

DEVELOPMENT OF SOCIAL BEHAVIOR IN FREE-LIVING NONHUMAN
PRIMATES

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INTRODUCTION AND BACKGROUND

Among primates, physical and behavioral maturation begin before birth and continue until an organism dies. Thus, primate behavioral development can be viewed properly only as a life-long process that results in a continual shaping and reshaping of the ways in which an individual responds to the myriad ecological and social features of its environment. Throughout life, a primate garners knowledge of contingencies and relationships thereof that enhances its abilities to avoid predators, conspecific aggression, accidental injury and inclement weather, to forage and rest efficiently, to acquire desirable mates and to raise offspring successfully. As social, demographic and ecological conditions change, individuals are able to promote their survival and reproductive potential by drawing on that store of knowledge, and often on the knowledge of fellow group members.

We seek to understand behavioral development and the processes of socialization in nonhuman primate species in part to enhance our understanding of these aspects of human development. Among extant organisms, nonhuman primates are phylogenetically our closest relatives. Like humans, they exhibit large brains, long prereproductive developmental phases, complex modes of parental care, long periods of adolescent sterility, long interbirth intervals and long lifespans in comparison to most non-primate mammals of

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similar body mass (see Sacher and Staffeldt 1974; Western 1979; Eisenberg 1981; Sacher 1982). Also, the proportion of the lifespan that is represented by the prereproductive period of their development is greater than that in species of comparable size in other orders of mammals. Relatedly, both human and nonhuman primates rely extensively on their prodigious learning capacities to acquire the skills needed to survive as immatures and to become flexible and effective adults. Finally, the maturation of nonhuman primates takes place within some of the most complex societies to be found in the animal kingdom (see below).

Clearly, the nonhuman primates are the best available animal models for the study of human behavioral development. Moreover, because nonhuman primate behavior patterns are relatively unconstrained and unembellished by cultural mores and traditional systems of beliefs, such as those that characterize human societies, our understanding of the adaptedness and variation of many behavioral systems among human societies can be given valuable perspective by investigation of the homologous systems among the nonhuman primates.

Tremendous progress in the past twenty-five years of research on primate social behavior has been potentiated by a productive union of laboratory and field work on many species. A large proportion of past laboratory and field work has been focused on questions about the ontogeny of primate behavior and, in particular, the development of social relations (see e.g., Hinde and Spencer-Booth 1967; Harlow and Harlow 1965; Harlow and Harlow 1969; Kaufmann 1966; Berman 1982a; Berman 1982b). Researchers working in laboratories have contributed significantly by evaluating hypotheses that have been difficult to test in the field (see e.g., Hines 1942; Young et al 1964; Goy and Phoenix 1972; Mason 1965). Simultaneously, field work on primate development has placed the findings of laboratory research into their natural context. Observations of several primate species in their natural environments have not only helped to illuminate the immediate effects and ultimate functions of several primate traits, but also they have revealed a wide variety of naturally-occurring environmental constraints on development in primates. The abundance, quality and distribution of food, the size and demographic composition of social groups, and social structure within

groups all mediate multifarious effects on the rate and form of lifelong behavioral development occurring in natural primate populations (Altmann and Altmann 1979). Consequently, we begin our review with a sketch of the diverse physical and social worlds within which primate development occurs.

Primate Ecology and Social Organization

Primate infants are born into a wide variety of social systems and an equally broad diversity of natural environments. Immature lorises and galagids develop with only their mothers for social partners, and infant orangutans are typically accompanied solely by their mothers and an older juvenile sibling (Rodman 1973; Horr 1977; Charles-Dominique 1977). Young callitricids, hylobatids and indris are attended by their mothers, fathers and one or more older siblings (Carpenter 1940; Castro and Soini 1977; Pollock 1977), whereas some infant squirrel monkeys begin life in groups that have hundreds of members (Baldwin and Baldwin 1971). Primates are found primarily in the tropics (Napier and Napier 1967); however, natural populations occur in habitats ranging from near desert conditions (Papio hamadryas and Papio anubis in Ethiopia, Kummer 1968; Kummer 1971) through tropical forests to high and northern regions that experience severe, snowy winters (Rhinopithecus roxellanae in China and Tibet, Napier and Napier 1967; Macaca fuscata in Japan, Izawa and Nishida 1963). Some primate species are considered to be virtually completely arboreal (e.g., the indriids, tarsiids, hylobatids, callitricids, and some colobines), while others spend the large majority of their waking hours on the ground (e.g., Papio spp. in savannah habitats, Theropithecus gelada, Gorilla gorilla berengei, Erythrocebus patas).

Primate species also exploit many different foods. Although many species can be classified as generalist omnivores that opportunistically feed upon fruits, flowers, seeds, leaves, grass corms, bulbs, gums, insects, eggs and small vertebrates, several primates have relatively specialized diets and select primarily insects, fruits and flowers, or foliage. Some callitricids and several of the small prosimians are primarily insectivorous (Hershkovitz 1977; Clutton-Brock and Harvey 1977). The atelines (spider monkeys), chimpanzees, orangutans and gibbons (Hylobates spp.)

rely most upon fruits for their subsistence (Rodman 1973; Rodman 1977; Chivers 1974; Ellefson 1974; Klein and Klein 1975; Wrangham 1977). To varying degrees, the colobine and *Alouatta* species feed primarily on foliage (Struhsaker 1975; Oates 1977; Milton 1980); these species have sacculated stomachs in which bacterial symbionts aid in the digestion of the large amount of cellulose in their diets (Bauchop and Martucci 1968).

What determines the size and kind of social group into which an infant is born? Over the last decade, research on primate foraging ecology and mating systems has helped to elucidate the adaptiveness and interspecific variation of primate social structures (Crook 1970; Crook 1972; Goss-Custard et al 1972; Rodman 1973; Clutton-Brock and Harvey 1976; Clutton-Brock and Harvey 1977; Clutton-Brock and Harvey 1978; Wrangham 1979; Wrangham 1980; Wrangham 1982). Recently, theorists have emphasized the significance of intrasexual competition and the relative importance of different resources for male and female primates. For female primates, and perhaps most other female mammals, relative reproductive success appears to depend primarily on females' success in garnering sufficient nutrition to support themselves and their offspring through successive periods of gestation and lactation (Dittus 1979; Altmann 1980; Cheney et al 1981; Wrangham 1981). In contrast, the reproductive success of males is primarily limited by factors that influence males' relative access to receptive, fertile females (Darwin 1871; Williams 1966; Trivers 1972). Hence, if primate social groups are primarily mechanisms whereby the reproductive success rather than the survival of individual adult males and females is maximized, then interspecific variability in group structure should reflect the species-typical optimal foraging strategies of females and optimal mating strategies of males (see Wrangham 1979; Wrangham 1980; Wrangham 1982).

Recent reviews of primate social systems and foraging patterns have provided compelling evidence to support this developing perspective on the evolution of primate social groups. Wrangham (1980; Wrangham 1982) and Moore (in press a) suggest that primate species should be classified with regard to the degree of female transfer that occurs between social groups. In "female-bonded" (Wrangham 1980) or "not-female transfer" species (Moore in press a), most females

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mature, reproduce, and live out their entire lives in their natal groups. Wrangham (1982) suggests that extended kin groups of primate females coalesce under conditions that favor large groups with a competitive advantage over smaller groups at valuable food sources that are either sparsely distributed or unpredictable in occurrence. Males in these species emigrate from their natal groups as adolescents and may continue to migrate between groups as adults (Packer 1979a). Emigration of adolescent males may function to mitigate intrasexual competition among males (Dobson 1982; Moore and Ali in press) and to reduce the probability of inbreeding (Bischoff 1975; Packer 1979a; Packer 1979b).

Most species of the cercopithecine monkeys (e.g., savannah baboons, mangabeys, macaques and guenons) exhibit female-bonded social organization. In these species, social relations among adult females are highly differentiated; affinity is more salient among female kin and their offspring than among unrelated females in these societies (Sade 1965; Sade 1972; Kurland 1977; Nash 1978b). Female dominance rank is generally matrilineally "inherited" (Kawai 1958; Sade 1967; Hausfater et al 1982), and it plays an important role in intragroup competition (e.g., Wrangham 1981). Dominance relations among matrilineal females are often stable over periods of many years (Hausfater et al 1982; Bramblett et al 1982).

Adult male membership is variable among female-bonded groups. In groups of red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*), a single male holds tenure for a period of time until he is replaced by an immigrant (Struhsaker 1977; Rudran 1978; Struhsaker and Leland 1979; Butynski 1982). Groups of these monkeys maintain territories by excluding from their ranges conspecifics that are not group members. Both females and males repulse invading conspecifics (Struhsaker and Leland 1979); however, additional research is needed to confirm that, in doing so, females defend their local food resources, while males prolong their tenure as reproductive males. In many other cercopithecine species, several fully adult males typically reside within social groups. In vervets, macaques, baboons and mangabeys, males maintain relatively unstable dominance relations among themselves, and high-ranking males have greater access to estrous females than do other males under some conditions (Hausfater 1975; Packer 1979a, Packer 1979b; Struhsaker and Leland 1979; Smith 1981; Rowell and Richards

1979; Strum 1982; Robinson 1982). Most multimale, female-bonded primate social groups do not defend territorial boundaries, but sometimes compete for localized sources of food. Finally, the available data are insufficient to determine whether some of the cebid species live in female-bonded groups (Oppenheimer 1968; Defler 1979; Defler 1982; Moore in press a).

The majority of female-transfer primate species subsist primarily on low-quality, abundant and evenly distributed food sources and live in smaller social groups than do female-bonded species (Moore in press a). Because of a considerable amount of female migration between social groups, a smaller proportion of adult females in these groups are closely related to one another than in the groups of female-bonded species (Wrangham 1980; Wrangham 1982; Moore in press a). Chimpanzees (Pan troglodytes), gorillas (Gorilla gorilla berengei), howler monkeys (Alouatta palliata and A. seniculus), hamadryas baboons (Papio hamadryas), bonnet macaques (Macaca radiata), the white sifaka (Propithecus verreauxi), and the colobines (Colobus and Presbytis spp.) have been characterized as female-transfer species (see review by Moore in press a). In several of these species, both affiliative and agonistic social relations appear to play less pervasive roles among adult females than among the females of female-bonded species (McKenna 1981; Kummer 1968; Harcourt et al 1976; Struhsaker 1975; Struhsaker and Leland 1979; but see also Jones 1980).

Female-transfer primate groups also contain either one or many adult males. In those cases in which only one male occurs and where day ranges are small (e.g., Colobus guereza, some populations of Presbytis entellus), the male defends the range of a group of females from invasion by other adult males. In other species in which long day ranges or other aspects of a species' behavioral ecology preclude territorial defense, a group male locally guards his females from the advances of other males (Gorilla gorilla berengei, Papio hamadryas, some Presbytis spp.). In other female-transfer species, males form kinship groups that are, in fact, the cores of their social groups (e.g., Colobus badius, Pan troglodytes and perhaps Macaca radiata, see Wade 1979; Shively et al 1982). Male chimpanzees rarely emigrate from their natal groups, and they aggressively defend their large

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territories from invasion by neighboring males (Bygott 1979; Goodall et al 1979). Red colobus monkey males discourage other males from joining their group by keeping them on the periphery (Struhsaker 1975; Struhsaker and Leland 1979; Marsh 1979).

Two other types of primate social systems exist: "solitary" life, which is typified by the nocturnal prosimians (galagidae, tarsiidae, lorisidae, Microcebus murinus and others) and the orangutan (Pongo pygmaeus), and monogamy, as exemplified by the hylobatidae, the callitricidae, Indri indri, Lemur mongoz mongoz, Aotus trivirgatus, and Callicebus species. Females of the "solitary" species generally range alone or in the company of their infants and juvenile offspring. There is, however, considerable evidence that the social interactions that do occur among the females of these species most frequently involve close relatives (see Rijksen 1978; Galdikas 1979; Charles-Dominique 1977; Clark 1978). Males' ranges are typically larger than those of adult females and they include the ranges of more than one female. As in those species discussed above, males in these species either maintain territories about some females' ranges (prosimians, Charles-Dominique 1977) or repulse other males primarily when females within their ranges come into estrus (orangutans, Rodman 1973; MacKinnon 1974).

In monogamous species, there is little or no sexual dimorphism, and the adult male and female of each group share the duties of parental care and territorial defense (diurnal species). Both male and female offspring disperse from their parents' range during juvenescence or adolescence, and dispersal often follows heightened aggression from parents toward offspring (Chivers 1974; Ellefson 1974; Tenaza 1975; Neyman 1977; Dawson 1977; Epple and Katz 1980; Tilson 1981). Tilson has described the process whereby gibbon parents (Hylobates klossii) help offspring to establish separate ranges.

In view of the compelling evidence from other primate species that females aggregate or disperse in response to the distribution, quality and abundance of food, and that male dispersion is a function of the distribution of adult females, the most likely cause of monogamy in primates is that females in these species are incapable of successfully

raising offspring on their own or that parental investment by males leads to substantially increased female fecundity (see Kleiman 1977; Kleiman and Malcolm 1981). Under these conditions, a male could most readily increase his relative reproductive success by helping to ensure the survival and reproduction of his offspring. It is widely believed that for precisely this reason the vast majority of avian species are monogamous at least during breeding seasons (Lack 1968).

A critical implication of past field research is that not only across species, but also across generations within species, immature primates can experience radically different social and ecological environments during their prereproductive years of development (Altmann and Altmann 1979). Additional field research is needed to discover the range of environmental conditions that are faced by various species and to elucidate the effects of different conditions on the development of behavior. Quite possibly, social, demographic and ecological conditions that exist during prereproductive development play important roles in determining the reproductive tactics that are exhibited by individuals upon attaining sexual maturity (see e.g., Harcourt and Stewart 1981; Draper and Harpending 1982).

Maturational Transitions and Phases of Development

Review of the literature reveals confusion of terminology and little consensus or even attention to diagnostic criteria that would facilitate comparative study of behavioral development across Primates and across Mammalia. To develop a comparative perspective, it will be useful to define developmental phases of broad applicability among mammals, despite the difficulties to doing so. This is not the same as saying that mammalian development proceeds in spurts or discrete stages between which there is little ontogenetic continuity; longitudinal study of development in any primate species unequivocally belies that notion. This chapter highlights the actual continuity of primate behavioral development. However, for primates it is also clear that the processes of maturation and socialization bring about several major changes in conditions of existence within the lifetime of an individual, changes that require considerable and often dramatic reorganizations of behavior. We refer to the developmental phases between these transi-

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tions as infancy, juvenescence, adolescence and adulthood. After these phases are briefly characterized below, each is detailed in the following sections of the chapter.

In the primate literature, there exists the implicit tenet that infancy is that period during which the individual is directly dependent on its mother and other possible caretakers for survival. We take this as our definition. Primate infants use their parents as sources of nutrition, warmth and transportation. Their mothers also provide secure bases for infant exploration to which infants return when their activities and encounters lead them to become agitated (Baldwin and Baldwin 1977). The infant can depend on its mother to protect it from inclement weather, predators, threatening conspecifics, rough-housing juveniles, and clumsy allo-mothers.

A mammalian youngster is no longer considered an infant when it attains the capacity to survive the death of its caretakers; generally, for primates, this means that the youngster is able to provide adequately for its own nutrition, thermoregulation and movement within the environment. In addition to daily foraging and travel with their social group, the predominant activities of juvenile primates include exploration of the environment and social play with age-peers and/or siblings. Although young juveniles no longer sleep with their mothers, they maintain relatively close relationships with them, which is evidenced by the relatively frequent grooming that the juveniles receive from their mothers. In some species young juveniles' relationships with particular adult males, established during infancy, may promote survival (e.g., Stein 1981; but cf. Dittus 1979). Throughout juvenescence, more complex forms of social interaction begin to occur with age-peers, older and younger immatures, and adults. As juveniles mature, sexual diethisms develop and feeding competition and agonistic relations with adults of both sexes play increasingly significant roles in their lives.

The beginning of adolescence is marked by puberty, and this developmental phase lasts until individuals attain the capacity to reproduce. For males, this entails the ability to impregnate an adult female when given opportunities to copulate; for females, adolescence ends with the birth of a live infant, or attainment of the capacity to bring a viable

pregnancy to term. Data on the behavioral changes that coincide with puberty in primates are few. Studies of captive, group-living adolescent male chimpanzees (Kraemer et al 1982) and rhesus monkeys (Rose et al 1978) have revealed interspecific differences in changes of aggressive and sexual behavior during adolescence that are concomitant with the attainment of high levels of circulating testosterone. Free-living adolescent female baboons and chimpanzees become attracted to adult males, particularly those that are unrelated or unfamiliar to them. The sexual behavior of adolescents becomes more effective as adolescence progresses, despite the fact that adolescents' sexual interactions are inhibited in most species by like-sex adults in natal groups. In every species, adolescent or young adult males or females or both emigrate from their natal group or ranging area, except in those species in which dispersal sometimes occurs earlier, during juvenescence (e.g., Pongo pygmaeus, Rijksen 1978; Saguinus oedipus, Dawson 1977; Neyman 1977; Galago demidovii, Charles-Dominique 1977).

This chapter reviews information on behavioral development from birth to adulthood in free-living nonhuman primates. Much field work has been done on infant behavioral development in primates, whereas few comprehensive studies of juvenile or adolescent development have been conducted. Consequently, the following sections provide an overview of important issues for infant behavioral development, and summarize, with greater attention to detail, information on primate juvenescence and adolescence from studies of particular aspects of these developmental periods. This information is supplemented where necessary, with data from research conducted on captive social groups of primates. Throughout this review, emphasis is placed on the major conceptual issues that have emerged from the past twenty-five years of field work on primate behavioral development.

INFANCY

Infancy begins dramatically with birth. Although no developmental transition thereafter occurs so conspicuously for primates, we can mark the end of infancy by a youngster's ability to survive without specific, directed provision of care, especially in the realms of nutrition and transportation. During juvenescence, the immature animal's survival and development continue to be enhanced by other

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group members; but this enhancement is increasingly through the general protection afforded by group-living and through selected opportunities for association and for observational learning. It is during infancy, in contrast, that survival depends additionally on regular and frequent direct feeding, carrying and protection, activities that are energetically costly, sometimes dangerous, and usually performed only by relatives, most commonly by mothers.

In natural populations, the period of infancy corresponds closely with the interbirth interval. Without food provisioning by humans, this period lasts from less than a year in some of the smallest prosimians and New World monkeys (see Charles-Dominique 1977; Hershkovitz 1977) to four or five years in the great apes and humans (Draper 1976; Konner 1976a; Clark 1977; Horr 1977; Rijksen 1978; Fossey 1979). In all these species, however, the period of direct parental support is longer than in other mammals of comparable size and involves relatively extensive forms of investment on the part of parents. Nonetheless, infancy remains the life stage of highest mortality for primates, as it is for all mammals (Eisenberg 1981); most individuals die before reaching adulthood and at least half of those deaths typically occur during infancy. It is within this context of high mortality that the adaptive importance of the behavior of infants and their caregivers comes into sharp focus.

Nutrition

Neonatal primate infants are physically unable to obtain, and in some cases to digest, the foods that constitute the diets of older species members. They require special foods that must be provided for them. While gestation and lactation are mechanisms whereby all mammals provide for fetal and infantile nutritional needs, many carnivorous mammalian parents regularly supplement infants' milk with whole or partially-digested foods (Schaller 1972; Kruuk 1972; Mech 1970; Frame et al 1979; Rue 1969; Kleiman 1977). No nonhuman primate parents have been observed to contribute significantly to their offsprings' nutrition in such ways; nor is the investment asymmetry of gestation and lactation compensated for by males providing mothers directly with food in any nonhuman primate species, as is common in some other taxonomic groups such as birds (Skutch 1976). Thus,

for most primate females, motherhood entails the full responsibility of providing for their infants' nutrition. In some monogamous species, however, males establish and maintain feeding territories to which unmated females are attracted (e.g., *Hylobates klossii*, Tenaza 1975; Tilson 1981).

The general primate pattern is for a female to produce a low-lipid, low-protein milk which necessitates frequent nursing (Jenness 1974). The single infant, born with strong grasping ability, accomplishes frequent nursing by clinging and riding on its mother's ventrum throughout her daily travels. Use of nests or "parking" of infants for considerable periods occurs primarily among nocturnal prosimians with small ranges and for whom multiple births are common (Charles-Dominique 1977). Most other primates live in social groups and range over larger areas than do solitary or monogamous species. They do not return to a "home site" repeatedly during the day, nor do they regularly return to the same single sleeping site on successive nights, making visitation to nest sites impractical. Thus, the provision of nutrition and transportation are closely linked for most primates, perhaps more so than for any other group of placental mammals (but see discussion of anthropoid exceptions below).

Irrespective of the differences in developmental time scale among primates, for each species there is a long overlap between the age at which the infant first experiments with solid food and the age at which weaning is complete. The transition from a milk diet to one consisting entirely of solid foods is a gradual one that occupies all except the earliest period of infancy (e.g., Richard 1976; Pollock 1977; Sussman 1977; Fossey 1979; Nicolson 1982). The weaning process itself is also gradual; the age at which the primate infant is first rebuffed from the nipple is often less than half the age at which weaning is complete (Struhsaker 1971; Clark 1977; Pollock 1977; Fossey 1979; Altmann 1980). Complete independence from mother's milk often does not occur in primates until the latter part of a mother's next pregnancy (Clark 1977; Rijksen 1978; Fossey 1979; Altmann 1980). This long period of infantile dietary overlap allows for quantitative adjustments, or fine-tuning, in the amount of milk a mother provides. A mother may increase the amount of suckling she allows, for example, if an infant becomes ill or if environmental conditions worsen

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(Altmann 1980). Simultaneously, sufficient time is made available for infants to learn the different foods that become available in each season and to develop the requisite skills for obtaining, and the digestive tolerance for assimilating, those foods.

The percentages of time spent suckling and spent in contact with a caregiver decrease regularly over time. In the few cases for which comparable data are available from different environments, these parameters seem to be relatively invariant across populations during the first portion of infancy (vervets Struhsaker 1971; Lancaster 1972; baboons Rowell et al 1968; Owens 1972; Nash 1978a; Altmann 1980; Nicolson 1982). The rate of acquisition of independence during early infancy may be limited by fairly invariant neurological or neuromuscular development (see Hines 1942). Within these populations, however, independence is probably further constrained for some young infants by social factors. The greater protectiveness and restrictiveness of socially low-ranking baboon and macaque mothers sometimes results in a slower rate of independence acquisition in their infants, which, in turn, may be associated with a delay of the mother's subsequent reproduction (Rowell et al 1968; Altmann et al 1978; Nicolson 1982).

It is after the first part of infancy, when infants become semi-independent, that ecologically relevant factors such as the length and speed of the day-journey, the environmental substratum, and the availability of "weaning foods" (Altmann 1980) may appreciably affect the rate of development of all infants and consequently affect the timing of their mothers' next reproduction. For example, Schaller (1963) observed that gorilla mothers encourage their infants to move onto surrounding vegetation early in life. Fossey (1979) has described an early mode of locomotion in gorilla infants, which she calls "rump-clinging", that introduces the infants to semi-independent terrestrial locomotion before one year of age. In contrast, the arboreal orangutan mother carries her infant almost constantly until about two and a half years following birth and does not begin to encourage her infant to explore its environment on its own until the infant is about two years-old (Horr 1977; Rijksen 1978; see also Chalmers 1972).

Other behavioral measures of infant independence may be both more closely related to phyletic differences and more sensitive to changes in the physical and social environment than is contact or suckling time *per se*. For baboons (*Papio anubis*, *P. cynocephalus*), the only species for which data are available, there are developmental changes in the way that infant contact and nursing are coordinated with a mother's other daily activities (Altmann 1980; Nicolson 1982). Changes in infant size, activity level and vulnerability change the compatibility between a mother's various maintenance activities (e.g., foraging, rest and grooming) and infant suckling, and change the costs and benefits of these activities for both mothers and their infants during development (see Altmann 1980; Altmann 1983 for a more complete discussion of these behavioral contingencies). About midway through infancy, baboon mothers restrict infant suckling primarily to periods of rest or social grooming. The baboon data suggest that subsequently infants become very sensitive to changes in their mothers' activities and modify their own behavior in accordance with these changes (Altmann 1980; Nicolson 1982; see also Berman 1978 for macaques).

During developmental periods in which mothers change the contingencies between their own and their infants' behaviors, infants experience appreciable psychological trauma. This trauma has probably been mistaken in some earlier research on primate mother-infant relations for weaning trauma. In Amboseli baboons, mothers' activity budgets do not, in fact, limit the contact time (roughly, the suckling time) of older infants; mothers reject their infants' suckling attempts primarily when these attempts do not conform to the new "rules" for suckling that the mothers make (Altmann 1980). We have speculated that an infant's learning of behavioral contingencies made by its mother may form an important model for the developing youngster's later social learning and behavioral coordination with others. Because the contingencies involve the mother's maintenance activities, their forms and occurrence in other generations, populations and species probably depend on environmental variability.

The time interval between nursing sessions is another non-traditional behavioral measure that may be of particular biological importance developmentally, as is suggested by

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research with humans (Konner and Worthman 1980). Although the benefit that can be gained by an infant through suckling is probably proportional to the time spent suckling, as would be the immediate energetic cost to the mother, the effect on the mother's future reproduction, due to endocrine-mediated lactational suppression of ovulation, is probably a function of the length of the interval between suckling bouts. Consequently, environmental and behavioral factors that affect intersuckling intervals, and parent or offspring control of these intervals, may have major developmental ramifications. Because mothers devote different amounts of time to their various maintenance activities, and because the time devoted to each occurs in bouts of different length (Post 1981), restrictions of an infant's nipple access to certain of its mother's activities will affect the length of both suckling bouts and the intervals between bouts. Recently, data for baboons was collected to examine these relationships (J Altmann unpub. data).

Transportation

Most young primate infants are carried during all of their mothers' activities. Infants cling to their mothers' ventrums, suckling at will, and view the world, social and ecological, virtually through their mothers' eyes. Opportunities for observational learning abound, and in this position of intimate contact the infant probably also becomes sensitive to its mother's tension or calm in social and other situations and becomes conditioned to those contingencies (see Loy and Loy 1974; Berman 1978; Berman 1980). One cannot help but speculate on the consequences of the modal patterns of infant care that are practiced in contemporary industrial societies which result in infants spending long periods out of contact with others and out of touch with the world and society that they are to join (Bronfenbrenner 1979; Kaye 1982). How much behavioral continuity and intergenerational transmission is lost thereby? How much more aggressive must an infant be to make its needs known?

The major nonhuman exceptions to constant maternal transport occur among those prosimian primates that leave their young "parked" in nests or in foliage near sequential feeding sites, and among the small, monogamous New World

monkeys in which fathers and siblings provide most of the transportation for their multiple offspring (Mason 1968; Epple 1975; Charles-Dominique 1977; Fragaszy et al 1982). Both of these systems result in less frequent nursing opportunities for the infants. Also, mothers are spared the energetic costs of transporting their infants.

The family-care system of the monogamous primates results in a very small and compact social group, and it may be appropriate for primates only when the home ranges of individual females must be defended as territories, or when, for this or for other reasons, female fecundity is radically enhanced by assistance from an adult male (see Sussman and Tattersall 1976; Wright 1978 for instances of non-territorial primate monogamy). Relatedly, large litter weight is associated with paternal transport in some taxa: among the callitricidae, the greater the litter weight at birth relative to mothers' weight, the earlier paternal transport begins (Kleiman 1977).

Among the larger monogamous primates, paternal transport of infants is variable. Whereas siamang fathers take over infant transport after the first third of infancy and carry infants into their early juvenile period (Chivers 1974; Alberts 1983), none of the adult male gibbons have been observed to provide transportation for their offspring in the wild (Carpenter 1940; Ellefson 1974; Tenaza 1975). Nor does the monogamous male *Indri indri* carry his infant offspring; however, following weaning, some young juvenile indris begin to sleep with their fathers at night (Pollock 1977).

As the young primate infant matures, it initiates breaks in contact from its caretaker. The first explorations occur when its mother (or father) is stationary, and later infants leave during foraging or group progressions, thus beginning to provide some of their own transport. However, independent infant locomotion begins while the infant is still totally dependent on its mother nutritionally, and consequently this apparent infant independence actually occurs at an energetic cost to its mother (Altmann 1980; Altmann 1983). This energetic cost may be one that a mother cannot afford under severe conditions, and in any case this partial locomotor independence involves a short-term cost with the "promise" of the long-term payoff of

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offspring independence, the "goal" of development for both parent and offspring. This is but one example of a behavior that is performed at an appreciable, short-term energetic cost that is offset by an important long-term benefit. Many behaviors may be of that sort during development, as Fagen (1977; Fagen 1981) has argued is the case for social play.

Protection from the Elements, Conspecifics and Predators

Persistent contact between the primate infant and its caregiver mitigates several potential threats to the survival of the small, weak and inexperienced infant. In animal species without multiple births and without dens or nests, thermal protection and thermoregulation could be major problems for small and slowly growing young (Galef 1981). The primate infant is protected from the cold at night by sleeping huddled with its mother. During hot afternoons in the glare of the equatorial savannah sun, a young baboon infant is protected from direct sunlight by its mother's body as it sits or rides ventrally. Older infants seek, and even compete for, the shade produced by larger animals, usually particular adult male associates. When its next sibling is born or if it is orphaned (Harding and Manziollo 1981), the baboon youngster usually seeks an older sibling or an adult male associate as a sleeping partner. In sudden downpours of rain, otherwise independent youngsters often run to huddle with their mothers, other family members or adult male associates (Altmann 1978; Altmann 1980).

In many group-living primate species, some conspecifics are potential threats to the well-being of infants through harassment, kidnapping, and even killing (Hrdy 1979; Altmann 1980; Busse and Hamilton 1981; Butynski 1982; Pereira 1983; Hausfater and Hrdy 1984). Whereas infanticide resulting from severe wounding or direct killing is caused most often by newly immigrant males, harassment and kidnapping are usually committed by unrelated female group members. In hierarchically-organized female-bonded groups, this threat is greatest to the infants of low-ranking mothers. Infants seem to learn from their mothers' restrictiveness and fear responses to avoid dangerous group members and to run back to their mothers at the approach of these individuals. Baboon neonates whose mothers are particularly restrictive

continue to stay in greater contact with their mothers for many months after their mothers' restrictive behavior has ceased (Altmann 1980; Nicolson 1982).

Predators, too, contribute to the high mortality of infancy. By maintaining contact or close proximity to its caregiver, a primate infant can benefit from the older animal's knowledge and experience, resulting in appropriate response and rapid flight when necessary. The advantages of immediate safety are thus supplemented by valuable learning for the times later in life when the youngster will have to fend for itself. The effectiveness of maternal protection in Amboseli baboons has been demonstrated by the virtual absence of deaths of young infants by predation except in cases where the mother has also died. In contrast, predation has been the probable cause of death for a number of older, fairly independent, infants and young juveniles (Altmann, Altmann and Hausfater unpub. data). Even after baboon youngsters are transported in no other situation, their mothers or associated adult males sometimes carry them to safety during attacks by predators. However, these immatures are not always sufficiently near a protector at the time of an attack to find help rapidly amidst the ensuing frenzy.

From Infancy to Juvenescence

The infant's transition to becoming a young juvenile involves obtaining its own food, keeping up with group travel and avoiding potentially dangerous conspecifics and predators unaided. These skills are not necessarily acquired at the same pace; when information becomes available from a number of species, the order of acquisition of various proficiencies might be found to differ among species. The various regimes of physical and behavioral maturation among primates, each influenced by particular opportunities for observational learning and for practice, surely determine rates of skill acquisition; but comparative studies focused on these aspects of behavioral development have yet to be conducted.

As the infant achieves competence in providing for its immediate daily survival, it also begins to develop those social and physical skills that it will need as a juvenile

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and, ultimately, as an adult. Prior to attaining nutritional independence, the infants of every primate species that has been studied begin to exhibit some of the behaviors and displays that characterize their species' behavioral repertoire, such as particular styles of greetings, leaping and branch-shaking displays, yawn and brow-stare threats, and some stereotypic vocalizations (see e.g., Chevalier-Skolnikoff 1974).

Primate sociosexual behavior begins during infancy (Goodall 1967; Owens 1976). Midway through infancy, baboons begin to present their hindquarters to other group members and to mount one another (Owens 1976; Young et al 1982). The large majority of infant males' mounts are disoriented; however, the proportion of their mounts of other males decreases while they more frequently mount immature female peers. Mounting by immature females wanes throughout infancy, and during their second year of life, females begin to present more frequently than their male peers (Ransom and Rowell 1972; Young et al 1982).

Older infants also begin to perform social grooming; at this stage an infant's grooming is often briefly directed to its mother as the infant attempts to gain nipple contact (Sade 1965; Altmann 1980). However, infants do begin to groom themselves, their siblings, their peers, and others, occasionally and briefly, as soon as their neuromuscular development allows them to perform the rudimentary movements that are involved in this behavior (Hines 1942). But, throughout infancy, their grooming relations with others are overtly asymmetric because older group members are often willing to groom infants, whereas the infants are primarily willing to receive -- until something else catches their interest, such as an age-peer, an insect or their mother's location and activity. Most of the literature cited in this section includes brief accounts of the onset of infantile grooming.

Although components of agonistic behavior appear in the infant primate's behavioral repertoire, aggressive behavior directed by infants toward other group members is very rarely seen (see Berman 1978; Berman 1980; Berman 1982a; Berman 1982b). Dominance patterns and some other behavioral sex differences sometimes emerge by the end of human and nonhuman primate infancy (see Kummer 1968; Owens 1972; Loy

and Loy 1974; Maccoby and Jacklin 1974; Bjerke 1981); however, even in highly dimorphic species such as baboons, most such differences are seen primarily later in development.

Increasingly, the older infant engages in both solitary and social play and in exploration. Group members that were first encountered while the infant's world was centered primarily on its mother now become the focus of the young juvenile's social life. Most important are the age-peers that are available to the youngster, along with siblings and the younger of older unrelated juveniles; a sibling or a large peer group may even have hastened the onset of nutritional independence for the youngster (Hansen 1966; Kaufmann 1966). Although the rising juvenile will long maintain important social ties with its mother, following weaning the young primate initiates its life as a unique member of its community.

JUVENESCENCE

What Is a Juvenile?

The definitive characteristics of mammalian juvenescence regard survivability and reproductive capacity: juveniles are prepubertal individuals that are no longer dependent on their mothers (parents) for survival. By weaning, immatures are no longer dependent on their mothers' milk as a source of nutrition, and commonly they require no further transportation or thermoregulatory support. In some species, a brief period of dependence follows weaning during which specialized skills must be learned from a parent (e.g., in some predators; see Schaller 1972 on behavioral development in cheetahs, *Acinonyx jubatus*, and Murie 1936; Murie 1944; Rue 1969 on red foxes, *Vulpes fulva*). Also, there is evidence from field studies of nonhuman primates that some degree of psychological independence must be attained before an immature primate can survive complete separation from its mother, and that this degree of independence is not attained in some species until after weaning (Clark 1977; Altmann 1980; Pusey 1983).

Juvenescence contributes substantially to the unusually long prereproductive period of development that characterizes most primate species, and it comprises an exceptionally

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large proportion of the estimated natural life-spans of primate species. Work by Cole (1954) highlights the evolutionary significance of protracted immaturity in primates. Cole demonstrated that a small change in the age of first reproduction could have a profound effect on a species' intrinsic rate of increase if all other life-history parameters remained unchanged (but see Mertz 1971). Analogously, a change in the age of first reproduction in a lineage within a species could have a large impact on the reproductive success of that lineage. Why, then, do primates live out 20 to 40 percent of their lives prior to attaining reproductive capacity?

Undoubtedly, different suites of selection pressures have resulted in extended periods of immaturity for various animal species. Presumably, in each case those individuals whose rate and form of development provide the highest age-specific survival rate and/or age-specific fecundity are among those that contribute the most progeny to subsequent generations (Fagen 1981; Wiley 1974b; Case 1978). There is some evidence to suggest that the selection pressures that led to a high degree of encephalization in primates simultaneously extended the period of primate immaturity (Sacher and Staffeldt 1974; Western 1979; Sacher 1982; Western and Ssemakula 1982). Sacher and Staffeldt (1974) revealed a strong correlation between neonatal brain weight and gestation length in placental mammals and suggested that, in general, the rate of mammalian somatic growth and development might be constrained by the developmental rate of the central nervous system. Also, species with high "encephalization quotients" (Jerison 1973), or high ratios of brain weight to mean mammalian brain weight for a given body weight class (Eisenberg 1981), typically exhibit delayed sexual maturation (but see Radinsky 1982).

Most researchers suggest that delayed sexual maturity in primates has evolved because it provides developing individuals the time required to learn about the complex contingencies of their societies and habitats prior to initiation of their reproductive efforts (see Gavan 1982). However, if the evolutionary increase in primate adult brain size entailed an increase in the proportion of the life-span during which critical aspects of brain growth and development occur, increasing adult brain size may have carried with it the evolutionary liability of delayed maturity (see

above). If the increase in adult brain size that has occurred during primate evolution is responsible for the increase in the prereproductive proportion of primate life-spans, then the importance of juvenile learning may not be so much a cause but more an important corollary of delayed maturity. From this perspective, natural selection should be expected to favor those individuals that "use their time wisely" during development by observing and learning from peers, older group members, and aspects of their environment. Thus, it appears that the advantages of increased learning and behavioral flexibility during both immaturity and adulthood have contributed both directly and indirectly to the evolutionary increase in the relative duration of immaturity in primates.

In contrast to the abundance of research that has been done on infant development and mother-infant relations in non-human primates, the ontogeny of primate behavior beyond infancy has been left relatively uninvestigated. This is particularly true for free-ranging primates. A few field workers (Cheney 1976; Pusey 1977) have focused on the intermediate developmental stages of immatures, and several have studied particular aspects of the lives of independent immature primates, such as social play, grooming, acquisition of dominance status and dispersal (see e.g., Sade 1965; Goodall 1967; Landcaster 1972; Missakian 1974; Wrangham 1979; Chalmers 1980; Walters 1980; Boggess 1982; Tilford 1982). However, at least four studies of juvenile monkeys living in natural social groups should add appreciably to our knowledge of primate juvenescence (Hayaki 1983, Japanese macaques; Pereira 1984, yellow baboons; Baker-Dittus in prep., toque macaques; Johnson in prep., olive baboons). Virtually all field work on juvenile nonhuman primates has been conducted with cercopithecine species; consequently, several of the conceptual issues that are discussed below have emerged primarily from consideration of cercopithecine life-history. The following discussion of primate juvenescence concludes by summarizing and comparing what is known about juveniles in some of the less-studied species.

The Tasks of Juvenescence: Survival and Preparation for Adulthood

For primates and many other mammals, early juvenescence, like infancy, is often a life stage of comparatively high mortality (Laws 1969; Laws and Parker 1969; Schaller

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1972; Blurton-Jones and Konner 1973; Sinclair 1977; Dittus 1979; Altmann 1980; Clutton-Brock et al 1982; Nicolson 1982). Whereas mothers and their infants cooperate to promote infant survivorship, young juveniles, lacking many skills and much experience, must provide all of their own nutrition and learn to recognize for themselves the resources and dangers of their surroundings. It is likely to be for this reason that mortality among savannah baboons and other primates remains particularly high following infancy into juvenescence, in spite of the advantages of group-living (Pulliam 1973). The limited available mortality data underscore the potential importance of the adaptiveness of juvenile primate behavior for promoting survivorship during the early juvenile years. Comparative data on behavior and survivorship during early juvenescence are needed for more natural primate populations.

Juvenescence in primates is also a period during which immature animals become progressively more independent members of their society. Primate infants are carried by and, later, follow their mothers into proximity with her associates (Altmann 1980; Berman 1982a; Berman 1982b); but juveniles determine for themselves the amount of time they spend in association and interaction with surrounding members of their group or population. Most immature primates live in social groups containing several individuals that differ in age, sex, dominance status, experience and temperament. Young juvenile primates should be expected to establish social relations with those conspecifics with whom they can most readily garner experience with species- and sex-typical maintenance and social behaviors and from whom they can learn about the social structure of their group or population. Even among the relatively solitary lorises and orangutans, a juvenile's chances of surviving and degree of future reproductive success are probably enhanced or diminished as a complex function of the patterns of social association and interaction that are pursued by the developing youngster (see Charles-Dominique 1977; Rijksen 1978). Juveniles that interact with conspecifics in a manner that enhances their chances of surviving and reproducing will be among those that are most likely to contribute progeny to subsequent generations. In short, the behavior of juvenile primates is expected to be adaptive not only to the extent that it enhances the survivability of the juvenile, but also to the extent that it prepares the developing individual for life as an adult of its sex and species.

Age Changes and Sex Differences in Juvenile Behavior: Baboons, Macaques and Vervet Monkeys

Our studies of the baboons of Amboseli, Kenya have suggested that the two primary "tasks" of juvenescence, survival and preparation for adulthood, are not problems of equal importance for young and old juveniles. Because young juveniles (one to three years-old) are subject to a high rate of mortality, whereas old juveniles (three to six years-old) constitute an age class with one of the lowest mortality rates (Altmann 1980; Altmann, Hausfater and Altmann unpub. data), the most successful individuals may be those that best employ behavioral tactics that safeguard them from important sources of mortality during their early juvenile years, and then develop and refine social skills later in juvenescence for use during adolescence and adulthood.

The very physical frailty and foraging ineptitude that render young juveniles susceptible to environmental hazards probably liberate them from some of the social hazards of life in their groups. For example, the stringency with which developing individuals are required to defer to adults is likely to increase with age because juveniles' abilities to compete with adult group members for food, space and other resources increase with age and size. The young juveniles of many primate species probably exploit the leniency that they experience from older group members by spending more time in close proximity with them than do older immatures, thereby gaining opportunities to feed at high quality food patches, to learn to identify and process different food items, and to acquire morsels that are discarded, rejected or overlooked by the adults. Younger juvenile baboons can also avoid feeding competition with older immatures or adult females by maintaining close proximity to adult males during feeding. Adult males that develop affiliative social relations with particular infants (see Ransom and Ransom 1971; Altmann 1980; Stein 1981; Nicolson 1982; Smuts 1982) later intercede on behalf of these individuals when the young juveniles are aggressed upon by others (Stein 1981; Pereira 1984).

Time spent in proximity to adults probably also serves to mitigate the dangers of unfamiliarity with other ecological hazards for young juvenile primates. Youngsters who spend time in close proximity to the older, more experienced

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members of their group can readily respond to the caution and alarm of these group members. Also, the adult males of some species sometimes retrieve older infants and young juveniles during groups' encounters with predators (Ransom and Ransom 1971; Ransom and Rowell 1972; Altmann 1980). Finally, young juveniles might, in fact, mitigate predator pressure by continually maintaining close proximity to any and all group members (Hamilton 1971). Data have been analyzed recently that describe whether age and sex differences exist in the social contexts during which baboon juveniles approach and spend time in proximity to adult and other group members (Pereira 1984).

For all primate species, the life-histories and adult social behavior of males and females differ to a considerable extent. These differences include patterns of dispersal and ranging, lifetime group membership, the social mechanisms of acquisition and maintenance of adult dominance status, and modes of parental behavior. Although these life-history differences have been well-documented, their significance for the development of social behavior in primates remains poorly understood. If the behavior of immature primates prepares individuals for lives as effective adults, we should expect to see differences in the developing social behavior of juvenile males and females that are related to differences in the social skills that are needed by the adult males and females of a species.

Below is reviewed from an evolutionary perspective, the literature on age changes and sex differences in the behavior of free-living juvenile primates. Some recent data on juvenile behavioral development in Amboseli baboons (Papio cynocephalus) are incorporated that allow going beyond a gross outline to some of the complex texture of development in this species.

Grooming Relations with Mother and Less-Related Adult Females. Both anecdotal and more systematic observations reported during the past twenty-five years of primate field research have consistently indicated that primate mother-offspring relationships normally persist far beyond infancy. Affiliative behaviors such as maintenance of close proximity, support during aggressive interactions, and mutual allo-grooming often occur between primate mothers and their offspring throughout offsprings' prereproductive development (Sade 1965; Struhsaker 1967; Goodall 1968; Miller et al 1973; Oki and Maeda 1973; Lindberg 1973; Chivers 1974;

Missakian 1974; Drickamer 1976; Cheney 1977; Cheney 1978a; Nash 1978b; Seyfarth 1980; Walters 1980; Walters 1981). In contrast, adult females much less frequently aid or groom immature group members other than their offspring (Sade 1965; Sade 1967; Cheney 1977; Cheney 1978a; Kaplan 1978; Massey 1978; Altmann 1980, Walters 1980; Walters 1981).

Field data collected recently from 20 juveniles of two baboon groups in Amboseli reveal age and sex differences in juveniles' grooming relations with their mothers as well as differences between juveniles' grooming relations with their mothers and their grooming relations with unrelated adult females. These data were collected during approximately 1000 hours of focal animal sampling (Altmann 1974) that were conducted throughout 1981; all subjects contributed comparable amounts of data for every half hour period between 0700h and 1800h, excluding the noon hour. Grooming episodes were initiated whenever one animal approached another and either began grooming or solicited and received grooming from the approacher. Grooming episodes were exchanges of one or more bouts of allo-grooming between two animals (Pereira 1984).

When juveniles groomed with adult females, they were disproportionately likely to groom with their mothers rather than with any of the 17 or 12 other adult females in the two groups. However, there were striking age differences in the extent to which juveniles focused their grooming toward their mothers. During weaning and the early juvenile period (one to three years of age), mothers were the partners for approximately 66 percent of youngsters' grooming with adult females (Figure 1; Table 1). In contrast, mothers were the partners for only about 35 percent of older juveniles' (three to six years of age) grooming with adult females. However, young juveniles' grooming relations with their mothers were less reciprocal than those between old juveniles and their mothers. Young juveniles were more likely than old juveniles to initiate grooming episodes by soliciting and receiving grooming (83 percent vs. 54 percent of young vs. old juveniles' episode initiations with mother median scores; see Table 1). Also, whereas mothers virtually never solicited grooming from young juvenile offspring, mothers initiated grooming episodes with old juvenile offspring by soliciting grooming 38 percent of the times. Finally, young juveniles typically performed about 11 percent of the grooming during episodes with their

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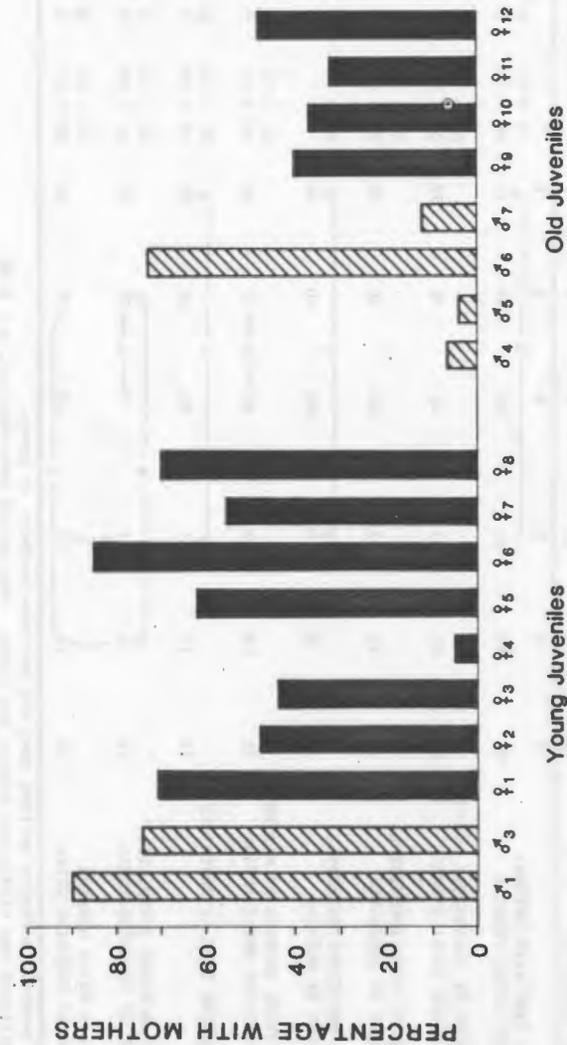


Fig. 1 Percentage of each juvenile's grooming time with adult females that was with its mother.

TABLE 1: Characteristics of Grooming Relations Between Juveniles and Their Mothers, Median Individuals' Scores.

NUMBER OF SUBJECTS*	YOUNG JUVENILES (YJ)		OLD JUVENILES (OJ)		A PRIORI HYPOTHESIS	RESULT
	MALES (M)	FEMALES (F)	MALES (M)	FEMALES (F)		
GROOMING TIME WITH MOTHER/ TOTAL WITH ADULT FEMALES	2	8	4	4		
	%	%	%	%		
	82	59	13	39		YJ > OJ OF > OM
INITIATIONS BY JUVENILES/ TOTAL EPISODE INITIATIONS	45	65	42	76		OJ > YJ OM > OF
JUVENILE SOLICITATIONS/TOTAL INITIATIONS BY JUVENILES	74	93	100	36		YJ > OJ OM > OF
MATERNAL SOLICITATIONS/TOTAL INITIATIONS BY MOTHERS	0	0	100	40		OJ > YJ
SOLICITATIONS REFUSED BY MOTHERS/ TOTAL OFFSPRING SOLICITATIONS	35	20	66	25		OJ > YJ OM > OF
MEAN GROOMING TIME BY JUVENILES/ EPISODE	11	17	36	65		OJ > YJ OF > OM
EPISODES IN WHICH JUVENILES DID ≥ 80% OF GROOMING/TOTAL	11	9	7	55		OJ > YJ OF > OM
EPISODES IN WHICH MOTHERS DID ≥ 80% OF GROOMING/TOTAL	90	79	60	28		YJ > OJ OM > OF

* - Two juvenile subjects omitted that did not have mothers in group.

a - Significant sex difference within age class: two-tailed Mann-Whitney, $p < 0.06$.

b - Significant age difference: two-tailed Mann-Whitney, $p < 0.05$.

c - Significant asymmetry in grooming relations: two-tailed Wilcoxon Matched Pairs, $p < 0.05$.

stages in every field of inquiry and because of frequent use of cross-sectional data to reconstruct species' natural histories. However, identification of alternative pathways in primate behavioral development and of flexibility within pathways is overdue. Age-dependent changes in modes of aggression, affiliation, courtship, mating, parenting, foraging and travel are all important candidates for future investigation.

Our brief sampling of parallels and contrasts between development in human and nonhuman primates has led to several interesting and important questions. As researchers begin to consult more frequently the literature from related fields of research, new perspectives and ideas will continue to flourish. The topics that have held center stage in past developmental research are not necessarily those of greatest importance to all human and nonhuman primates, nor to any particular species of interest. Rather, to a considerable extent, they reflect particular preoccupations of the academic disciplines and societies from which researchers emerge. An important benefit of cross-species research and cross-discipline communication will be a continuing identification of new research topics, especially, one hopes, those of primary importance to the lives of our research subjects.

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their knowledge of inter-individual social dynamics and their own social relations with adult females to employ nonaggressive reproductive tactics that gain them sexual consortships. The more powerful, but inexperienced young males are unable to predict the probable reactions and attractions among the adult members of their new groups, and cannot benefit from social relations they have yet to establish with the adult females.

Of course, an individual animal's experiences from birth to adulthood also have great potential to influence the development of adult behavioral tactics and strategies. Studies of experiential effects on prereproductive individuals have suggested that particular experiences during immaturity can lead members of some species to adopt different "ontogenetic trajectories" (Wiley 1981) that lead to different behavioral strategies later in life (see also Bekoff 1977; Draper and Harpending 1982). In other populations, frequency-dependent natural selection produces consistent proportions of individuals that exhibit different behavioral repertoires. Investigators studying insects (Alcock et al 1977; Borgia 1979), fish (Semler 1971), anuran amphibians (Wells 1977; Perrill et al 1978; Howard 1978), birds (VanRhijn 1973, Wiley 1974a) and some nonprimate mammals (Darling 1937; LeBoeuf 1974; Clutton-Brock et al 1982; Wirtz 1981) have begun to describe alternative life-history tactics among animals of different genotypes and/or phenotypes. Primatologists have the opportunity to initiate research into these developmental issues with species whose behavioral flexibilities are, perhaps, the broadest in the animal kingdom, and whose learning capacities most closely resemble our own.

Our knowledge of behavioral development during adulthood and of alternative life-history swaths in nonhuman primates is -- in its infancy. Future studies of adult male and female primates will benefit from employing developmental and lifespan perspectives. We predict that studying individuals from infancy through adulthood will consistently reveal proportions of species members that follow ontogenetic trajectories that do not conform to current conceptualizations of "normal" primate behavioral development. These alternative modes of development have undoubtedly been overlooked and underreported because of the appropriate preoccupation with modal patterns that typifies initial

TABLE 2: Characteristics of Grooming Relations Between Juveniles and Less-Related Adult Females (Mothers and Known Sisters Excluded). Median Individuals' Scores.

	YOUNG JUVENILES (YJ)		OLD JUVENILES (OJ)		A PRIORI HYPOTHESIS RESULT	
	MALES(M)	FEMALES(F)	MALES(M)	FEMALES(F)		
NUMBER OF SUBJECTS	3	8	11	4	5	9
MEAN GROOMING PER ADULT FEMALE (PER CAPITA)	7	7	7	7	7	7
INITIATIONS BY JUVENILES/TOTAL EPISODE INITIATIONS	1	2 ^d	2 ^d	5	5	5 ^d
JUVENILE SOLICITATIONS/TOTAL INITIATIONS BY JUVENILES	50	87	80	67	93	93
ADULT SOLICITATIONS/TOTAL INITIATIONS BY ADULT FEMALES	75	7 ^d	14	33	0	3 ^d
SOLICITATIONS REFUSED BY ADULTS/TOTAL JUVENILE SOLICITATIONS	0	0	0	0	80	55
EPISODES IN WHICH JUVENILES DID ≥ 80% OF GROOMING/TOTAL	50	60	55	92	88	92 ^d
EPISODES IN WHICH ADULTS DID ≥ 80% OF GROOMING/TOTAL	14	80 ^d	71 ^d	25	91	77
	86	19 ^d	21 ^d	30	0	0

a - Significant sex difference within age class: two-tailed Mann-Whitney, $p < 0.05$.

b - Significant age difference: two-tailed Mann-Whitney, $p < 0.05$.

c - Significant asymmetry in grooming relations: two-tailed Wilcoxon Matched Pairs, $p < 0.05$.

d - Significant difference from comparable score with Mother as partner: two-tailed Wilcoxon Matched Pairs, $p < 0.05$.

mothers, whereas old juveniles typically performed about 56 percent of the grooming during grooming episodes with their mothers (Table 1).

Juvenile baboons' grooming relations with less-related adult females in Amboseli differed dramatically from their grooming relations with their mothers (known sisters were excluded from these analyses; Table 2). The juveniles initiated 87 percent of their grooming episodes with these adult females (vs. 68 percent with mothers; two-tailed Wilcoxon Matched Pairs, $n=18$, $T=21$, $p < 0.05$), and only 9 percent of these 251 initiations were solicitations for grooming. Responses to these solicitations also differed. Whereas mothers refused only 29 percent of solicitations from their own juveniles, adult females responded to grooming solicitations from other juveniles by refusing to groom approximately 71 percent of the times (Table 2).

Groomer and groomee roles were unequally shared in most grooming episodes involving juveniles, and this asymmetry further revealed differences in relationships. In 91 percent of all complete grooming episodes observed between juveniles and adult females, one partner performed 80 percent or more of the grooming. Juveniles typically performed this majority of the grooming in episodes with other females (74 percent vs. 15 percent of episodes), but rarely did so in episodes with their mothers (16 percent vs. 67 percent of episodes; Tables 1 and 2).

Thus, young juvenile baboons continue to depend on their mothers for substantial proportions of the grooming that they receive. Moreover, young juveniles are not required to reciprocate much of this grooming; baboon mothers in Amboseli receive very little grooming from their young juvenile offspring and virtually never solicit grooming from them. As juvenile offspring mature, they begin to reciprocate most of their mothers' grooming, and mothers begin to solicit grooming from them to initiate grooming episodes. In contrast, unrelated adult females do not favor young juveniles during grooming interactions (as they do young infants; Altmann 1980; Nicolson 1982). In fact, if juveniles of any age engage in grooming with unrelated adult females, it occurs at the juveniles' initiative, and they perform the large majority of the grooming during those episodes.

cence; but rather, like adult growth in other mammal species (e.g., bovids, see Geist 1971), it slowly declines (e.g., Hopf 1979; Altmann et al 1981; Sackett et al 1982). Thereafter, important physiologic changes occur such as those that impair adults' abilities to rebound from injuries, illnesses and extraordinary exercise (see Fagen 1981). Also, throughout adulthood, experience accrues that enables individuals to accommodate changes in conditions of existence brought about by physical aging. For many primates, perhaps most mammals, at least three developmental phases of adulthood could be recognized that would comprise young, mature and aged individuals. Individuals in these adult developmental periods probably employ different behavioral tactics that exploit their respective strengths and mitigate their respective weaknesses in their efforts to survive and to enhance their relative fitnesses.

Savannah baboons provide an excellent example of different reproductive tactics used by young and mature-to-aged adult males. Following immigration, young males commonly assume relatively high agonistic dominance status (Packer 1979a; Strum 1982; Pereira 1983); however, under some conditions these males do not mate with the high frequency that would be predicted by dominance rank alone (Strum 1982; cf. Hausfater 1975; Packer 1979a). Strum (1982) recently reported a period of several months during which male mating success was only weakly related to agonistic dominance rank in a group of savannah baboons. Often in Strum's study group, the winner of a fight between adult males over access to an estrous female did not then consort with the female; sometimes, neither combatant but rather a third adult male took over consortship with the female (see also Packer 1977). Adult males that had been residents of the study group for several years garnered a disproportionately large number of the sexual consortships with estrous females.

Strum suggests that immigrant (young) and resident (mature and aged) adult male baboons employ different reproductive tactics, especially when dominance relations among adult males are unstable. The older, resident males are familiar with the social relations that exist among the adult members of their group and have established strong affiliative relationships with particular adult females (see Ransom and Ransom 1971; Altmann 1978; Altmann 1980; Smuts 1982). Strum believes that resident adult males exploit

Consideration of social structure and the importance of dominance relations during different phases of development in primate societies identifies several questions that deserve additional study in both human and nonhuman primates. Because adult females in many primate species do maintain significant dominance relations among themselves, we might expect that human females also tend to do so. What is the nature of adult female-female hierarchial interactions across species and cultures, and how are these relations established or foreshadowed during prereproductive development? Aspects of the development of dominance relations should be expected to differ across groups in which adult roles differ considerably and across environments in which immatures must compete for resources to different extents and at different ages. In undisturbed groups of children, girls are capable of dominating boys, and some are capable of dominating all of their peers (Missakian 1980; see also Strayer and Strayer 1980). But, how do the content and patterning of female-initiated agonistic interactions differ, if at all, from those of male-initiated interactions? Do they differ as a function of the sex of the aggression recipient and/or as a function of the type of resource over which competition occurs? Do children of the two sexes differ with regard to their attraction to or avoidance of the highest-ranking same-sex and cross-sex peers? Are males or females more likely to form a coalition in order to challenge a superior? Are these patterns aligned with adult sex roles and are they influenced by the intensity of socialization within a society? How do these ontogenetic patterns compare across species?

Behavioral Development during Adulthood and Ontogenetic Trajectories

Research on aging and adult behavior constitutes an entire subdiscipline in the study of human development (see e.g., Neugarten 1968), whereas behavioral development during adulthood has received virtually no attention from researchers of nonhuman primates. Traditionally, animal behaviorists have treated reproductive maturity as the end-point of behavioral development when, in fact, mammalian adults exhibit significant, if ever more gradual, behavioral changes over time. Several researchers have noted that primate body growth does not stop abruptly after adoles-

Previous research on free-ranging macaques and baboons has identified sex differences in juveniles' grooming relations with their mothers. Mothers groom their young juvenile sons and daughters equally frequently while sons reciprocate smaller proportions of their mothers' grooming than do daughters (Missakian 1974; Cheney 1978a). However, macaque mothers of old juvenile males groom their offspring significantly less frequently than do mothers of old juvenile females (Missakian 1974; see also Sade 1965).

The Amboseli data were examined for comparable differences. These data indicate that young juvenile male and female baboons spend similar amount of time grooming with their mothers, and, in general, experience similar filial grooming relations (see Table 1; Figure 1). Among old juveniles, however, females spent significantly more time grooming with their mothers than did males (two-tailed Mann-Whitney, $n, m = 4, 4$, $T = 10$, $p < 0.03$). Also, several aspects of the Amboseli data combine to reveal appreciably more reciprocity in the mother-offspring grooming relations of old juvenile females than of old juvenile males (Table 1). Daughters began 64 percent of the episodes that they initiated with their mothers by grooming rather than soliciting grooming. In contrast, every grooming episode initiation exhibited by old juvenile sons with their mothers was a solicitation for grooming ($n = 16$). Conversely, mothers initiated 60 percent of their grooming episodes with their daughters by grooming, whereas three of the four observed maternal initiations of episodes with old juvenile sons were solicitations for grooming. Mothers rejected 25 percent of their old juvenile daughter's solicitation attempts to initiate grooming episodes, while mothers of old juvenile males responded to their offsprings' solicitations by refusing to groom on 66 percent of the occasions. Finally, old juvenile females performed at least 80 percent of the grooming during 55 percent of their grooming episodes with their mothers, while old juvenile sons did so in only 7 percent of their episodes with their mothers.

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did their female age-peers in the two study groups (two-tailed Mann-Whitney, $n,m=2,8$, $T=18$, $p < 0.09$; Figure 1). In contrast, three of the four old juvenile males directed smaller proportions of their grooming with adult females toward their mothers than did all four old juvenile females that were studied (Figure 1).

In summary, the general developmental pattern is one of declining exclusivity and increasing gender differences in mother-offspring grooming relations. Also, with increasing offspring age and primarily with daughters rather than with sons, mother-offspring grooming relations become more stable and more symmetric. Mother is overwhelmingly a young juvenile's primary adult grooming partner in cercopithecine species, particularly for males. During this phase of development, youngsters initiate grooming episodes with their mothers by soliciting grooming, and they reciprocate little of their mothers' grooming. As juveniles mature, mothers remain the primary focus of juveniles' grooming with adult females; however, mothers now share a much smaller proportion of their offsprings' total grooming: old juveniles more frequently initiate grooming episodes with adults other than their mothers and with other immatures.

Interestingly, some features of the grooming relations of old juvenile male baboons with their mothers resemble mother-offspring grooming relations involving young juvenile offspring of either sex. Whereas older juvenile females' grooming relations with their mothers foreshadow daughters' futures as their mothers' peers and partners in reciprocal, affiliative social relations, old juvenile sons appear to strive to continue exploiting the simple role of offspring in their grooming interactions with their mothers. Older juvenile males and their mothers are less willing to perform the first bout of grooming in their grooming episodes with one another than are old juvenile females and their mothers, and, in general, the data suggest that mothers of old juvenile males protect themselves from the tendency of their offspring to reciprocate smaller proportions of their grooming. The frequency of grooming between baboon mothers and sons probably begins to decline as mothers more frequently refuse to engage in asymmetric grooming episodes with their sons.

Attainment of Dominance Status. As juveniles grow and gain experience, the degree to which the resources that they exploit overlap with those of adult group members increases,

certain ecological conditions. Dominance relations among male primates are likely to be most important in conferring differential access to estrous females. Competition among adult males is the probable evolutionary link between the propensities of human and nonhuman primate juvenile males to engage like-sex peers in physical competition. It is, in fact, unlikely that direct physical competition among human males within social groups for access to reproductive females has contributed appreciably to differential male reproductive success in most recent and contemporary societies (Durham 1976a; Larsen 1976; Alexander et al 1979; but see Dickemann 1979). But, throughout recent evolutionary history, the importance of males' aggressive and competitive proclivities for man's ability to wage successful war and thus appropriate other groups' resources (sometimes including females or at least pregnancies) has probably helped to perpetuate aggressive, competitive male children (and adults) in our species (Davie 1929; Chagnon 1968; Durham 1976b; Larsen 1976; Alexander et al 1980; Borgia 1980).

It is useful to recall at this juncture that chimpanzee community structure exhibits interesting similarities to the structure of patrilocal human societies. Chimpanzee communities are based on extended male kin groups that defend their large territories, and thus mating privileges, from infringement by non-resident males (Nishida 1979; Wrangham 1979). Males of a community sometimes even kill male intruders from neighboring territories (Bygott 1979; Goodall et al 1979). Social relations among males of a community are highly complex and are structured by degrees of consanguineal relationship (Bygott 1979; Bauer 1976; Tutin 1979). Females migrate between communities upon attaining sexual maturity and sometimes again during adulthood, and interact with one another much less frequently than do males (Bauer 1976; Nishida 1979; Pusey 1979; Pusey 1980; Pusey 1983). Interestingly, the nature of dominance relations among adult female chimpanzees, gorillas and humans remains poorly understood. As in chimpanzee communities and in many human cultures, female gorillas are the individuals that migrate between social groups (Harcourt et al 1976; Harcourt 1978); there is also some evidence that with age silverback (leader) males sometimes yield their leadership to a son (Harcourt 1978; Harcourt and Stewart 1981).

Consideration of social structure and the importance of dominance relations during different phases of development in primate societies identifies several questions that deserve additional study in both human and nonhuman primates. Because adult females in many primate species do maintain significant dominance relations among themselves, we might expect that human females also tend to do so. What is the nature of adult female-female hierarchical interactions across species and cultures, and how are these relations established or foreshadowed during prereproductive development? Aspects of the development of dominance relations should be expected to differ across groups in which adult roles differ considerably and across environments in which immatures must compete for resources to different extents and at different ages. In undisturbed groups of children, girls are capable of dominating boys, and some are capable of dominating all of their peers (Missakian 1980; see also Strayer and Strayer 1980). But, how do the content and patterning of female-initiated agonistic interactions differ, if at all, from those of male-initiated interactions? Do they differ as a function of the sex of the aggression recipient and/or as a function of the type of resource over which competition occurs? Do children of the two sexes differ with regard to their attraction to or avoidance of the highest-ranking same-sex and cross-sex peers? Are males or females more likely to form a coalition in order to challenge a superior? Are these patterns aligned with adult sex roles and are they influenced by the intensity of socialization within a society? How do these ontogenetic patterns compare across species?

Behavioral Development during Adulthood and Ontogenetic Trajectories

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counterparts (Emmerich et al 1971; Bee 1967; Bronfenbrenner 1970; Serbin et al 1973; Minton et al 1971), and that recent studies of children receiving little adult socialization have revealed little or no difference in the degree to which boys and girls exhibit aggression and become dominant (Blurton-Jones and Konner 1973; Draper 1976; Draper 1980; see esp. Missakian 1980; also Strayer and Strayer 1980). Draper (1980) has discussed some of the socialization processes that produce the common patterns of aggressive male and male-dominant-to-female in western societies; but much research on the etiology of dominance relations in human and nonhuman primate societies is needed.

Finally, researchers who design investigations of the development of dominance relations in primates should consider strongly what aspects of life for their species are affected most by dominance status. Investigators who have stressed the dominance of boys over girls in western societies may have overlooked more essential aspects of competitive social relations among children. What resources are most important to immatures of either sex? How does society influence the social contexts and ages at which attempts to exert dominance or control over others first appear in males and females? Although primate males are hormonally predisposed to exhibit aggression more readily than their female peers, in the absence of any limiting resource one might predict that conflict would not occur. Past observations of infant and juvenile monkeys support this expectation. Prior to weaning, aggression among baboon and macaque infants is infrequent and dominance relations often seem not to exist; following weaning, dominance ranks can be assigned among young juveniles on the basis of individuals' abilities to supplant peers at feeding sites (Pereira 1984). Once aggression among peers can influence survival via differential access to important resources such as food, dominance relations emerge among immatures.

The type of competition that will be most significant for males and females upon reaching adulthood might also affect the ontogeny of dominance relations among immatures. Studies of nonhuman primate societies have suggested that intrasexual competition is a crucial phenomenon underlying primate social behavior. Females grow to compete primarily over access to food because for them differential access to food can lead to differential reproductive success under

intensifying the competitive aspects of social interactions between adults and developing juveniles and increasing for juveniles the importance of acquisition of adolescent or adult social status. The cercopithecine system of social association among female kin and matrilineal dominance rank "inheritance" has been the focus of much primate field work. Several researchers have demonstrated that deployment of apparent altruism in cercopithecine social groups occurs primarily among closely-related females (Sade 1965; Sade 1967; Sparks 1967; Lindberg 1973; Oki and Maeda 1973; Seyfarth 1976; Drickamer 1976; Cheney 1977; Kaplan 1978; Massey 1977; Dunbar 1979; Walters 1980; Walters 1981). The primary altruistic behaviors that have been quantified include aid during aggressive interactions and the exchange of allo-grooming.

Whereas female age peers become dominant or subordinate to one another near the end of infancy in strict accordance with their mothers' relative dominance ranks (Loy and Loy 1974; Cheney 1976; Lee and Oliver 1979; Berman 1980), attainment of dominance status adjacent to adult female kin requires that a juvenile female reverse her dominance relations with unrelated adult females of families that are lower-ranking than her own. Cheney (1977) suggested that immature female baboons acquire their adult dominance status primarily by receiving support from their mothers during aggressive interactions with unrelated adult females of lower-ranking families. Walters (1980), examining data from Amboseli baboons, stressed that juvenile female baboons receive aid during agonistic interactions not only from their female kin, but also from unrelated higher-ranking adult females (see also Lee and Oliver 1979; Horrocks and Hunte 1983). He noted that female interventions in ongoing agonistic interactions nearly always support existing dominance relationships among matrilineal, and suggested that this pattern of support among unrelated females perpetuates the long-term stability of cercopithecine female dominance hierarchies (Hausfater et al 1982; Bramblett et al 1982).

Less attention has been paid to the changes in dominance status that occur during development for cercopithecine juvenile males. Lee and Oliver (1979) have provided some evidence that young juvenile male baboons initially assume the dominance rank of their mothers among adult females and eventually become dominant to all females in their group as they approach the size of adult females (see

Koford 1963; Loy and Loy 1974; Cheney 1976; Sugiyama 1976; Berman 1978; Berman 1980 for other baboon and macaque data). Within their peer group, juvenile male baboons and macaques may dominate all females or may assume ranks that are isomorphic with their mothers' relative ranks. Also, in some populations juvenile males differ from juvenile females by assuming relative dominance ranks among age-sex peers on the basis of age or size: males become dominant to slightly younger peers even when their mothers are low-ranking (Lee and Oliver 1979; Hausfater, Altmann and Altmann unpub. data; Pereira 1984; but see e.g., Koford 1963; Koyama 1967; Cheney 1976).

The available data suggest an important question for future research: what are the mechanisms whereby juvenile female macaques and baboons assume relative dominance ranks among age-sex peers that are isomorphic with those of their mothers and whereby juvenile males are often not as constrained by maternal dominance status, but sometimes attain dominance ranks among peers that are predicted by slight differences in their relative ages, sizes and strengths? It is possible that adult females begin to support subtly and perhaps even passively the young juvenile females from higher-ranking families (see also Horrocks and Hunte 1983). Juvenile females may be able to exploit adult females' propensities to intercede on the behalf of higher-ranking females during skirmishes (Walters 1980) by foraging near high-ranking adult females when juvenile females from relatively low-ranking families are also nearby. Conversely, juvenile females may strive to avoid foraging near high-ranking adult females when high-ranking juvenile females are also in close proximity. By employing these tactics, juvenile females might exploit immature females from lower-ranking families during feeding competition, reinforce their developing dominance status and avoid situations in which they would be at a competitive disadvantage. Juvenile females might also enhance the probability of receiving support from higher-ranking adult females by selectively greeting and grooming these females (Cheney 1976; Cheney 1978a; Cheney 1978b).

If the support of unrelated, higher-ranking females is critical to acquisition and maintenance of dominance status for cercopithecine females but not for their male peers, the social interactions of juvenile females with the adult females of their natal group should differ from those of juvenile males. Whereas juvenile females are expected to

parent insignificance and instability of dominance relations among the boys' female age-peers and stressed that these findings were fundamentally similar to dominance relations seen among the adult males and females of nonhuman primate societies (Edelman and Omark 1973; Omark and Edelman 1975; Waldrop and Halverson 1975; Savin-Williams 1977; Savin-Williams 1980; Savin-Williams and Freedman 1977).

There are several problems with this cross-species comparison. First, although some primatologists originally reported that dominance relations among female baboons and macaques were unstable and insignificant in comparison to dominance relations among adult males, unequivocal evidence has accumulated for all studied species in these genera demonstrating not only that dominance relations do exist among the adult females of these species, but also that these relationships are much more stable than those among adult males. Unfortunately, the myth of unstable and insignificant dominance relations among female primates, females that are primarily subordinate to males, has yet to be completely dispelled (see e.g., Cronin 1980). We refer the uninitiated reader to Hrdy (1981) for a review of adult female agonistic relations and the primate societies in which adult females are equal or superior to adult males with regard to dominance status.

Second, comparison of the dominance relations among the immature individuals of one species (*Homo sapiens*) to those among adults in others (nonhuman primates) is, at best, a difficult first step for comparative analysis. It is essential to compare first the dominance relations of the immatures in each group, and to make similar comparisons of the adults. As yet, however, comparisons between children and immature nonhuman primates are hindered by gaps in our knowledge for all species. Among baboons, as we discussed earlier, females appear to be socialized early in life to conform in their dominance relations with peers and with older group members to the established adult female social structure. Males, in contrast, are often liberated from this system and from a very early age are subordinate only to those group members that they cannot independently physically dominate. From this perspective, it is indeed interesting that past studies of children in western societies have shown that boys are more aggressive and more likely to try to dominate or disobey adults than are their female

which, in turn, produces a greater propensity toward aggression and competition among immature males than among their female peers. The interested reader should consult the excellent reviews that are available on behavioral sex differences in children (Freedman 1974; Maccoby and Jacklin 1974; B. Hamburg 1978; Ember 1981; see also Cronin 1980; Bjerke 1981).

Whereas the benefits from practicing fighting skills during juvenile play primarily accrue to males, both male and female juveniles gain experience with non-aggressive --communicatory, sexual and care-taking -- behaviors during play (see Dolhinow and Bishop 1970; Baldwin and Baldwin 1977). The children of industrial societies play at home-making, dining, dating, child-care, war, hunting, sports, cops-and-robbers, and teacher-and-pupil; similar games are seen in the play of children in preindustrial cultures. The learning of essential skills such as those used in hunting begins during children's play in hunter-gatherer societies. Among the Kalahari !Kung-san, young boys construct weapons with which they learn to hunt insects and small game; later, fathers make hunting accessories such as bows, quivers and arrows that are scaled down to an appropriate size for their sons' practice (Lee 1979).

Dominance Relations

Studies of the development of dominance relations among preschool children, older children and adolescents have increased steadily in number and quality since the early 1970's (see Omark et al 1980; see esp. Missakian 1980); throughout this period, research on free-living nonhuman primates has considerably influenced work in this area of child development. Early research on children in western societies demonstrated that boys are commonly more aggressive and more competitive than girls and that boys tend to be dominant to girls, although overlap between the "tougher" girls and the lower-ranking boys was not uncommon (see McGrew 1972; Edelman and Omark 1973; Omark and Edelman 1975; review by Maccoby and Jacklin 1974; see also Blurton-Jones 1967; Blurton-Jones 1972 for conflicting data). Several authors highlighted the pervasiveness and stability of dominance relations among boys from preschool age through early adolescence, contrasted these phenomena with the ap-

interact in ways that expedite their assimilation into the adult female social structure of their group, the social behavior of juvenile males should reflect greater independence from the hierarchical social relations among females.

Cheney (1976; Cheney 1978a; Cheney 1978b) studied the interactions of juvenile males and females with adult females in a small group of chacma baboons (*Papio ursinus*). Three of the four juvenile females that she studied groomed adult females other than those presumed to be their mothers at higher rates than did any immature male. Two of three juvenile females (the fourth was the apparent daughter of the highest-ranking adult female) directed appreciably greater mean proportions of grooming toward higher-ranking adult females than toward lower-ranking adult females. These three juvenile females were also found to play most frequently with the infants of high-ranking females, although the initiators of play bouts were unknown (Cheney 1976; Cheney 1978b). Juvenile males in this group more frequently groomed adult females that were lower in rank than females that were higher in rank than their presumed mothers (Cheney 1978a), and did not prefer infants of high- or low-ranking mothers as play partners (Cheney 1978b), but rather preferred to play with like-sex age-peers. There is need for data from other populations and species, and particularly from groups for which familial relationships are known.

Social Play. Several studies of social play in free-living macaques and baboons and in captive cercopithecines have shown that among these Old World monkeys immature males tend to play longer, more frequently and more roughly than do immature females (Hinde and Spencer-Booth 1967; Owens 1972; Owens 1975a; Raleigh et al 1979; Bramblett 1978; Symons 1978; Levy 1979; Chalmers 1980; Coelho and Bramblett 1982). Levy's (1979) study of the development of social play in the rhesus monkeys of Cayo Santiago provides the most detailed field data on primate play behavior to date (see also Symons 1978). Levy found that the frequency of play in immature rhesus macaques decreases continually between twelve months of age and adulthood. At every age, males were found to play more and to exhibit a higher proportion of wrestling bouts in their play than did their female peers; these differences between male and female players increased with age. Play between males was characterized by a higher proportion of contact time than was play between females, and a higher proportion of males' contact

time consisted of "rough" styles of contact. Males were the initiators of most mixed-sex play bouts. Finally, the play of older immatures was found to "breakdown" into true aggressive interaction more frequently than play between younger partners; this was particularly characteristic of play between males.

Most of the investigators that have gathered play data from free-ranging baboons have not been primarily concerned with age and sex differences of the sort discussed by Symons (1978) and Levy (1979) for rhesus macaques, but thus far their data have corroborated the sexual diethisms discovered in immature macaque social play (Owens 1975a; Owens 1975b; Rose 1977; Cheney 1978b; Chalmers 1980). In particular, Owens (1972; 1975a; 1975b), who studied primarily infant olive baboons (*Papio anubis*), found that males initiated play more frequently, played longer and exhibited higher proportions of wrestling, mock-biting and sparring in their rough-and-tumble play than did their female peers. Data from a few juveniles suggested that the social play of older males change more readily into aggression than does the social play of older females (Owens 1975b). After examining the amount of time each of his subjects spent playing with other group members, Owens (1975a) concluded that infant and young juvenile baboons prefer to play with partners of comparable size and strength.

The initiators of rough-and-tumble play bouts among juvenile baboons in Amboseli were identified to illuminate further the nature of age-sex differences in baboon play. Because the first analysis concerns sex differences in play interactions among juveniles within age classes, the data for one male and two females that were six to 12 months younger than all of the other young juveniles were omitted (see above references for age effects on partner choice). In each of two study groups, there were three young juvenile females and a single male that were all born within a four-month period. The young juvenile male in each group initiated rough-and-tumble play with a larger number of frequent partners than did his female age peers: Play initiations with more group members were needed to account for 80 percent of the males' rough-and-tumble initiations than were needed to account for 80 percent of the initiations exhibited by their female age-peers (Figure 2). This pattern is less clear among older juveniles, but does not run contrary to the results for the young juveniles (Figure 2).

sexual interactions with adults hasten the maturation of their sexual performance. In most primate species, the sexual interactions of infants and juveniles among themselves and with adult partners are ignored by adult group members. However, in many species, once immatures reach adolescence, same-sex adult group members begin to interrupt their attempts to copulate with adults. This is particularly evident among males, but aggression toward adolescent daughters is commonly observed in the adult females of territorial monogamous species.

Although many human societies have proscriptions against extramarital sexual activity among adults, the children and/or adolescents in a majority of Murdock's (1949) sample of 150 preindustrial societies are allowed premarital sexual license. In many other societies, such as among the !Kung hunter-gatherers, children are only mildly discouraged from engaging in juvenile sex-play and from observing parental coitus (Shostak 1976). In contrast, in virtually all contemporary industrialized societies, taboos against extramarital sex include sexual activity by children and adolescents (Nye and Berardo 1973). Perhaps as a consequence, preadolescent boys in America spend a large proportion of their time together talking and learning about sexual matters (Fine 1980).

Social Play

The play of immature human and nonhuman primates is similar to that of most mammalian species in that it occurs most frequently in environments that can support this energetically costly behavior and that one of its valuable consequences is the promotion of growth and development of muscle, bone, locomotor skills and coordination. Although these are factors that should be expected to influence the play of immature males and females alike, one of the most consistent findings in studies of social play in children and in juvenile nonhuman primates is that young males play more frequently and more aggressively than do their female age-peers (see JUVENESCENCE and Blurton-Jones and Konner 1973; Whiting and Pope 1973; Freedman 1974; Omark et al 1975). It is apparent that perinatal androgen activity in mothers and their male offspring results in a sex-typing of males' central nervous systems (Resko 1970; Resko 1975)

Future studies of juvenile nonhuman primates may reveal that processes of selective attention and behavioral focus on like-sex adults are critical for the development of sex-typical behavior patterns as seems to be true for human children (cf. deBenedictus 1973; Fectau and Strayer 1980). Kindergartners who have attained the understanding that boys incontrovertibly grow up to be men and girls develop into women choose to observe same-sex models, whereas other children of the same age do not discriminate in their observations of adults of the two sexes (Slaby and Frey 1975; see also B. Hamburg 1978). Maccoby et al (1958) and Maccoby and Wilson (1957) have demonstrated that junior high school boys and college men observe male actors more than female actors in choice situations during film screenings, whereas females of these ages attend more to the female actors. Developing children and nonhuman primates may also perceive different aspects of the adult behavior that surrounds them. Studies by Bandura (1965), Maccoby and Wilson (1957), Moore (1966) and Kagan and Moss (1962) suggest that girls do not notice and retain details of aggressive interactions between adult males to the extent that boys do. Data from juvenile nonhuman primates could reveal similar phenomena: for example, juvenile female baboons may be more attracted to mothers and infants that are in contact or near to one another than they are to either the mother or the infant alone. Such data would suggest that it is mother-infant interaction and not infants *per se* to which the young females are attracted. Future studies of behavioral development in nonhuman primate species should be designed to discover whether juvenile males and females attend not only to different adult group members but also to different types of social interactions.

Sociosexual Behavior

Research on captive and free-living primates has demonstrated that extensive learning is involved in the development of effective sexual behavior in monkeys and apes. The first sexual advances of male and female primates emerge and become oriented primarily toward cross-sex age-peers during infancy; however, in every species that has been studied thus far, sexual interactions only gradually approach adult efficiency during adolescence. Both juveniles and adolescents attend to adult sexual interaction and seek opportunities to interact sexually with adults of the other sex;

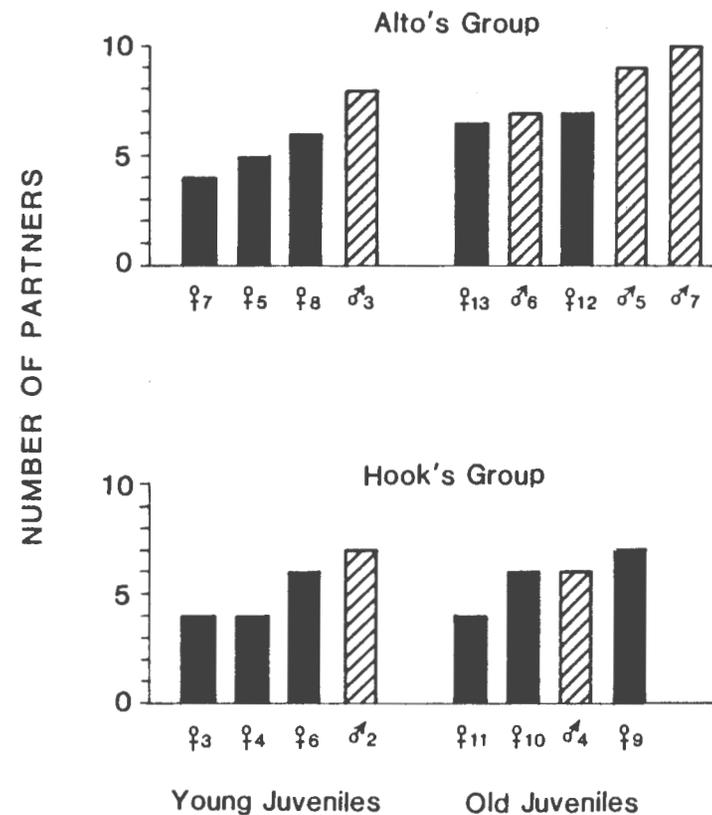


Fig. 2 Number of partners needed to account for 80 percent of rough-and-tumble play bouts initiated by subjects.

For each of all seven male and 13 female juveniles, the five most-preferred rough-and-tumble play partners were identified by calculating the rate at which subjects initiated rough-and-tumble play with each group member, taking into account the amount of time that each partner was present in their group. On the average, the five most-preferred rough-and-tumble play partners accounted for 71 percent of a juvenile's initiations ($n=20$ subjects).

Among both older and younger juvenile baboons, males consistently preferred more challenging partners for rough-and-tumble play than did females. The younger juvenile males of both groups preferred the older juvenile males, male peers and the oldest male infants as partners in rough-and-tumble play, whereas younger juvenile females preferred primarily infants of either sex and female age peers for their rough-and-tumble play. Among the preferred partners of each of the three older juvenile males in Alto's Group were his two age-sex peers and the oldest young juvenile male. The lone older juvenile male of Hook's Group initiated rough-and-tumble play more frequently than did any other juvenile under study, and he directed the large majority of his rough-and-tumble play initiations toward the only available younger juvenile male, the oldest male infant, and toward the most aggressive young juvenile female. In contrast, the data from the five older juvenile females in the two study groups reveal that none of these females preferred to play rough-and-tumble with their male or female age-peers or with the oldest of the younger juvenile males. Rather, these females preferred to play primarily with younger juvenile females and with infants of either sex. Finally, within groups without exception, every juvenile male subject directed a larger proportion of his total rough-and-tumble play initiations toward adolescent males (5 and 1/2 to 8 years old) or juvenile males from an older age class, and initiated a greater proportion of his rough-and-tumble play bouts that involved adolescent or older juvenile males than did any female age peer.

All of the play data that we have discussed support the hypothesis that one of the functions of cercopithecine social play is to provide practice of fighting skills and strategies for developing males (see Symons 1978). Social play is undoubtedly important for the growth and neuromuscular development of young primates of both sexes (Bekoff et al 1979; Bekoff and Byers 1981; Fagen 1981). However, the data reported here also confirm expectations based on

These observations, along with the cross-cultural ubiquity of marriage as the only socially-accepted condition for child-birth, suggest that sharing of parental responsibilities between mothers and fathers has a long evolutionary history for *Homo sapiens*. They may also explain why studies of contemporary hunter-gatherers have been unable to show appreciable sex differences in the infant-caring behaviors performed by children (Draper 1976). Whereas a juvenile female catarrhine monkey may benefit from her early curiosity about interactions between infants and their caretakers because infant-rearing will later be almost solely her responsibility, when parental duties are shared between mother and father (e.g., among the callitricidae and the hominidae) male and female immatures are predicted to exhibit similar degrees of interest in infants. That the female children of many contemporary cultures exhibit more nurture toward infants and toddlers than do their male counterparts (Whiting and Pope 1973; Blurton-Jones and Konner 1973) may be, in large part, a result of widespread selective social enhancement of the nurturing capacity of girls (see Draper 1980; Ember 1981).

Sex-Typing

What are the mechanisms whereby male infants and boys gradually assume the mannerisms and behavioral repertoires of men and maturing females adopt the behaviors of women? Answering this question has long been a major concern of students of child development (Sears et al 1965; Mischel 1966; Kohlberg 1966). Children's increasing comprehension of gender constancy and gradual expansion of identification to include like-sex peers, caretakers and adults is fundamental in the process of sex-typing (Kohlberg 1966). Positive and negative reinforcement of sex-appropriate and sex-inappropriate behavior by adult authorities and imitation of older like-sex role models also play important roles (Maccoby and Jacklin 1974; Hamburg 1978; Ember 1981). While the ontogeny of sex-typing in humans remains only partially illuminated, the primary processes that augment and extend inherent behavioral sex differences in nonhuman primates are virtually unknown (e.g., Young et al 1982). Research on the ontogeny of sex-specific behavior in nonhuman primates would be of considerable value toward deepening our understanding of sex-typing in children.

Offspring Care

In human societies all over the world, a woman attains adult social status when she reaches menarche, becomes pregnant or gives birth to a viable infant. Interestingly, in virtually all known cultures, both monogamous and polygynous, pregnancy mandates being permanently associated with the offspring's father through marriage (Malinowski 1962; Daly and Wilson 1983). It is apparent that a species-typical characteristic of *Homo sapiens* is that the responsibilities of child-rearing are shared between mother and father, either directly or indirectly.

In many nonhuman primate species, adult males also contribute to the rearing of infants. Although adult males of most species are not as involved in the direct nurture of infants as are mothers, in many, males provide considerable care in the form of protection from strange males, predators, or rough females, or by attending to or tolerating infants while mothers are elsewhere (see Redican 1976; Parke and Suomi 1981; Snowden and Suomi 1982 for reviews of paternal behavior in primates). The adult males of monogamous species regularly provide appreciably more infant care, but even the males of species in which very little adult male behavior is typically directed toward infants are capable of developing a high degree of nurturance under experimental conditions (Parke and Suomi 1981).

Most important, paternal care in most primate species, including humans, comprises forms of investment that are complementary to those from mother, rather than only substitutive forms of care (Snowden and Suomi 1982). Research on both humans and nonhuman primates indicates that infants develop distinct and strong relationships with their male caretakers that are only partially similar to those with their mothers (e.g., Fragaszy et al 1982; see also Draper and Harpending 1982). Several studies of humans have documented fathers' emotional and psychophysiological responses to offsprings' vocalizations and distress signals that are comparable to maternal responses (Frodi et al 1978; see Parke and Suomi 1981), although other studies show that American fathers more readily "tune out" their infants than do mothers (LaRossa and LaRossa 1981).

cercopithecine life-history that males should seek varied and challenging experience in physical competition early in life, whereas such experience, having much less potential to affect females' future reproductive success, is not pursued by juvenile females. In particular, males' use of a larger number of regular opponents in rough-and-tumble play and more frequent play initiations with opponents of equal or superior competitive abilities support the hypothesis that males benefit later in life by perfecting skills and strategies in fighting during juvenile play. The fact that similar sexual diethisms have been found in the social play of other mammal species in which adult males compete physically for access to estrous females (see review in Fagen 1981; also Moss 1982 for a qualitative account of sex differences in elephant play, *Loxodonta africana*) also supports this evolutionary interpretation of the social play diethism in cercopithecine primates.

Interaction with Infants. Cheney (1976; 1978b) has shown that rates of social play in juvenile female baboons (*Papio ursinus*) increase considerably with an increase in the number or availability of infants. This finding reflects a common sexual diethism in immature and adult primates -- females typically exhibit greater interest in neonates and young infants than do males (Spencer-Booth 1968; Struhsaker 1971; Lancaster 1972; Konner 1976b; Singh and Sachdwa 1977; Altmann 1980; Hasegawa and Hiraiwa 1980; Berman 1982b). Vervet monkeys (*Cercopithecus aethiops*) represent an extreme case: juvenile female vervets are strongly attracted toward young infants, whereas juvenile males often exhibit virtually no interest in the infants of their group (Struhsaker 1971; Lancaster 1972).

No data from free-ranging primates are yet available that demonstrate increased infant survivorship for mothers that exhibited greater interest in infants during juvenescence than did their peers. Interestingly, however, among captive tamarins (*Saguinus fuscicollis*, *Leontopithecus r. rosalia*), if either member of mated pairs does not gain experience in caring for infants prior to the pair's first reproductive effort, the probability of infant abuse, neglect and death is considerably increased (Epple 1975; Hoaga 1977; Kleiman 1979). The potential adaptive value for females of seeking early experience with infants is highlighted for field workers who must watch a neonate die after its mother failed to orient the infant properly and support its efforts to find the nipple during its first day or two of life.

Sociosexual Behavior. Only a single quantitative account of the ontogeny of sociosexual behavior in free-ranging juvenile primates is available: Owens (1976) studied the emergence of mounting behavior in immature baboons (*Papio anubis*) in Gombe National Park, Tanzania. After the infrequent and disoriented mounts of infancy, the large majority of juveniles' mounts were properly oriented, and a significantly higher proportion of male juveniles' mounts were accompanied by pelvic thrusting. Around one year, males' properly-oriented mounting of adult females increased dramatically, apparently as a result of intromission (see also Young et al 1982). Males up to four years of age mounted immature partners of either sex using the characteristic foot-clasp on mountees' legs with about 28 percent and thrusting with about 17 percent of mounts, whereas the foot-clasp and thrusting were observed with over 93 percent of the immatures' mounts of adult females. The first ejaculatory pauses appeared in males' mounts around 15 months after birth, and occurred in about 25 to 30 percent of males' mounts thereafter until puberty. After puberty (about 60 to 70 months in Gombe baboon males; Owens 1976; Packer 1979a) the proportion of males' mounts that included ejaculatory pauses doubled.

The immature female baboons that Owens studied mounted much less frequently than did immature males; only once was a female observed using a foot-clasp during a mount, and thrusting was never observed in mounts by females. Immature females never mounted adult group members. Also, although male-male mounting persists into adulthood among baboons, adult females in Gombe were never observed to mount other group members. In Amboseli, however, although adult females virtually never mount males, they commonly greet one another by mounting (Pereira unpub. data). Adult and immature females' mounts of other females typically lack thrusting and are brief and often "sloppy" in appearance, grading into other types of greeting such as embraces. Ransom and Rowell (1972) and Young et al (1982) have reported that during their second year of life immature female baboons begin to present their perineum more frequently than do their male peers. Whereas immature females in Gombe typically exhibit "foot-back" behavioral components in their presentations (Ransom and Rowell 1972), the presentations of immature female baboons in Amboseli are more individually variable with respect to this component.

Our answers to these questions are: yes -- important parallels and fundamental contrasts to human behavioral development have been discovered in studies of behavioral development in the nonhuman primates. And, yes -- future field work could unquestionably provide an invaluable comparative database with which to design and interpret studies of human development. These answers seem incontestable in spite of the fact that we have only begun to illuminate the ontogeny of behavior in nonhuman primates. Indeed, we have seen that little research has yet been done on development beyond infancy in free-ranging primates. Nonetheless, students of nonhuman primate development and of child development have each identified important fundamental issues and have developed methodology that, if duly considered, will enrich studies in each counterpart system.

It is beyond the scope of this chapter to provide a complete comparative treatment of parallels and contrasts in the development of human and nonhuman primate behavior; rather, we highlight below selected illustrative aspects of behavioral development in human and nonhuman species. In particular, we include discussion of topic areas in which students of human or nonhuman primate development have progressed sufficiently to provide heuristic perspective for future studies of other species.

Both human and nonhuman primates are born completely dependent upon their mothers' and others' nurturance for survival. Infantile dependency and subsequent periods of prereproductive development in primate species constitute larger proportions of lifespans than in most species of other mammalian orders. Protracted prereproductive development in primates is probably due, at least in part, to selection that has favored individuals with considerable learning capacity and behavioral flexibility at every stage in development. As they mature, nonhuman primates and children learn much about the complexities and nuances of the social behavior of their species and sex as well as skills in feeding and other maintenance behaviors. Species- and sex-specific behaviors develop through observation of elders and by practice, in interaction with physical and behavioral predispositions (see below).

These are the conditions to which adolescent primates must accommodate. Recent observations suggest that adolescent primates employ behavioral tactics that mitigate certain social and ecological hazards of adolescence. For example, in some baboon and macaque populations, adolescent males sometimes migrate together (Boelkins and Wilson 1972; Cheney and Seyfarth 1977; Meikle and Vessey 1981). This tactic may mitigate the risks of predation and minimize young males' period of low reproductive status. (See Froelich et al 1981 for demographic evidence of similar relationships among adolescent male howler monkeys; see Caine 1980 on the development of sibling and peer relationships in macaques). Adolescent male langurs, chimpanzees and rhesus monkeys appear to groom high-ranking adult males to establish affiliative relationships that could facilitate a rise in dominance rank (Sade 1972; Simpson 1973; Merrick 1977; Moore in press b). High rank may help to ensure residence and promote reproductive success for male and female rhesus and howler monkeys (Chepko-Sade and Sade 1979; Jones 1980) and male chimpanzees (McGinnis 1979; Tutin 1979). Finally, in primate species in which females commonly migrate between large social groups, potential resistance to immigration from resident females is often mitigated by minimal feeding competition among females (some colobines, gorillas), but female chimpanzees may exploit resident males as buffers against aggression from resident females (Pusey 1979).

DISCUSSION

Nonhuman primates are the subjects of much endocrinological, immunological and pharmacological research because of the homologies that exist between their physiological systems and our own. More than twenty-five years of research on nonhuman primate behavioral development has proceeded under the often tacit assumption that the ontogeny of behavior in nonhuman primates provides an equally amenable model for human behavioral development. What are we discovering? Are there important parallels to human development in the behavior of immature nonhuman primates that merit further investigation? Will additional field work provide a still more robust perspective for research on human development?

Owens' (1976) data from free-ranging baboons are comparable to those from studies of sociosexual development in captive juvenile male macaques (Harlow 1962; Hinde and Spencer-Booth 1967; Hanby and Brown 1974; Wolfe 1979) and baboons (Young et al 1982). All of these studies emphasize the importance of learning in the development of proper orientation and more mature patterns of copulation in juvenile males and females. However, learning of the behavioral components of effective sexual interaction is not complete until adolescence in primates.

Juvenile Behavioral Development in Other Nonhuman Primates

Whereas quantitative descriptions of some aspects of juvenile behavior are beginning to accrue for some macaque and baboon species, no comparable information is currently available for juveniles living in the widely divergent societies of most other cercopithecinae, hylobatidae, callitricidae, cebidae, prosimii, colobinae, and pongidae (but see Pusey 1983). Such data are needed to substantiate current perspectives on the nature of primate juvenescence.

The life-histories of the less-studied primates provide excellent opportunities to test further hypotheses that have come from the study of baboons, macaques and vervet monkeys. For example, if interest in infants by juvenile females has evolved to ensure maternal competence during adulthood, the prediction follows that juvenile behavioral sex differences concerning infants should not be as consistent or as large in species in which males contribute substantially to infant care. Studies of captive callitricids have shown that both male and female immatures carry infant siblings (see e.g., Epple 1975; Hoage 1977; Kleiman 1979), and Hoage (1977) suggests that appreciable sex role differentiation with regard to infant care occurs during development in *Leontopithecus r. rosalia*. Currently, there are no data available on the relative rates at which juvenile male and female callitricids, hylobatids, callimiconids, and *Callicebus* monkeys initiate interactions with related and unrelated infants during development in the wild. These are the data that would be singularly useful to illuminate the nature of juvenile-infant interaction in all primate species (see also Konner 1976b).

That female macaques and baboons develop stronger and more reciprocal social relations with their mothers than do juvenile males of these species seems consistent with the

life-histories of these cercopithecines (see above and Cheney 1976; Cheney 1978a; Silk et al 1981; Silk 1982). For primate species in which not only males but also or only females disperse (e.g., the callitricidae, some prosimii, the hylobatidae, *Alouatta* spp., the pongidae, *Papio hamadryas* and some colobines; see Moore in press a), one would predict that reciprocity in social relations between juvenile males and their mothers will be found to rival or exceed that found between mothers and their juvenile daughters. Moreover, in species in which males infrequently emigrate from natal groups, the development of affinity in fraternal social relations should exceed that seen in male-dispersing primate species.

Pusey (1983) has reported that grooming relations between chimpanzee mothers and juvenile offspring of the two sexes are equally frequent and reciprocal ($n=4$ males and 4 females), and that male and female juvenile chimpanzees appear equally dependent on their mothers until puberty. Also, several researchers have reported that male-male social relations are unusually affiliative in chimpanzees, red colobus monkeys and bonnet macaques, species in which male dispersal from natal groups is minimal (see e.g., Simonds 1974; Struhsaker 1975; Bauer 1976; Struhsaker and Leland 1979; Wade 1979). Studies of monogamous primates have reported that adult females aggress most or only toward daughters among offspring that attain puberty within the family group, although females in some of these species are known to be capable of repelling adult males (e.g., Tilson 1981). These examples appear to support the predictions made above; however, we need studies that are designed specifically to compare the fine details of filial and sibling relationships of free-ranging juveniles in these and other species.

Many researchers find compelling the functional interpretation of sexual diethisms in social play found among cercopithecine juveniles that we discussed earlier (see Symons 1978). However, data on the social play of juveniles of other primate species are desirable to substantiate further this perspective. In several prosimian, callitricid and hylobatid and some cebid and cercopithecoid species, adult females are equal or superior to adult males in agonistic dominance status. The study of social play in these species would be valuable for testing an alternative hypothesis explaining sexual diethisms in social play: aggres-

sive for adults to repulse adolescent competitors and, consequently, for adolescents to avoid crippling injury and to risk a period of solitude by emigrating. In other species, where no other factor has selected strongly for or against adolescent dispersal, those individuals that seek unfamiliar sexual partners might most successfully reproduce due to avoidance of inbreeding depression. The aggression of monogamous primate parents toward like-sex adolescent offspring is likely to be ubiquitous precisely because of its dual adaptive value: for the parents, it simultaneously reduces feeding and/or sexual competition and the likelihood of inbreeding by their offspring (see Tilson 1981).

Adolescents that remain in their natal group must continue to assimilate themselves into their group's established social structure. Affinitive intrasexual social relations are commonly observed among adolescent and adult members of the sex that usually remains in the natal group. Throughout adolescence in cercopithecine species, females further develop and maintain affinitive social relationships with female kin, and, perhaps, unrelated, higher-ranking adult females, that were established during juvenescence. Similarly, in species in which males infrequently disperse from natal groups, male-male association or social bonding is prevalent, male kin groups sometimes maintain breeding cooperatives, and adolescent males assimilate themselves into their group's male social structure (e.g., chimpanzees, Simpson 1973; Bauer 1976; Merrick 1977; Pusey 1983; red colobus monkeys, Struhsaker and Leland 1979; bonnet macaques, Simonds 1974; Wade 1979; Ali 1981 as ref. in Moore in press a).

In contrast, the majority of social interactions that occur among the adult males of male-dispersing species (e.g., baboons) is neutral or agonistic in nature, although some males do form coalitions with peers during agonistic encounters (Hausfater 1975; Packer 1977; Packer 1979b). Similarly, social relations among the adult females of female-dispersing species (e.g., gorillas) are typically much less pervasive than those found among females in most cercopithecine social groups (Harcourt 1978; Sigg 1980). Currently, little is known concerning the potential differences in social skills needed for intersexual social relations by members of a given sex across species in which that sex does and does not usually transfer between groups.

Researchers who emphasize the importance of intrasexual competition for adolescent emigration stress that the aggressive interactions that begin between adults and immatures during juvenescence typically intensify during adolescence, often "peripheralize" adolescents, and sometimes seem to peak in frequency and intensity immediately prior to dispersal (see Nishida 1966; Chivers 1974; Ellefson 1974; Tenaza 1975; Sugiyama 1976; Mohnot 1978; Packer and Pusey 1979; Jones 1980; Tilson 1981 for data). Direct aggression toward adolescents is considered a mechanism whereby adults minimize the potential for adolescents to exacerbate sexual and/or feeding competition by remaining within their natal group or ranging area. Moore and Ali (in press) argue reasonably that avoidance of inbreeding cannot easily explain dispersal for both sexes in those group-living species in which both sexes commonly emigrate. Tilson's (1981) observation of naturally-occurring mother-son incest following the disappearance of the adult male from a family of Kloss' gibbons are consistent with this perspective (Moore in press a). Other researchers note that aggression is not a necessary precursor of dispersal for some species; dispersers often leave without having received heightened aggression or even after attaining high agonistic dominance status, and they sometimes encounter greater aggression following migration from peers in their new social groups than they did in their natal groups (Hausfater 1975; Packer 1979a; Pusey 1980; Hausfater, Altmann and Altmann unpub. data). It seems clear that neither ejection nor prevention of reproduction by adults are primary causal factors of dispersal for these primates.

It is unlikely that there exists a unitary explanation for adolescent dispersal in all primate species. Undoubtedly, for every species a balance among several selective forces guides the evolution of dispersal among males and females. For most adolescent primates at least four factors are likely to play significant roles: a) the density of potential mates or non-natal social groups in the environment, b) the probability of long- and short-term survival outside of any social group, c) whether aggression from familiar adults is more or less likely than that from unfamiliar adults to result in injury or reproductive suppression, and d) whether reproductive relatives of the other sex are more or less likely to be encountered elsewhere than in the natal group. In some environments, it may be crit-

sive social play functions to prepare developing individuals of one sex to become the dominant adults of their societies and thus to control the behavior of adults of the other sex in situations of contest or social disruption. To our knowledge, only one study has provided details concerning the social play of juveniles in a primate species in which adult females are dominant to adult males: Wolfheim's (1977) study of captive talapoin monkeys (Miopithecus talapoin). Wolfheim found that the juvenile male talapoin monkeys more frequently initiated and participated in rough social play than did the females, just as in the male-dominant cercopithecine societies. The author concluded that juvenile social play does not function to prepare individuals of the "more aggressive sex" in cercopithecine groups to dominate members of the other sex during adulthood. We agree; however, of particular significance is that the study did provide support for the prediction that juvenile males play more aggressively than do juvenile females in species where intragroup (sexual) competition is most intense among adult males (see Rowell and Dixson 1975).

The monogamous primates differ considerably from macaque and baboon societies in that intrasexual dominance relations are not "inherited" among females, and intrasexual agonistic interactions often appear to be as significant among females with regard to individuals' lifetime reproductive success as they are among males. Unfortunately, for these species we lack both detailed developmental data and knowledge of normative patterns of life-history (see Dawson 1977; Neyman 1977; Pook and Pook 1981). However, if social play functions to provide practice of fighting skills, future research should reveal that the frequency and roughness of juvenile females' social play rival those of juvenile males' play in species in which the reproductive success of adult females depends on individuals' effectiveness during intrasexual agonistic interaction or in which the importance of skills in physical competition are of little relevance to male reproductive success.

Primate species of widely separate phylogenetic heritage but similar life-histories should be compared to discover the significance of developmental sexual diethisms and age changes in behavior. The immatures of such similar species can be expected to face similar problems and, perhaps, to effect similar solutions during development. Consider, for example, Charles-Dominique's report (1977) that juvenile male galagines (Galago demidovii) sometimes

leave their mothers to follow the most dominant adult male that ranges in their natal area, whereas juvenile females have not been observed to do this. The data from young galagos suggest an hypothesis for other "solitary" primates: following dispersal, juvenile males more often seek out, follow and observe the movements of adult males than do juvenile females. An affinity of independent immatures to like-sex adults may be an important behavioral mechanism to provide maturing members of relatively solitary primate species opportunities to observe and learn from appropriate role-models. Although no data have yet been reported for orangutans that demonstrate a propensity in developing males to follow or observe adult males, such a system could occur in this species: Rijksen (1978) has reported that orangutans are adept at moving in parallel with conspecifics even when they are separated in a forest by hundreds of meters, and that adult male orangutans typically tolerate and ignore the presence of juveniles.

ADOLESCENCE

Although little research has been focused on a comprehensive understanding of juvenescence in nonhuman primates, still less information is available concerning the behavioral changes concurrent with the rapid physiological and morphological development of primate adolescence (Kraemer et al 1982). Although this chapter is concerned primarily with behavioral development in free-ranging nonhuman primates, due to the paucity of field work on adolescents we have drawn more information from studies of captive groups of primates for this section than we have for previous sections. Readers are referred to Caine (in press) for a thorough taxonomic review of reported behavioral changes in wild and captive adolescent primates.

Hobson et al (1980: 410) defined female primate puberty as "all of the events which lie between the first changes in patterns of reproductive endocrine hormones and the acquisition of the capacity to carry pregnancy to term." The critical events of puberty according to these authors begin with sleep-related gonadotropin spikes that are induced by incipient hypothalamic secretion of luteinizing hormone-releasing hormone (LHRH), and include rising basal levels of gonadotropins and sex steroids, menarche, estrogen-induced gonadotropin release, first ovulation and competent luteal function. Their definition is satisfying in its clinical

Dispersal and Social Integration for Adolescent Primates

In most primate species, adolescent males commonly disperse from their natal groups, and in many species, females usually remain in their natal groups for their entire lives. Because this is the pattern observed among the best-studied species, the cercopithecine primates, it is commonly considered the primate pattern. However, in many primate species, some adolescent females emigrate, and in several species, most females transfer between groups at least once in their lives, while it is less common for the males of these species to do so (e.g., red colobus monkeys, chimpanzees and gorillas; see Harcourt 1978; Wrangham 1980; Moore in press a; see INTRODUCTION & BACKGROUND).

Migration between social groups is assumed to be a risky endeavor for primates because during migration an individual relinquishes whatever advantages group-living has to offer, and because entry into another social group may be assiduously and aggressively opposed by resident adults. A solitary primate is often forced to subsist in marginal habitat (Tilson 1981; Hamilton and Tilson 1982), and during migration the individual cannot benefit from the additional protection from predators conferred by the eyes and ears of associated conspecifics (Pulliam 1973). Finally, upon entry to a new group, immigrants in some species are often low-ranking (Drickamer and Vessey 1973; Jones 1980; Meikle and Vessey 1981) or poorly socially-integrated for as long as a year (pers. obs. and see Strum 1982).

A controversy exists in primatology over the proximate causes and ultimate functions of dispersal among adolescent primates. Some researchers suggest that in most species adolescents disperse from natal groups primarily because they are prevented from copulating or are, in fact, ejected by adult group members (Dobson 1982; Moore and Ali in press). Others have implicated apparent attraction to cross-sex conspecifics outside the social group as the primary proximate cause of emigration (see e.g., Cheney and Seyfarth 1977; Packer 1979a). Finally, some researchers discuss the importance of avoidance of inbreeding and de-emphasize the significance of proximate precipitating factors (see e.g., Howard 1960; Packer 1979a; Pusey 1980).

remain poorly understood, and the significance of these phenomena for individuals at different stages of development is virtually unknown (Hayama 1966; Levine et al 1970; Chamov and Bowman 1978; Leshner and Candland 1972; Rose et al 1972; Rose et al 1978; Epple 1982; Epple and Katz 1980; Eberhart et al 1980; Eberhart et al 1983). Data from adolescent male rhesus monkeys and chimpanzees living in captive social groups suggest that the behavioral effects of pubertal hormone changes are different in these two species; more data are needed to evaluate fully the nature of such differences. There are no developmental data on the relationships between changes in reproductive endocrinology and dispersal from natal groups or natal ranges.

The effects of unfamiliar cross-sex adult conspecifics, i.e. immigrants or members of neighboring groups, on the endocrine activity, aggressive behavior, dispersal and overall reproductive potential of adolescent and young adults are important life-history phenomena that deserve substantial research. Recent work on callitricids, squirrel monkeys and lemurs demonstrates that whereas the presence of parents or natal group adults can suppress the reproductive potential of adolescent primates, the presence of unfamiliar adults can accelerate adolescent sociosexual maturation in some species. Epple and Katz (1980), Epple (1981) and Hopf (1979) have found that both male and female adolescent tamarins and squirrel monkeys court conspecifics and reproduce considerably earlier when they are housed with an unfamiliar adult of the other sex than when they are raised among age-peers. Vandenberg (1974) reviews this phenomenon as it was originally described for rodents (see also Kummer 1968; Wiley 1981; Foerg 1982). Epple (1981) has demonstrated that an entire suite of adult aggressive and territorial behaviors is elicited from adolescent male or female tamarins that are housed with an unfamiliar adult of the other sex. Interestingly, a recent cross-cultural investigation of maturation rates in human societies has revealed that young women living in polygynous societies not only marry but also reach menarche at earlier ages than do the women of monogamous cultures (Bean 1983; see also Dickemann 1979).

The effects of familiar and unfamiliar adults on the sexual maturation of adolescent primates is directly related to the problems of social integration within, and dispersal from, natal groups. We turn now to a brief review of field research that has dealt with these issues in primates.

precision for female primates, and it serves to highlight the need for the documentation of externally observable morphological and behavioral correlates of puberty and adolescence in both sexes.

We consider primate adolescents to be pubertal, pre-reproductive individuals. The onset of puberty in the immature males of many primate species can be reliably detected in the field by observation of rapid testicular growth or descent (Rowell and Dixson 1975; Pusey 1978; Glick 1980; Nigi et al 1980; Altmann et al 1981). Testicular growth is among the first of several morphological responses to pituitary release of lutenizing hormone in pubescent male primates. Maturation of ovarian tissues in response to LH cannot be readily observed in the field; however, the females of many primate species exhibit slight to dramatic tumescence of the perineum and/or changes of facial and perineal skin coloration during gonadarche (Gillman 1939; Rowell 1977; Fossey 1982; see Caine in press for review). Pubertal perineal swelling is obvious in many of the species in which adult females do not undergo distinct estrous swelling (see e.g., Rowell 1977; Nigi et al 1980).

Neither initial testicular growth nor perineal swellings or menarche are signs of full sexual maturity in primates (Montagu 1957; Rowell 1972; Wolfe 1978; Hopf 1979; Nigi et al 1980; Rostal and Eaton 1982). The first and often several of the early menstrual cycles of adolescent macaques, baboons, chimpanzees and humans are irregular and anovulatory (Montagu 1957; Hobson et al 1980). Even after regular ovulation begins, other factors may contribute further to adolescent infertility. Complete maturation of luteal function, necessary for maintaining implantation of a developing embryo, is among the last of prereproductive maturational developments in the female primate reproductive system (Hobson et al 1981).

In many primate species, males attain puberty later and experience a longer period of pubescence than do their female counterparts. For example, female savannah baboons typically reach menarche by five to five and one half years of age, whereas testicular growth in males does not usually begin until a half-year later (Altmann et al 1977; Altmann et al 1981; Packer 1978a; Packer 1979b). Once testicular development and the growth of seminiferous tubules begin, males' testosterone secretion and sperm counts increase (Glick 1979; Nigi et al 1980; Kraemer et al 1982) and ejacu-

lation becomes more easily observable in the field (see Pusey 1977; Pusey 1983). Following menarche, female baboons normally experience about 10 to 12 months of estrous cycling prior to becoming pregnant (Scott 1979; Scott in press; Altmann 1980), and, in Amboseli, primiparous females are as successful at bringing their pregnancies to term as are multipara (Altmann et al 1981). In contrast, morphological and physiological development continue in adolescent males along with the development of reproductive and social behavioral skills over a period of at least two years (Altmann et al 1977; Altmann et al 1981; Rowell 1977; Fossey 1982; see Nigi et al 1980 and Rostal and Eaton 1982 for quantitative physiological and behavioral data from Japanese monkeys, *Macaca fuscata*). In populations in which young females have a high probability of losing their first fetus or infant (e.g. La Paguera rhesus, Drickamer 1974; squirrel monkeys, Hopf 1979; gorillas, Fossey 1982; Amboseli baboons, Altmann, Hausfater and Altmann unpub. data), male age-peers often have still not attained reproductive capacity by the time these females conceive a second time.

What behavioral changes coincide with adolescence for primates? Two obvious changes in the lives of adolescents involve progressive reduction in social experience: adolescents much less frequently play than do juveniles (Owens 1975; Gard and Meier 1977; Symons 1978; Levy 1979; Fagen 1981), and adults less frequently tolerate the proximity of adolescents, particularly in feeding contexts. The peripubertal growth spurt (Watts and Gavan 1982) or simple increased overall body size of adolescent primates may be partially responsible for both of these changes. Froelich et al (1981) have argued that the rapid anabolic growth of adolescence can make puberty a period of nutritional stress and sometimes high mortality for primates like the mantled howler monkey (*Alouatta palliata*). During periods when foraging requirements are high, social play in primates and other mammals declines or disappears (Baldwin and Baldwin 1976; Fagen 1981; see also Loy et al 1978 on testosterone suppression of primate play). The increased foraging skills and feeding requirements of adolescents of both sexes also heighten the degree to which adolescents must compete with adults for food. As the competitive nature of relations between adults and immatures intensifies, so too do the agonistic interactions between adolescents and adults. Thus, the clemency that adolescents were accustomed to receiving from adults during juvenescence wanes as immatures approach adulthood (Pereira 1984).

Recent laboratory research documents physiological suppression of adolescent reproductive capacity in captive callitricids and lemurs. Rates of scent-marking and ovulation are significantly lower in adolescent females that are housed with their mothers (*Callithrix jaccus*, Abbott 1978; *Saguinus oedipus*, French and Snowden 1982; *Saguinus fuscicollis*, Epplé and Katz 1980). Foerg (1982) reported that the testicles of two three-year-old male ruffed lemurs (*Varecia variegatus*) housed with their families did not differ in size from those of two-year-old males, whereas two three-year-old males housed separately with unrelated adult females exhibited adult testicular development and each sired offspring.

The sexual behavior of adolescent male baboons and macaques living in their natal groups might also be inhibited at the physiological level. Packer (1979a) showed that the rates at which adolescent and young adult male baboons (*Papio anubis*) consort and copulate with adult females following immigration into a new social group far exceed those which are exhibited by males prior to emigration from their natal groups. The fact that several of these males had attained high agonistic dominance status in their natal groups prior to emigration suggests that aggression from like-sex adults is not the only factor contributing to the suppression of adolescent reproductive capacity in this species. Rose et al (1978) studied adolescent males in three captive groups of rhesus macaques and found that the onset of seasonal adult testosterone cycling was delayed for adolescent males living in groups containing more fully-adult males. Observations of black-back male mountain gorillas (*Gorilla gorilla beringei*) following the disappearance of their silverback males (D. Watts pers. comm.) suggest that the change of young adult males' social status in this situation is probably associated with changes in baseline levels of circulating androgens and thus reproductive capacity (Eberhart et al 1980; Eberhart et al 1983).

Much information is needed that would illuminate the prevalence and diversity of social and physiological mechanisms that suppress sexual maturation in nonhuman primate species. Although the secretion of adrenal and gonadal steroids and several pituitary hormones is known to be intimately related to dominance relations and sociosexual behavior in primates, causes and effects in these systems

males and estrous females, adolescent males leave their mothers to join these groups. As adults, males associate with their mothers more than they do with other anestrus adult females, but less than do females that stay in their natal community (Pusey 1980; Pusey 1983). However, adolescent and adult male chimpanzees spend the majority of their time in association with other mature males of their community (Bauer 1976).

Social Suppression and Acceleration of Adolescent Reproductive Capacity

The end of adolescence and the onset of young adulthood are not easy to discern for some primates. Old adolescent males and females of many species are inhibited in their sexual performance either by their own disinterest in the available sex-partners in their natal groups (see e.g., Spiro 1958; Shepher 1971; Bischoff 1975) or by direct sexual suppression by adults.

Reports of potential adult behavioral interference are common. In cercopithecine social groups, adult males often inhibit the sexual behavior of adolescent males by directing aggression toward adolescents that are in proximity to or interacting with sexually receptive adult females (*Cercopithecus aethiops*, *Macaca fuscata*, *Papio cynocephalus* pers. obs.; *Papio hamadryas*, Kummer 1968; *Theropithecus gelada*, Dunbar and Dunbar 1975; *Erythrocebus patas*, Rowell 1977; Chism et al 1982). Fathers in captive family groups of the lemur *Varecia variegatus* (Foerg 1982) begin aggressing upon male offspring that mount adult females primarily after the immatures' testicles have begun to enlarge. In captive tamarins (Kleiman 1979; Hoage 1977) and at least one lemur species (Foerg 1982), mothers begin to aggress frequently upon their female offspring when these daughters undergo their menarcheal estrus cycles. Like-sex parents in family groups of gibbons (*Hylobates* spp.) and siamangs (*Symphalangus syndactylus*) also begin to direct heightened aggression toward their offspring that reach adolescence (Aldrich-Blake and Chivers 1973; Ellefson 1974; Tilson 1981), and the reproductive male in groups of gorillas (*Gorilla gorilla berengei*), interrupts the copulation attempts of the adolescent and young adult males in his group (Fossey 1982).

Although primates play less frequently during adolescence than during juvenescence, the sexual diethism in the social play of cercopithecine juveniles increases during adolescence: males continue to play well into adolescence, whereas in several species, adolescent females play rarely if at all (Owens 1975b; Bramblett 1978; Bramblett 1980; Levy 1979). Because males in these species exhibit more marked growth than do females during adolescence (see Coelho this volume), and consequently probably experience greater nutritional pressure, one would expect just the opposite diethism; thus, other factors beside absolute feeding requirements must influence rates of adolescent play. Levy (1979) demonstrated that adolescent male rhesus monkeys continue to choose primarily age-sex peers as partners for social play, and that this play is more likely than play among juveniles or adolescent females to change into bonafide agonistic interaction (see also Owens 1975b; Cheney 1976; Chalmers 1980 for baboon data). When adolescent females do play, they often choose infants or young juveniles as their play partners (see Cheney 1978b; Caine in press). These findings further support the perspective that social play among immature cercopithecine males functions to promote the development of fighting skills.

Adolescent Sociosexual Behavior

A characteristic of the development of nonhuman primate sexual behavior is that it begins during infancy and continues through juvenescence and adolescence. Wolfe (1978; 1979), Scott (in press) and Hopf (1979) have demonstrated that whereas adolescent male and female monkeys are nearly sexually mature physiologically, in most cases they require considerable experience prior to attaining behavioral sexual maturity (see also Michael and Wilson 1973; Hanby and Brown 1974; Rostal and Eaton 1982). Scott found that copulations involving adolescent female savannah baboons (*Papio anubis*) were often incomplete because these females more frequently interrupted males' copulation attempts by avoiding bipedal hip grasps, leg mounts and copulation prior to ejaculation than did adult females. Wolfe (1979) reports that in Japanese macaques (*M. fuscata*), in which multiple brief mounts occur between adults prior to ejaculation, adolescent males and females tend to wander away from their partners between mounts and often leave mount series before ejacu-

lation. Adolescent Japanese monkey males require many more thrusts to ejaculation than do adult males, and adolescent male baboons (*P. anubis*, single mount ejaculators) ejaculate on a smaller proportion of their mounts than do adult males of their species (Owens 1976). Hopf (1971; 1979) has shown that the sexual behavior repertoires of adolescent male and female squirrel monkeys (*Saimiri sciureus*) are not complete until two years (breeding seasons) after the adolescents are physiologically capable of reproducing.

At puberty, female baboons' interactions with adult males take on a dramatically new character. Whereas prior to gonadarche females only infrequently interact with adult males, pubescent females persistently approach, groom and present their hindquarters to the adult males of their group (Cheney 1976; Scott 1979; Takacs 1982; Pereira unpub. data). Observations of immature female chimpanzees (Pusey 1980; Pusey 1983) and gorillas (Fossey 1982) have shown that female sexual attraction to adult males in these ape species also begins primarily during adolescence. However, adult males rarely show much interest in copulating with adolescent females during the latter's early estrous cycles (baboons, Packer 1979; Scott 1979; Scott in press; Pereira unpub. data; Japanese macaques, Wolfe 1978; chimpanzees, Pusey 1977; Pusey 1980; gorillas, Fossey 1982). During this period, adolescent female and older juvenile or adolescent male olive baboons engage in their first sexual consortships together (Scott in press). Wolfe (1978) reports that pre-pubescent and pubescent male Japanese macaques form brief consortships with both adolescent and adult females. Adult male baboons and macaques usually begin to copulate with adolescent females after a few cycles, and soon thereafter (one to a few cycles), adolescent females experience their first consortships with adult males (Wolfe 1978; Wolfe 1979; Scott 1979, Scott in press; Packer 1979b; Hausfater, Altmann and Altmann unpub. data).

Adolescence in Chimpanzees

A detailed investigation of puberty and adolescence in the chimpanzees of Gombe National Park, Tanzania (Pusey 1977; Pusey 1978; Pusey 1979; Pusey 1980; Pusey 1983) is one of the few field studies that have focused on the behavioral development of adolescent primates (see also Scott in press).

Pusey (1983) noted that unlike most anthropoid species, for chimpanzees (*Pan troglodytes*) the transition to independence involves, to a great degree, learning how to live alone, particularly for females. Juvenile chimpanzees associate with their mothers almost constantly for several years after being weaned from suckling at about five years of age. When the mothers of the young juvenile chimpanzees that were studied by Pusey engaged in sexual consortships with adult males, their juveniles accompanied them to the outskirts of their range. In contrast, two six-year-old juveniles were observed accompanying their mothers on only the first of several sexual consortships. During subsequent consortships these juveniles spent most of their time visiting the feeding station in Gombe where they could be certain of meeting other community (Goodall 1968) or unit-group (Nishida and Kawanaka 1972) members. Of these two juveniles, the female rejoined her mother between subsequent consortships, whereas the male never resumed high levels of association with his mother, although he met her often at the feeding station.

The onset of adolescence is the primary cause of waning of non-nutritional dependence in the chimpanzee (Pusey 1983). Immature female chimpanzees reach gonadarche about eight and a half to nine years of age but do not experience their first full estrus swellings and menarche for another one to three years (Pusey 1980, pers. comm.). Adolescent females begin to leave their mothers during these first estrus cycles to mate with males of their community (Pusey 1978; Pusey 1983). Adolescent females often associate with their mothers between estrus cycles; however, some young females visit neighboring communities during sexual receptivity, and some of these females take up permanent residence in these other communities. Pusey (1983) reports that adult females in Gombe have not been observed to transfer out of their community; however, adult female chimpanzees living in the Mahali mountains of Tanzania migrate between unit-groups (Nishida and Kawanaka 1972; Nishida 1979).

Puberty begins for the male chimpanzees of Gombe between eight and 10 years of age (Pusey 1977; Pusey 1983). Males' first noticeable ejaculations occur about 12 months after incipient testicular growth. By this time, males' association with their mothers begins to decline. Whereas juvenile males try, usually unsuccessfully, to lead their mothers into association with nearby sub-groups of community