliparous females that take infants most often and keep them longest

Figure 4.5 Babysitting in Indian langur monkeys. Here, two unrelated juvenile females take care of a three-week-old female infant. Her unencumbered mother uses the opportunity to supplement her diet by plucking flowers from an Acacia tree, something that would be difficult to do if she were carrying the infant herself. Photo used with permission from Volker Sommer.

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(Hrdy 1977, chapter 7). However, experienced mothers, too, will take care of other babies, and juvenile males may (rarely) carry them around despite the fact that as adults, males will never again hold or groom a baby. In any case, the langur example reminds us how ecology and social structure are entwined and how these dynamics will influence the interactive network of infants.

Vervets

Vervets are an African monkey species living in multimale/multifemale matrilineal social groups in woodland and forest fringe habitats. In the wild, vervets have a varied, mostly vegetarian, diet that includes fruit, pods, flowers, bark, and young shoots, supplemented by insects, lizards, eggs, and baby birds. Research on social relationships between vervet mothers, infants, and others was conducted for three decades at the UCLA-VA Vervet Research Colony, a captive facility managed to approximate the natural social conditions for this species in the wild. Research at the colony confirmed the strong interest in infants by allomothers that has been observed for vervets in the wild (Lancaster 1971) and provided the opportunity to collect detailed longitudinal data on the costs and benefits of an extended caregiving system for mothers, infants, and allomothers (Fairbanks 1990).

When a vervet infant was born in the colony, other group members typically came over to touch and inspect the new group member as early as the first day of life. All group members showed interest in young infants, including immature and adult males, but the most avid caretakers were juvenile females. If a juvenile female had an infant sibling, she was its most frequent caretaker; if she did not, she found another infant to hold and carry. There was variability in how comfortable mothers were with all of this attention, with low-ranking mothers being more protective and some high-ranking females allowing their infants to be carried by others up to 40% of the time.

Observations at the Vervet Colony are consistent with fitness benefits of caretaking for both mothers and allomothers. The mothers benefited from the time their infants spent with caretakers as it increased the time between nursing bouts, thus reducing the effects of lactational amenorrhea, increasing fertility, and shortening the next interbirth interval. Benefits were found for juvenile female caretakers when they produced their first infant several years later. First-time mothers who had above-average caretaking experience as juveniles were more likely to produce a surviving infant on their first pregnancy compared to females with less caretaking experience—a correlation that might also follow from differences in capacities and preferences that affect both juvenile caretaking and success as first-time mothers. Infant mortality in the colony was not related to the percentage of time that infants were carried by nonmothers, indicating that, at least with no predators and ample food, mothers who used caretakers were not reducing their infants' chances of survival.

Another group member with an important impact on the mother-infant relationship in vervet societies is the infant's grandmother (Fairbanks 1988). Just as the mother provides a secure base for the infant, the maternal grandmother provides a secure base for the mother-infant pair. Mothers who had their own mother in the group restrained their infants less and were more relaxed in infant care. Infants with grandmothers available were more exploratory and began their forays away from close proximity to the mother at an earlier age. Infants formed special relationships with their grandmothers and were groomed by them more often than by any adult female, other than the mother (Fairbanks 1988). Vervet grandmothers also had a significant effect on their daughters' fitness. Young mothers whose offspring had grandmothers in the group produced more surviving infants than comparable mothers without grandmothers (Fairbanks and McGuire 1986).

This example of the extended caregiving system of vervet monkeys illustrates that the mother-infant dyad is embedded in the larger social world. Mothers who can effectively take advantage of the help and security provided by others in caring for their current infant can benefit by increasing their lifetime reproductive success. Juvenile female allomothers promote their own fitness by gaining experience in infant care, and grandmothers contribute to the welfare of their descendants in the next generation.

The captive setting at the Vervet Colony also provided the opportunity to observe how vervet infants responded to a version of the Strange Situation Procedure used to measure attachment in human children (Fairbanks, unpublished). The following test was conducted when the infants were six months old, roughly equivalent to a preschool age child, and an age when they were spending most of the day away from the mother playing and interacting with other group members. The outdoor corrals at the colony each had a small, connected wooden shelter. When a six-month-old subject spontaneously entered the shelter area, the drop door was closed and it was separated from the group for five minutes. When the door was opened, every infant tested immediately ran over and contacted its mother. So, it appears that even in a species with multiple infant caretakers, the mother has a special role as the primary source of comfort.

Small Apes

The hylobatids have been traditionally described as living in small, stable groups, comprising a sexually monogamous adult breeding pair and their offspring (Leighton 1987). Thus, group size is drastically smaller than in great apes, with close social bonds between the two partners and no pronounced dominance hierarchy (Carpenter 1940; Chivers 1974). While gibbons are frugivorous and highly selective eaters (McConkey et al. 2002; Harrison and Marshall 2011), siamangs mostly feed on leaves (Gittins and Raemaekers

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1980; MacKinnon and MacKinnon 1980), although there is considerable variation among populations (Chivers 1974; Mackinnon 1977). The traditional notion of mandatory nuclear families might fit a classic Bowlbyian view.

This textbook picture of a monogamous pair with dependent offspring, however, has been increasingly challenged (Fuentes 2000; Reichard 2009; Reichard et al. 2012) after groups with more than two adult individuals have been reported for several species (Malone et al. 2012). For example, two thirds of the males and almost half of the females of white-handed gibbons at Khao Yai National Park in Thailand live in at least one other type of group structure in addition to pair living, which is still the most frequent type of social organization (Reichard et al. 2012:242). Furthermore, hylobatid females are sexually polyandrous: they engage in extra pair copulations while living in pairs, which can result in fertilization (Kenyon et al. 2011; Barelli et al. 2013), or copulate with both males in multimale groups (Palombit 1994; Reichard 1995; Barelli et al. 2008). Thus, hylobatids are characterized by a considerable degree of social flexibility, with females taking an active role in pursuing their reproductive interests (Sommer and Reichard 2000; Reichard et al. 2012).

There is no strict dominance hierarchy between pair partners. However, several studies mention that partners might take different roles, with females usually leading the group while traveling and males more dominant in encounters with other groups (Chivers 1976; Reichard and Sommer 1997; Barelli et al. 2008). Intergroup interactions can account for up to 9% of the daily activities in white-handed gibbons at Khao Yai Nationalpark in Thailand (Reichard and Sommer 1997), with the majority representing chases between males, but only little contact aggression (Reichard and Sommer 1997; Bartlett 2003).

In addition to the adult pair, groups include up to four offspring of different ages, with interbirth intervals of two to four years. Infants are usually carried by the mother (Figure 4.6), with siamangs differing from gibbons because of their direct paternal care for the infant (Lappan 2008). When an infant reaches eight months of age, males do some of the carrying, although this behavior might not occur in all siamang pairs (Chivers 1974). In the rare event of twins, it has been reported that other group members, such as brothers (in addition to the father), might carry the infants (Dielentheis et al. 1991). Infants are usually weaned around 12 months of age (Chivers 1976); however, others have reported weaning to occur at 15–19 months (Fox 1977). Upon reaching maturity, original descriptions claimed that the oldest offspring becomes increasingly isolated from group activities and finally leaves its natal group (a process called "peripheralization"; Fox 1977) to establish its new group. However, recent studies challenge this generalization, showing that sexually mature individuals often remain in their group if inbreeding or delayed reproduction is not an issue (Brockelmann et al. 1998). Alternatively, they may directly immigrate into another existing group without a solitary period (Sommer and Reichard 2000).

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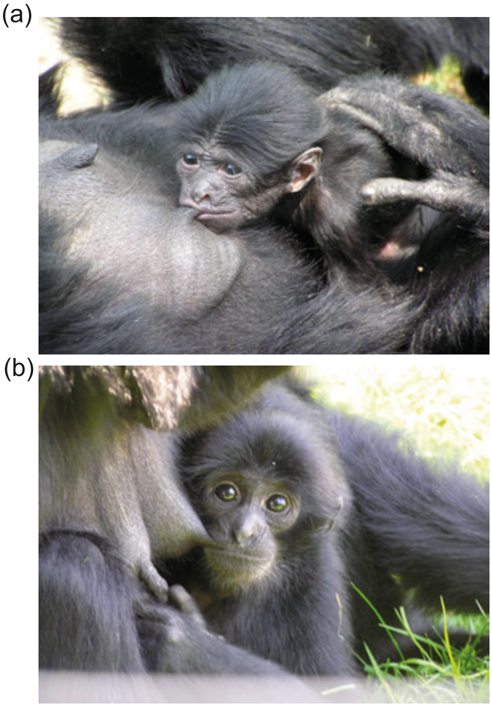

Figure 4.6 Gibbon mothers and infants. Infant at three weeks of age (a) and at six months (b). Photos used with permission from Manuela Lembeck.

Chimpanzees

Chimpanzees are largely frugivorous and complement their diet of fruit with insects, honey, and occasionally mammals, including other primates (e.g., Goodall 1986; Stanford 1992). At some study sites, they have been observed to use a variety of tools, such as sticks to extract honey from beehives and ants from their nests, and hammers and anvils to crack nuts (Whiten et al. 1999). Predation by leopards and lions is a risk for some populations (Boesch and Boesch-Achermann 2000).

Chimpanzee multimale/multifemale communities can consist of more than 200 members (Wood et al. 2017), but individuals travel and forage in small, often changing, subgroups. Males stay in their natal community and females usually disperse to other communities at adolescence (Goodall 1986; Boesch and Boesch-Achermann 2000). Adult males as well as females exhibit a linear dominance hierarchy, with males dominant over females (Goldberg and Wrangham 1997; Wittig and Boesch 2003). One explanation for male philopatry and female emigration may be that male alliances provide protection from infanticide in preventing trespassing males from neighboring groups from entering the communal range (van Schaik 1996). Several cases of infanticide by

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neighboring males have been documented (Goodall 1977), and females avoid boundary areas when they have infants (Goodall 1986).

Male chimpanzees form parties that patrol the boundaries of a home range and respond highly aggressively toward male strangers (Manson et al. 1991). Adolescent females trying to enter neighboring communities face substantial costs from the aggression of females previously established there. The dispersal attempts of the young females follow development of their first anogenital swellings, which may serve as "social passports," gaining them tolerance from males and thus protection from females. As a consequence of female dispersal, male chimpanzees are more strongly associated with one another than with females, and association between males and females is more pronounced than that among females (Goodall 1986; Boesch and Boesch-Achermann 2000).

Chimpanzee mothers provide continuous care and contact (Figure 4.7) during at least the first three months of their infant's life (Plooij 1984; Goodall 1986). While infants are initially in constant ventroventral contact with their

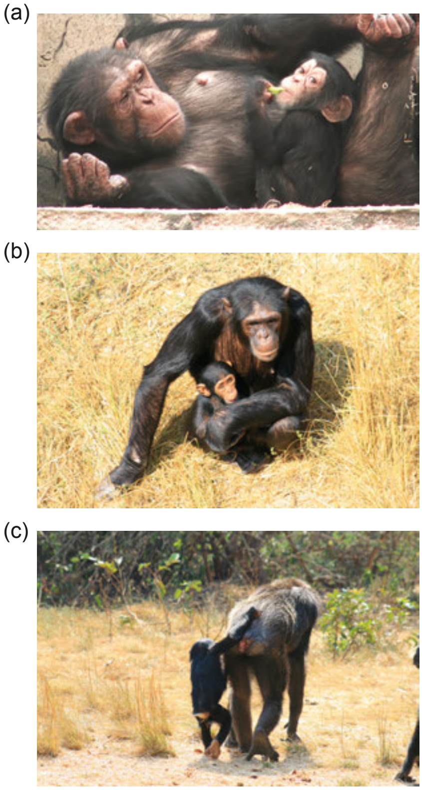

Figure 4.7 Chimpanzee mothers and infants. In (a) and (b) infants are 6 months old. In (c) the infant is about 30 months old and still remains very close to his mother. Photos used with permission from Manuela Lembeck (a) and Linda Scheider (b) and (c).

mothers, they start riding on her back by the age of five months (Bard 1995). Mothers gradually force their infants to walk and feed by themselves during their fourth and fifth year of life but continue to nurse, carry, and sleep in the night nests with them until they are five years of age. Allomothering is essentially absent, although older siblings may be allowed to carry infants (Goodall 1986). Following a mother's death, adoptions by older siblings and even unrelated adult males have been reported in chimpanzee communities at the Tai study site in Ivory Coast (Boesch et al. 2010; Myowa and Butler, this volume) Juveniles remain in association with their mothers and younger siblings, reaching adolescence at around eight to ten years. In some cases where adolescent individuals have been separated from their mother accidentally, they whimper and search for the mother even at this age. Females' age at first birth ranges from 11–14 years (Goodall 1986; Boesch and Boesch-Achermann 2000) and the mean interbirth interval ranges from 4–6 years (Sugiyama 2004; Barrickman et al. 2008).

Absence of allomaternal care may be a consequence not only of the lack of related adult females close by, mothers may also be protecting against the risk of infanticide by other females (Goodall 1986; Townsend et al. 2007). Risk of infanticide by males of their own community may be low because females mate with all the males. Widespread possibility of paternity may be protective, while low probability of paternity for particular males reduces fitness benefits for direct care, such as holding and carrying the infant.

In addition to this summary of behavioral observations in the wild, details of mother-infant interactions observed at the Primate Research Institute at Kyoto University are reported below (see section on "Long-Term Consequences of Infant Experience").

Humans

Humans live in household units within multimale/multifemale communities, clearly standing out from other primates for their abundance and ecological diversity of habitats across the globe (Brown et al. 2011; Keller and Chaudhary, this volume). Human ecological success has been linked to the evolution of human life history, which differs in several ways from that of other great apes (Hrdy 1999, 2009; Robson et al. 2006): While maturation in humans is slower—including a long childhood, late adolescence, and a remarkably increased life span—interbirth intervals are shorter and infants are weaned well before the age of independence (see below). Moreover, despite close birth spacing, the proportion of offspring that survive to adulthood is usually greater in humans, even among traditional hunter-gatherer populations (i.e., those not dependent on domesticated foods or public health care), than most corresponding estimates available from wild populations of apes (Wood et al. 2017). Obviously, humans can produce more costly offspring more efficiently in a shorter period

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of time, although this initially seems to contradict a fundamental life history trade-off between offspring quantity and quality.

A possible solution to this evolutionary paradox, as proposed by many researchers, is to consider offspring production in humans as "team work." In ecology, *cooperative breeding* describes a mode of reproduction in which individuals other than parents contribute to rearing dependent young (Hrdy 2009).

Of course, fathers can provide significant resources to mothers and also be engaged in directly caring for their children. However, the view of humans as characteristically living in nuclear families with fathers provisioning their wives and offspring ignores the extremely wide variation in paternal investment within and across human societies (Hrdy 2008). So the question arises: Who provides the support that allows mothers to produce new offspring while the previous ones are not yet independent (Sear and Mace 2008)?

As argued by Reiches et al. (2009), any member of a breeding group trades off direct and indirect reproduction, since contributions or withdrawals from pooled resources affect the budget available for fertility and survival. Natural selection justifies the expectation that investments are generally driven by net fitness advantages to individuals. So, researchers expect contributions to vary with genetic relatedness between donor and receiver as well as with donors' opportunity costs. For example, the opportunity cost of caring for younger siblings or providing some economic value to the family can be quite low for older children and adolescents (Kramer 2005).

In addition to older children and adolescents (not to mention childless adults), grandmothers past their childbearing years are another category of kin that constitutes a significant proportion of any human population particularly suited for providing kin support (Figure 4.8). For example, the proportion of postmenopausal women among the adult female population is about one third in the Tanzanian hunter-gatherer population of the Hadza, compared to a

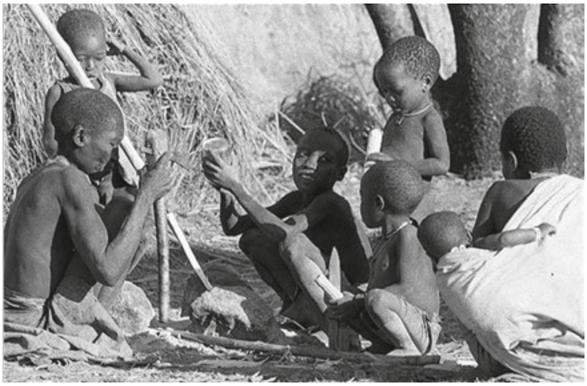

Figure 4.8 A Hadza grandmother prepares her foraging tools. She is surrounded by dependent grandchildren while her daughter (the mother of two of them) watches with her new infant. Photo used with permission from James F. O'Connell.

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corresponding estimate of about 3% for chimpanzees (Hawkes 2010; Blurton Jones 2016). According to the grandmother hypothesis, human reproduction takes place in a three-generation enterprise, with postmenopausal mothers assisting their offspring in reproduction (Hawkes et al. 1998).

Although this characterization has received much empirical support, there is also considerable variability among populations in the specific outcomes of grandmothering, with some studies finding contradictory effects (Hawkes and Coxworth 2013; Johow et al. 2013). One reason for the variation may be that grandparents can be related to their grandchildren either through their sons or their daughters, with different effects of (maternal) grandmothers on their daughters than of (paternal) grandmothers on their daughters-in-law (Leonetti et al. 2007). Since even parents and their offspring have conflicting fitness interests in resource allocation (Trivers 1974), it follows that the interests of genetically more distant members, such as in-laws, may be laden with much more conflict. In line with this, Voland and Beise (2002) found opposite effects of maternal and paternal grandmothers on the survival of grandchildren in a historical population of the Krummhörn region located in northwestern Germany. Here, the presence of the maternal grandmother (slightly) reduced infant mortality, whereas the presence of the paternal grandmother actually raised it.

When considering effects on maternal behavior and child development, the genetic relatedness of co-resident kin matters, and not only in the case of different genetic lineages: grandmothers' effects on grandchild survival has also been shown to vary with the probability the child inherited one of her X chromosomes (Fox et al. 2009). While most studies suggest that maternal kin are, on average, more beneficial to child survival than paternal kin, some do not fit this pattern (Sear and Mace 2008). Under some circumstances, mothers themselves opt not to invest in an offspring (Hrdy 1999, 2009). Demographic and socioecological context, along with genetic relatedness, affect whether supporting dependent young is likely to increase the supporter's own fitness, for example, by raising maternal fertility, offspring survival, or even economic productivity (Beise 2005; Kushnick 2012; Blurton Jones 2016). Varying access to resources, overall mortality risks, mating systems, and residence patterns between and within human populations provide a wide range of factors that affect rearing decisions (Lawson and Mace 2011). Depending on context, kin effects may either contribute directly to infant survival or future reproductive success (direct care) or enable parents to invest more or less in a child themselves (Kushnick 2012). Furthermore, individuals can also differ in their power to exert leverage on a mother's fertility, parenting behavior, or socioemotional development of the offspring (Houston et al. 2005). As suggested by the classic socioecological model, the fitness-maximizing consequences of behavior depend on context, and parenting in particular is known to be highly responsive to changes in environment (Royle et al. 2014). Reviewing published data on the impact of kin on offspring survival, Sear and Mace (2008) argued that investment

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decisions cannot easily be generalized, even if potential helpers are differentiated according to their age, sex, and genetic lineage. Further, they document high variability in the observed effects of different categories of kin on infant welfare (although in the studies reviewed, loss of the mother always reduced infant survival during the first two years). This variation highlights complexity associated with measuring reproductive success (Grafen 1988; Blurton Jones 2016), let alone inclusive fitness (West and Gardner 2010). Nevertheless, disentangling ways that direct and indirect reproduction contribute to fitness differentials within families seems feasible for the socioecologies where relevant data are available on genealogical relations, spatial proximity, and births and deaths over generations (e.g., Voland 2000; Smith and Mineau 2003).

Evolution of Human Life History

Bowlby's initial conception of the central role of early mother-infant attachment in later emotional health, and social and parental competence, has been revised, at least in some quarters: the concept of "mother" has been replaced with "caregiver" (inter alia), multiple definitions of "attachment" are allowed, and diverse cultural and individual forms of infant-caregiver interactions are acknowledged (Konner 2010; Quinn and Mageo 2013; Otto and Keller 2014). Still, the idea persists that early "attachment" after birth is uniquely important for humans. In support of a special role for early attachment, the period of postnatal helplessness is relatively long in humans, although some have noted similar helplessness in infant chimpanzees (reviewed in Hawkes 2006). Direct comparison of the features of human development with other primates indicates the timing of birth with respect to the infant's maturational state is somewhat early, but not remarkably so (Bard et al. 2011; see also below). It is the timing of weaning that stands out as a human distinction. Weaning is extremely early in humans compared to every other primate, occurring while the toddler still requires full provisioning and protection. The human child is thus separated relatively early from the special mother-infant bond of nursing and becomes dependent on a network of others, which can consist of multiple siblings, the mother, father, grandmothers, and a wealth of other potential alloparents, genetically related and unrelated. Below, we review information about the state of human maturation at birth and at weaning, initially with particular attention to brain maturation, so as to place early human development in a comparative context. The comparisons link brain size to the pace of development. For predictors of developmental pace, we review the coevolution of weaning age, age at feeding independence, age at maturity (first conception), and longevity from the demographic perspective of evolutionary life history theory. These lines of evidence converge on the likely fundamental importance of uniquely early weaning on the emotional, cognitive, and social characteristics of humans.

From "The Cultural Nature of Attachment: Contextualizing Relationships and Development,"
Heidi Keller and Kim A. Bard, eds. 2017. Strüngmann Forum Reports, vol. 22,
series ed. J. Lupp. Cambridge, MA: MIT Press. ISBN 978-0-262-03690-0.

Principles of Brain Maturation in Mammalian Development

Brain construction, maturation, and the very first behavioral capacities in placental mammals are surprisingly predictable and species-uniform (Figure 4.9) in nonhuman primates and humans, if maturational events are allometrically scaled—from conception, not from birth—with respect to eventual

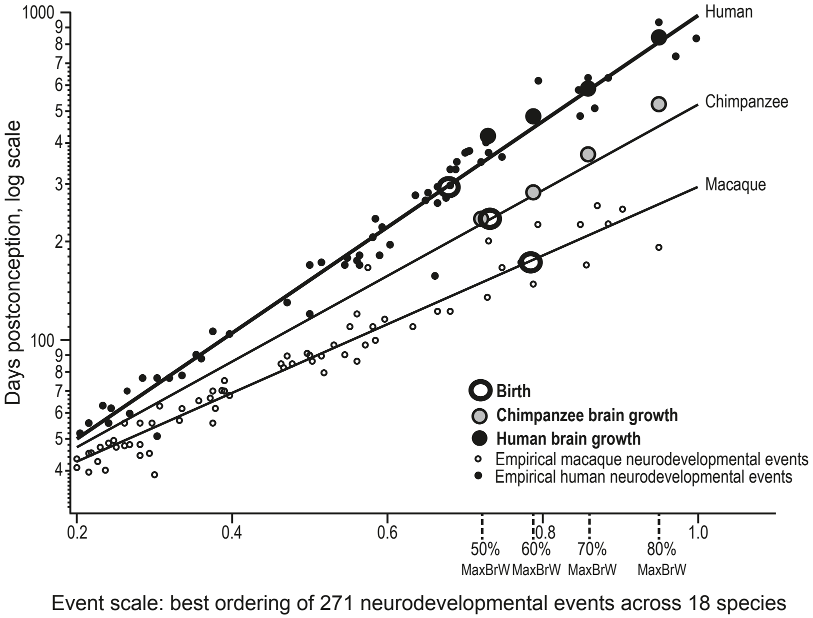

Figure 4.9 Comparison of predictable patterns and rates of maturation for the rhesus macaque, chimpanzee, and human brains around birth. The x-axis represents the "event scale," a statistical best ordering of 271 events in neural development in 18 mammalian species set to range between zero and one (data from Workman et al. 2013). These events include onsets, peaks and onsets of neurogenesis, axon extension and synaptogenesis, early physiological and behavioral events, and myelogenesis as well as specific brain volume milestones (data from Finlay and Workman 2013; Sakai et al. 2013). The y-axis is days postconception (log scale). On this representation, a steeper line for one species compared to another represents a longer time required to reach any specified maturational milestone—for example, humans take about 900 days to reach 80% of maximum brain weight, while chimpanzees take about 500 days. The linear model of the developmental "schedule" for humans, chimpanzees, and macaques are plotted with human and macaque lines generated from their empirical data (plotted) in combination with the additional data from 16 other mammalian species, while the chimpanzee line is estimated based on its brain size and gestational length (formulas in Workman et al. 2013 and http://www.translatingtime.net/). Data from the supplementary materials of Sakai et al. (2013) were used to determine the postconceptional day that percentages of maximum brain weight were reached in humans and chimpanzees. Large open circles represent the position of birth in each species on the neural maturational scale, showing considerable variation (see also Figure 4.10) compared to the high predictability of neurodevelopmental events between species.

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brain volume (Workman et al. 2013). Passingham (1985) first noted that graphs of changes in brain volume versus postconception day are virtually superimposable across mammals, and that the difference between them was duration, with larger brains requiring absolutely longer to produce. The reason for the surprising uniformity of basic brain construction in mammals (not true for all vertebrate taxa) is not yet known. Perhaps, the complexity of any individual brain permits a limited range of alterations in the timing of deployment of its developmental processes, with the basic scaffolding of neurogenesis, initial tract formation and myelogenesis, and initial synaptogenesis highly conserved.

By contrast, the events of life history—birth, weaning, feeding independence, dispersal, first parenthood, and so forth—are transactional and social, defined by the competing interests and multiple goals of individuals, the tradeoffs mentioned at the outset of this chapter. The timing of life history events such as birth or weaning depends not only on the maturational state of the offspring, but also on the competing and aligning interests of offspring and mother, in both individual variation and cross-species contexts (Royle et al. 2012).

Overall, long gestation requires more investment of resources from the mother than a short one. This investment involves not only the transfer of nutrients to the fetus, but also a lengthening of the interval to the next conception, and hence a decrease of maternal reproductive rate. Mothers might invest in long gestation and produce precocial offspring for many reasons, such as the need for ungulate offspring to avoid predators independently. Because adult brain mass is a power-law function of developmental duration, gestational length in combination with the degree of brain maturation at birth will also reflect adult brain mass. As Figure 4.10 shows, precocial guinea pigs have much more mature brains at birth than do altricial mice. This results from longer gestation in guinea pigs than in mice, combined with different rates of brain development during gestation. Further, brain maturation postbirth continues the unique developmental rate that is indicated by neural maturation at birth in each species and results in the adult brain mass that is predictable from total duration of development in both species.

Humans have been widely viewed as a secondarily altricial species (e.g., Martin 1990) among the primates due to the large proportion of brain growth that occurs after birth, which is frequently credited for humans' unusual cognitive abilities. Prolongation of a fetal rate of development far beyond birth is offered as an explanation for the volume increase (e.g., Coqueugniot et al. 2004), or a special adaptation for learning postbirth in humans (Sakai et al. 2013). These interpretations assume that birth occurs at the same stage in fetal development across different species, and that changes observed in development after birth are the result of evolutionary modifications of the development schedule itself. However, an evolutionary reshaping of the developmental schedule is not necessary to account for human maturation (Figure 4.10). Rather, the position of birth in humans occurs somewhat earlier on a neurodevelopmental

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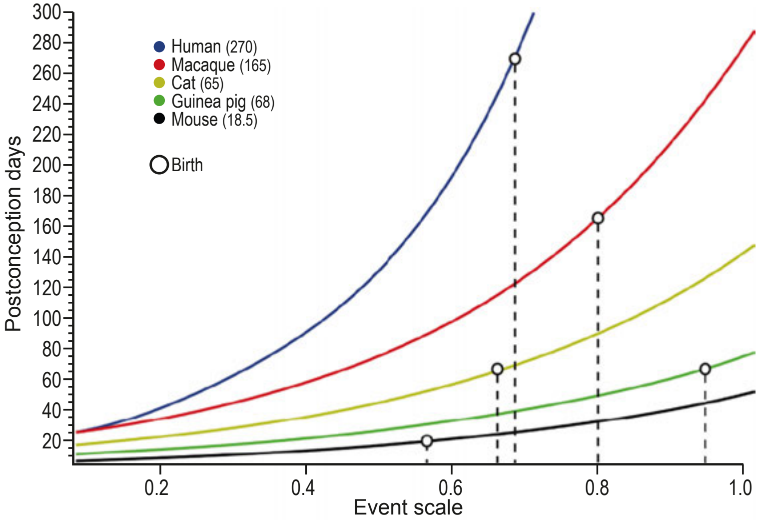

Figure 4.10 Variability in timing of birth with respect to neural maturation in five mammals. The position of birth (open circle, listed after each species name) for five placental mammals relative to the event scale (x-axis; the derivation of this scale is described in the caption for Figure 4.9); the age of each mammal in postconception days can be read for birth (or any neurodevelopmental event scale value) on the y-axis. The five placental mammals are chosen to represent close to the full range of the data set for both adult brain size and the altricial to precocial dimension of placement of birth with respect to neurodevelopment (Workman et al. 2013). The relative slope of the curves is highly correlated with adult brain mass: steeper slopes represent longer durations to reach maturity. In the most highly precocial mammal, the guinea pig, all neurogenesis and most myelination is complete at birth and brain mass is close to its adult value. For comparison, cortical neurogenesis in the altricial mouse at birth is still underway and synaptogenesis in the forebrain is only beginning. In humans and rhesus macaques at birth, cortical neurogenesis, cortical cell migration, and basic axonogenesis are entirely complete, and the succession of myelination of various tracts is in progress. The domestic cat is intermediate. From Workman et al. (2013), republished with permission of *The Journal of Neuroscience*.

schedule that is highly conserved across mammalian species. Further, the particular shape of the curve of brain growth must be calculated from the "allometrically expected" extension of human brain development required to produce a large brain (Finlay and Workman 2013). When these two factors are considered, human brain growth around birth can be seen to be very similar to that observed in other primates, appropriately scaled (Figure 4.9).

The functional state of the brain at birth is not very different across primates. In every primate studied, including humans, the basic construction of the nervous system is well over at birth, including generation of neurons, establishment of axon pathways, and initial excitatory and inhibitory synaptogenesis. The principal event underway over the range of neural maturation that primate births span is the sequential myelination of multiple brain components (Workman et al. 2013). The production of myelin, the sheathing of axons to increase their conduction velocity, is the cause of most of the perinatal increase of brain volume in primates. Each component being myelinated—spinal cord, cerebellum, optic nerve, corpus callosum and so forth—has its distinct timetable, which is experience-independent, not known to reflect ongoing learning directly. Because of a whole-brain "synaptic surge" linked to birth and independent of the conserved timetable of neural maturation and myelination, all primates appear to be relatively similarly placed in their abilities for early environmental learning (Rakic et al. 1986).

Yet, humans appear motorically incompetent compared to the great apes, perhaps more so than a somewhat earlier point of myelination would suggest. Note that the inability to walk until (typically) a full year after birth has been dissociated from neural maturation and linked instead to an insufficiency of the musculature to support body weight: infants suspended in water can produce organized stepping "reflexes" at birth (Thelen et al. 1984) with a timing characteristic of other mammals (Garwicz et al. 2009). Achievement of a critical height/weight ratio is the best predictor of walking onset (Thelen et al. 1984). The simple weight of the head may be the basic reason for the inability of human infants to support their heads at birth. By contrast, sensory and other integrative abilities can be well advanced or even sophisticated. For example, features of language structure can be learned by the human fetus *in utero* (Jusczyk et al. 1983; Mehler et al. 1988). Newborns selectively attend to contrastive stimuli and faces (Johnson 2005), with very rapid postnatal appreciation of the environment and intermodal interactions (Gibson et al. 1979; Walker et al. 1980). Statistical regularities of speech are also learned with extreme rapidity (Saffran et al. 1996). Whether delayed motoric abilities compared to general perceptual and learning abilities are "bugs" or "features" of human development remains to be determined.

The classic explanation for human altriciality at birth has been cephalopelvic disproportion. In this scenario, the transition to bipedal locomotion in human evolution led to a narrowing of the skeletal structure of the birth canal, conflicting with selection pressure toward larger brains that make passage through the birth canal more difficult, thus necessitating early birth so that a substantial portion of cranial expansion could take place outside the womb (Schultz 1949; Rosenberg and Trevathan 1995). A recent competing explanation is that maternal metabolic constraints rather than cephalopelvic proportion may determine the timing of birth in humans (Dunsworth et al. 2012; Huseynov et al. 2016). We might also view the shortened gestation in humans, with respect to fetal neural maturation, as part of the same forces that produce early weaning and increase the mother's overall reproductive output. All interpretations converge, however, on the idea that birth timing is a negotiation between the requirements of the fetus and the mother.

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Remarkably Early Human Weaning and Infant-Caregiver Interactions

The transition from suckling to independent feeding constitutes a major shift in the behavioral and cognitive capacities required for survival (Lee 1996). Knowing the stage of brain maturity at which weaning takes place is therefore of clear benefit for understanding the relationship between development of the nervous system and life history adaptations. Across species, weaning, like birth, is an event that can be uncoupled from the highly coordinated schedule of brain development. The evidence that weaning is earlier in humans compared to other great apes is clear. In a cross-cultural survey of weaning practices, the median age of weaning across 133 nonindustrial societies was reported to be 29 months postbirth, with a standard deviation of 10 months (Sellen 2001). In traditional societies, earlier weaning is associated with shorter interbirth intervals. Early weaning should be conducive to higher reproductive output, all other things held equal. As an illustration of how late weaning can be when initiated by the child, in a large sample of U.S. mothers it has been reported that the average age of child-led weaning is 4.4 years, or 53 months (Dettwyler 2004), much later than the nonindustrial average noted above and significantly later than the median weaning age for U.S. mothers, which is around seven months (as reported by the CDC). If we compare any of these measures to reported weaning ages for other great apes (e.g., gorillas at around 3–5 years, chimpanzees at 4–6 years, and orangutans at seven or more years), we see that weaning is earlier in humans, as has been emphasized by many researchers studying human life history evolution (e.g., Kennedy 2005). These observations, however, are based on absolute duration. Allometrically corrected predictions for these species compared to brain maturation show that humans are weaned even earlier than the linear projections indicate.

So, humans have made two alterations in reproduction: (a) a relatively shortened gestation with respect to neural maturation and (b) much earlier weaning. Both are methods of reducing unique maternal investment to tractable levels, depending on biparental care, grandmothers, or other alloparents in the early postnatal period and progressively more as childhood continues (Hrdy 2009). Early weaning also serves to redirect the early learning potential of the child. From early childhood to adolescence, the brain is organized for maximum learning, but the human child is neither feeding independently nor provisioned solely by its mother. As noted above, subsidies come from a larger array of allomothers beyond the minimal nuclear family including related and nonrelated others. Humans have an extended childhood where language, custom, and allegiance are being defined by that larger social group, not by the immediate parents. Allegiance to a peer group develops even in spite of complaints from the parents (Harris 1995; Locke and Bogin 2006).

The availability of subsidies from others, which allows mothers to bear a next baby while the previous one is still dependent, may be the foundation of our extensive and unusual sociality. Because human mothers can wean early

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without suffering unsustainable penalties in offspring survival, they increase their own fitness while thrusting the human child into dependence on a wider network of relationships. Even though many other primates are handled by allomothers soon after birth, infants' primary dependence on nursing continues until they can feed themselves. Human infants, in contrast, are displaced from the small society of mother and child into dependence on the community of age peers, other relatives, and any number of unrelated others in the early parts of "sensitive periods" of development of any number of sensory, cognitive, motor, and social abilities. Although much evidence suggests relatively greater attunement of the human child for social interaction, imitation, and cooperation (e.g., Tomasello 1999; Bullinger et al. 2011; Haun et al. 2014; Hawkes 2014), it may be the rearing context more than motivations and preferences of the child that differ from its primate ancestors and cousins (Bard and Leavens 2014). Possessed of an exceptionally large brain constructed on a primate-typical schedule, with an allometrically predictable extended period of maturation, the human child exercises those motivations and preferences in social environments more variable in every respect than those of any primate relative.

The Evolution of Slow Human Life History

The developmental niche we inhabit is a curious mixture of a conserved neurodevelopmental schedule and a specially adapted life history. Brain size, rate of brain growth, age at maturity, and longevity all covary (e.g., Sacher 1959, 1975), but the direction of influence among these several factors remains in question. Perhaps it is larger brains that require longer development and propel increased longevity (e.g., Kaplan et al. 2000, 2003; Barrickman et al. 2008; Isler and van Schaik 2014). The causal arrow can be drawn the other way, however, using demographic life history theory (Stearns 1992), with adult mortality risk the fundamental driver of life history evolution (Charnov 1993). That demographic approach explains the range of mammalian ages at maturity and durations of offspring dependence as evolutionary consequences of variation in average adult life spans (Charnov 1993).

Among nonhuman primates, great apes have the longest life spans, oldest ages at first conception, latest ages at feeding independence, and largest brains; and compared to those hominids, longevity is much greater, first conception later, and brains larger in humans (Barrickman et al. 2008). Female fertility, however, ends at the same age in humans as it does in other great apes (Robbins et al. 2006; Robson et al. 2006), grounds for assuming this was also true of our common hominid ancestor (Figure 4.1, lower right panel). Yet unlike other great ape females, women remain productive for decades longer (Blurton Jones et al. 2002; Blurton Jones 2016), suggesting that postmenopausal longevity, not an early end to fertility, is the derived feature in our lineage (Hawkes 2003, 2010). As noted above, great apes become frail and rarely survive to menopause (Hawkes 2010), whereas even in hunter-gatherer

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populations (where mortality is relatively high) about one third of the women live past the childbearing years (Hawkes 2010; Blurton Jones 2016). Our postmenopausal longevity is combined with weaning ages that are remarkably early when scaled allometrically to brain maturation *and* when compared to weaning ages expected for a primate with the longevity and age at first conception of humans. The grandmother hypothesis links the evolution of our postmenopausal longevity to our early weaning (Hawkes et al. 1998).

The human lineage evolved in an ecological context where staple foods are difficult for youngsters to handle for themselves. Under those circumstances, subsidies for dependent offspring allow mothers to bear next babies sooner. The economic productivity of postmenopausal Hadza grandmothers (Figure 4.8), considered in light of demographic links among mammalian life history traits identified in Charnov's (1991) model, suggest the coevolution of these distinctive features of human life history (Hawkes et al. 1998; Hawkes and Coxworth 2013). In a two sex, agent-based mathematical model of this grandmother hypothesis (Kim et al. 2012, 2014), a life history like the other great apes evolves into a human-like one propelled by postfertile females' subsidies for weaned dependants. At the initial great ape-like equilibrium, fewer than 1% of females survive their fertility. However, when they can subsidize their dependent grandchildren, slightly longer-lived grandmothers can help more and increased longevity evolves in subsequent generations. Grandmother effects drive model populations to new equilibrium longevities with fractions of postfertile females very like those of modern hunter-gatherer populations.

These simulations do not model brain growth directly, but the links between greater longevity, longer duration of dependence, later maturity, and mammalian brain size outlined above suggest a mechanistic link. If increasing longevity did evolve as grandmothering subsidies allowed mothers to wean earlier, concurrent retardation in maturation rate would result in brains developing more slowly to larger size along an allometrically conserved primate schedule. This combination of features makes human infants more dependent on a social environment beyond their mothers earlier in development than any of our primate relatives.

Long-Term Consequences of Infant Experience

Bowlby's concerns about attachment included consequences for the infant's subsequent social behavior. Here we review observations on nonhuman primates that investigate those links. Findings on several species of monkeys—especially rhesus—have been well published. After summarizing those, we give more detailed attention to less well-known observations on chimpanzees made possible by the unusual protocol at the Primate Research Institute of Kyoto

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University, which provides a window into maternal styles and the antecedents and contexts of their variation in one of our closest evolutionary cousins.

Variation in Monkeys

In rhesus macaques, the nonhuman primate central to the development of Bowlby's attachment theory, a majority of females reared without mothers are not able to provide adequate maternal care themselves: they are indifferent to their first infant or even display abusive behaviors. They can learn, however, adequate mothering skills and most turn out to be competent mothers for subsequent offspring (Suomi and Ripp 1983). Even in group-living animals, some mothers appear to be repeatedly abusive, dragging their infant by its tail or leg, pushing the infant against the ground, throwing, hitting and biting the infant, and stepping or sitting on it (Maestripieri 1998; Maestripieri and Carroll 1998). Abusive mothering occurs not only in captive populations of rhesus but also in pigtail macaques and sooty mangabeys, where up to 10% of the mothers physically abuse their infants (Maestripieri et al. 1997a, b; Maestripieri and Carroll 1998). Maternal abuse has also been observed in free-living Japanese macaques, most frequently among mothers who were orphaned after weaning and had no experience of younger siblings (Hiraiwa 1981).

Maternal style is transmitted across generations from mothers to daughters in rhesus macaques (Berman 1990). This also holds for physical abuse of infants. Cross-fostering studies in this species showed that infants who were born to, and raised by, abusive mothers as well as those who were born to non-abusive mothers but raised by abusive mothers became, in most instances, abusive mothers themselves. Contrary to that, infants born to and raised by non-abusive mothers as well as infants born to abusive mothers but raised by non-abusive mothers all became non-abusive mothers (Maestripieri 2005). This seems to echo the variation in steepness of dominance hierarchies across the macaque radiation noted above (see section on "Broader Variation in Macaques"). Tolerant species persist in their tolerance as hierarchical species persist in their maintenance of steep rank differences. The social style that infants experience sets their continuing expectations and responses in relationships.

This type of abusive mothering is noteworthy but rare in normally reared monkeys (<10% of cases observed), even in macaques. In contrast, variation in maternal style within the normal range is common and has been described along the dimensions of rejection and protectiveness for macaques and other primate species (Hinde and Spencer-Booth 1971b; Simpson and Datta 1991; reviewed in Fairbanks 1996). A relatively rejecting mother initiates fewer contacts when the infant is away, is more likely to break ventral contact, and puts limits on her infant's access to the nipple. Infants of more rejecting mothers, however, do not just passively take it. They increase their efforts to maintain contact with their mothers. They also have higher rates of contact with

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other group companions and begin exploring the environment at an earlier age. These differences continue into the juvenile years when daughters of relatively rejecting mothers are more likely to actively approach and spend time near others (Fairbanks and Hinde 2013). While extreme deprivation is expected to have lasting negative effects on development, overcoming challenges within the normal range of early experience can increase resilience and the ability to cope with stressors in later life (Parker et al. 2006).

Maternal protectiveness, in contrast, teaches infants that the world is a risky place. Primate mothers respond to perceived environmental risk by increasing contact with their infants, inspecting, grooming, and restraining their attempts to leave. Low-ranking mothers, mothers in groups with new adult males, and mothers who lost their last infant all have relatively high rates of maternal protectiveness (Fairbanks 1996). High levels of early maternal protectiveness delay the timing of exploring the world beyond the mother, and overprotected infants are significantly more cautious in response to novelty as juveniles (Fairbanks and McGuire 1993).

Research on early experience of the mother within the normal range supports the persistence of maternal style from mother to adult daughter described above for abusive mothering. While mothers do modify their style in response to circumstances, long-term studies of rhesus macaques and vervets confirm the significant continuity of mother-infant contact and maternal rejection across generations, even after controlling for correlated features like family dominance rank (Berman 1990; Fairbanks 1996).

Great Apes in Captivity

Incompetent or even absence of maternal care (e.g., ignoring, not nursing, or mistreating the infant) occurs not only in monkeys that lack sufficient experience but is common in captive great apes. Among chimpanzees in captivity, one out of every two mothers does not care for her infant, a stark contrast with the close attachment of mothers to infants in the wild (Matsuzawa 2006). An international survey on the breeding success of zoo-living gorillas, chimpanzees, orangutans, and bonobos, conducted by Abello and Colell (2006), revealed that the maternal skills of great ape females are associated with their own rearing histories. Incompetent mothering seems to be intergenerationally transmitted, as hand-reared mothers and/or those who lack the experience of observing maternal behavior are those who fail most often in providing appropriate care for their infants. Conversely, factors that contribute most to becoming a competent mother are being mother-reared and raised in a mixed-sex, mixed-age group where maternal and social behavior of conspecifics can be observed and/or experienced. Moreover, the presence of conspecifics shortly after parturition seems to be important in encouraging the mother's interest in her infant and stimulating caring. Intervention programs as well as the early

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integration of human-reared infants into a group (under rigorous supervision) may help to break the cycle.

In Japan, over half the chimpanzees kept in captivity live in groups of five or fewer. This is quite different from the wild where communities typically range from 20 to 100 members. Small groups mean that most captive chimpanzees have little chance to observe or interact directly with infants. A lack of social learning during an early period in life may be the primary reason why some captive mothers abandon their offspring (i.e., "sensitive period" for leaning to parent). In 2000, the Primate Research Institute of Kyoto University (PRI) initiated a longitudinal study on chimpanzee cognitive development (Matsuzawa et al. 2006). That year, when three chimpanzee infants were born (Figure 4.11), researchers had arranged to provide conditions of

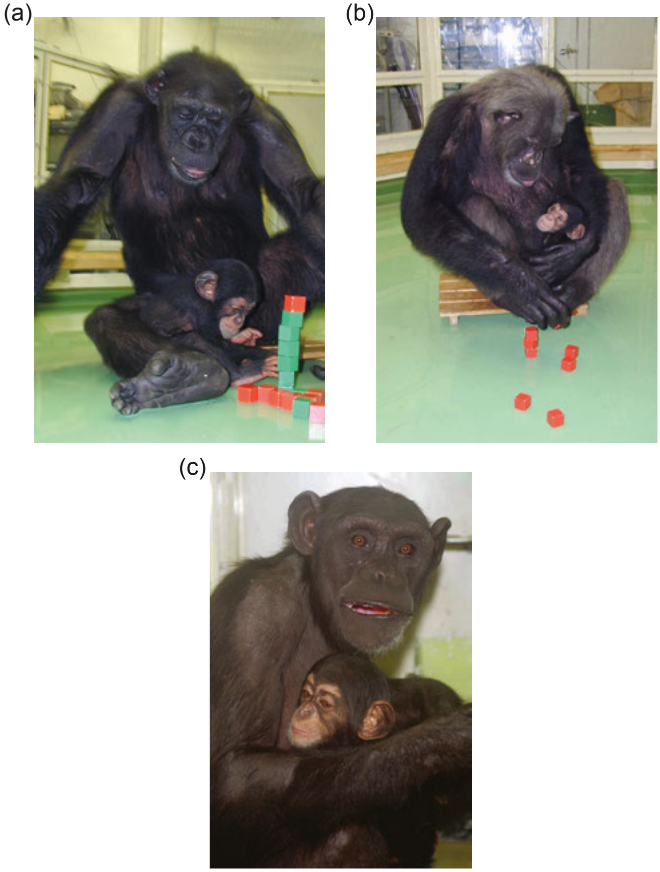

Figure 4.11 Three mother-infant pairs of chimpanzees at the Primate Research Institute, Kyoto University: (a) Ai and Ayumu (male, born in April 24, 2000), (b) Chloe and Cleo (female, born in June 19, 2000), and (c) Pan and Pal (female, born in August 9, 2000). Photo used with permission from Tetsuro Matsuzawa.

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community- and mother-infant bonds to facilitate the natural development of chimpanzees, given the limitations imposed by captivity.

With the pregnancies of Ai, Chloe, and Pan, researchers sought ways to prevent them from abandoning their infants. All the females had few, if any, opportunities to observe or interact directly with the offspring of other individuals. Ai's mother was killed in the forest in Africa several months after her birth, and she was reared by multiple human caretakers. Chloe had been born at the zoo in Paris and was likely reared in a poor social environment. She came to PRI several years after birth. Pan was a daughter of Puchi, who had been born at PRI and rejected by her mother. Puchi was reared by humans from just after birth (in a human house as a human infant).

Although the mothers had already passed the likely sensitive period for learning parenting behaviors from other social group members, researchers instructed the females how to hold and take care of their infant by the following three methods. The females were shown videos of wild chimpanzees taking care of their offspring (holding, nursing, grooming) to provide observations of parenting. Second, researchers gave the mothers tactile experiences with infants by holding infant gibbons and monkeys in front of the females and encouraging them to touch them through the mesh of the cage. Third, a researcher who had reared the chimpanzee entered the mother's room and instructed her to hold a stuffed chimpanzee. Fortunately, each mother then successfully held her baby and demonstrated good maternal competence (Bard 2002).

Quantitative measures of mother-infant interactions found that in the special setting of PRI, these mothers on average protectively cradled their infants less than mothers in other captive settings (Bard et al. 2005). Of special interest here are the individual differences in protectiveness among the three mothers:

- Ai (mother) permitted only a very limited number of human caretakers who had reared her to touch Ayumu (her son) right after birth. Ai continued close proximity with Ayumu 24 hours a day for the first three months of the baby's life.
- Chloe (mother) never permitted even the human caretaker most familiar with her to touch her daughter (Cleo). Chloe also continued to keep close to Cleo 24 hours a day for over six months, and held her even after Cleo had developed her own motor competence.
- Pan (mother) easily permitted many humans to touch or hold her daughter (Pal), and often put her baby on the floor beside her just as human mothers do (Figure 4.12). Pan, who had been raised in a human home, even handed her offspring over to human caretakers.

Differences in protectiveness among the mothers may be linked to differences in their own experiences during childhood.

Before Ai, Chloe, and Pan gave birth, two others had done so at PRI: Reiko and Puchi. Reiko was born in Africa in 1966 and arrived at PRI in 1968 when she was 19 months old; she could have observed other group members

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Figure 4.12 Pan with infant down. Pan put her offspring on the floor and lay with the infant from just after birth. Photo used with permission from Tetsuro Matsuzawa.

parenting in the wild. Puchi was born in West Africa in 1966. After her capture by human hunters, she was kept as a pet for 12 years in an ordinary human family. She arrived at PRI in 1979. She started social living with her conspecifics with no experience of learning or interacting with other individuals' offspring. Puchi, but not Reiko, refused to take care of her infants. Although she gave birth twice, both of Puchi's offspring were raised by human caretakers.

Following the success of rearing instructions with Ai, Chloe, and Pan, Puchi gave birth to her third offspring and again abandoned it. After artificial rearing began, researchers started instructing Puchi to hold her infant. Seven days after the birth, a researcher entered the same room with Puchi, holding her infant, and enticed Puchi to smell and touch the infant step-by-step. In the process of the instruction, Puchi gradually began to show interest in her infant. The instructions continued, and 20 days after she had given birth, Puchi successfully held her baby. These examples show that chimpanzees can learn parenting behavior by active human instruction, even when they have no experience of infant rearing early in their lives.

Concluding Remarks

An evolutionary perspective makes both phylogeny and natural selection central to explanations for variation among living things. Fitness trade-offs are everywhere, and conflicts of interest can powerfully shape social life. Primatologists do not all agree about the words used to describe social relationships, including whether "attachment" should even be used. Yet all agree that phylogeny, ecology, and social systems affect the interactions that primate infants have with their mothers and others, and that social relationships involve inevitable conflicts of interest. As shown here in a variety of primates, rearing

From "The Cultural Nature of Attachment: Contextualizing Relationships and Development,"
Heidi Keller and Kim A. Bard, eds. 2017. Strüngmann Forum Reports, vol. 22,
series ed. J. Lupp. Cambridge, MA: MIT Press. ISBN 978-0-262-03690-0.

circumstances have long-term effects on behavior later in life. In addition, infants play a role in finding the care they need and are resilient to "less than the perfect" mothering when raised in species-typical social groups with opportunities for interaction with other group members. In the detailed examples provided, later experience (at least in our closest cousins) as well as context continues to matter after infancy.

Could it be that parallel links between experience and parenting fuel the American advice industry in baby care? Among hunter-gatherers, other traditional societies, and in many non-Western cultural contexts (e.g., Keller and Chaudhary, this volume), babies are part of the daily lives of other children. Just as mothers rely on help from other adults as they bear new babies before the previous one can feed itself, young girls have continuing intimate experience with the infants before their own first conception. Even then, at least in the case of Hadza foragers, children survive better when their mothers gained experience before maturity through their own infant siblings (Blurton Jones 2016:413). In many parts of the industrial Western world, including much of the United States, contrasts with most of human experience are striking: direct exposure to babies is minimized by closely spaced births with limited family sizes, small households, and workplaces that (again unlike most of human experience) are inhospitable to babies and distant from the home.

The examples presented in this chapter show that individuals across the primate order often interact with infants they did not bear and, conversely, that the experience of primate infants often includes handling by nonmothers. By relinquishing their infants to others, mothers face risks and benefits that vary both with group composition and the mother's particular social position. Mothers, allomothers, and infants face different fitness trade-offs that include varying opportunity costs around these possibilities. While offspring might benefit from more maternal investment than is in the mother's fitness interest to give, infants can also gain from the wider interactions that shape their development. This appears nowhere more important than in our own lineage, as mammalian comparisons point to developmental correlates of the uniquely early displacement of human infants from the special mother-infant nursing relationship. Where attachment specialists and public health workers seek to implement policies that—often laudably—prioritize the welfare of infants and young children, the trade-offs and conflicts of interest faced by infants, children, mothers, and others may be relegated largely to afterthoughts. For evolutionary explanations of variation, those trade-offs and conflicts of interest are central. They make the distinctly early weaning of human infants deserving of increased attention for likely importance in expanding the capacities to adjust to varying social circumstances that we share with other members of our primate order.

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