
FATHER-CHILD RELATIONS

CULTURAL AND
BIOSOCIAL CONTEXTS



BARRY S. HEWLETT

EDITOR

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Introduction

Throughout much of Europe and America, the past 20 years has been a period of increased involvement by fathers in the direct care of their children (Lamb 1981; 1987). Contemporary American fathers are characterized by their nurturant and caregiving roles (Pleck 1984; Lamb 1987), while fathers during earlier stages of American history were characterized by their roles as moral teachers, breadwinners, or sex-role models (Pleck 1984). This increased paternal involvement has generated interest in the nature of fathers' roles and has resulted in a proliferation of popular and academic publications about fathers. The increase in fathering research has led Lamb (1987:xiii) to state that fathers are no longer the "forgotten contributors to child development" (Lamb 1975).

While the number of studies and publications about European and American fathers has increased exponentially since the early 1970s, relatively little is known about fathers in the rest of the world. The problem with focusing so much attention on predominantly white middle-class fathers from highly stratified societies is that the studies often suggest, implicitly or explicitly, that the patterns that are identified in the research are universal and natural, and, consequently, often become the basis for public policy. The American or European infant becomes the "universal" infant. For instance, current American research and literature indicate that father's participation in childbirth and father's playful interaction with infants or young children are natural or important aspects of the paternal role. Father's active participation in childbirth contributes to an easier delivery for his wife and facilitates infant-father bonding, which is in turn considered important for the infant's emotional and social development. Father's vigorous play with his infant is suggested to be the means by which the infant becomes attached to the father and the way in which the infant first learns social competence (i.e., the father's vigorous play is the first interactive style that is different from that of the mother, therefore the infant first learns how the deal with an alternative interactive style). Public policy changes have taken place as a result of these research findings. Hospitals and physicians now encourage if not expect fathers to participate in childbirth (prior to the 1970s hospital regulations excluded fathers from the delivery room), and pediatricians and child psychologists are emphasize-

ing the importance of father's "quality" time (i.e., playful and caring attention to child) with his child, rather than the amount of time he spends with his child, so that secure child-father attachment takes place.

In the middle-class American and European cultural contexts, these are important aspects of father's role. Infants are usually placed in their own crib after birth, fathers are seldom around their infants, the father's role as cultural transmitter is minimized since the state provides education, and children leave the family when they go to college or get married. Consequently, participation in childbirth and playful interaction become important mechanisms by which child-father attachment can take place. But studies in non-Western populations indicate that these are not universal or natural features of the father's role. Fathers in non-Western populations are seldom present at childbirth and never direct the mother's birthing process (Hewlett and Hannon 1989), and the few studies that have investigated father's versus mother's interactive style with infants in non-Western populations indicate that vigorous play is not central to infant-father attachment (Hewlett 1991; Roopnairine, 1991). Cultural contexts in non-Western populations are often dramatically different: fathers often sleep with their wife and newborn shortly after birth, fathers are active cultural transmitters, especially with sons, and not all household members leave the family when they get married.

While cross-cultural studies question some of the European and American research, this does not mean that all aspects of father's role are culturally relative. Fathers in all parts of the world do share certain characteristics: fathers provide less direct caregiving than mothers (but there may be some fathers within a culture that take on primary caregiving), fathers are expected to provide at least some economic support for their children, and fathers are expected to support the mother economically and/or emotionally.

This volume aims to elucidate both the diversities and commonalities in the father's role. The volume identifies factors that influence intracultural and intercultural variability in the father's role, and describes how economic, ecological, ideological, and reproductive factors influence both intracultural and intercultural variability.

The volume has three distinct features. First, the volume examines the father's role in several natural and social environments. Hunting-gathering, horticultural, pastoral, and highly industrialized societies are represented; matrilineal, patrilineal, and bilateral descent systems are considered; societies known for their peaceful, nonviolent nature (e.g., Aka, Batek, Ongee) can be compared to societies known for their frequent and extensive warfare and violence (Yanomamo, Agta,

Ache). A diversity of natural environments is also represented: people that have adapted to tropical forest, desert, mountain, and island environments are included in the volume. Considerable emphasis is given to fathers in hunting and gathering societies (Chapters 2, 6, 7, 11, 12, 13, 14) because this way of life characterizes about 90% of human history and it is rapidly disappearing. If we are going to try and understand the nature of fathers' roles it seems that the few remaining hunter-gatherer populations may provide some invaluable clues.

While the volume spans tremendous cultural and environmental diversity, most of the populations are "preindustrial" or what anthropologists sometimes call traditional or band and tribal level societies in the sense that the populations are from relatively rural and some of the least economically developed areas of the world. The frequency and nature of contact with industrialized and hierarchical societies tend to be limited, but these societies are by no means isolated or untouched by industrialization; all of the societies participate in the world economy at some level and they are all part of contemporary nation-states.

The second distinguishing feature of the volume is that it recognizes the importance of understanding both biological and cultural forces that influence the father's role. Contributors in the first section of the volume examine the father's role in evolutionary or biosocial frameworks, while contributors to the second section analyze the father's role in symbolic and cultural contexts. Both sets of authors recognize that ideology and biology are intertwined; both together influence the father's behavior and the effects of his behavior.

The final distinguishing feature is that all of the contributors are fieldworkers. Their research has been field oriented, rather than library or laboratory oriented. Quantitative or qualitative descriptions of father's role are based on long-term naturalistic observations. All of the authors have lived intimately with the people they are writing about.

Investment versus Involvement

It is important to distinguish father (or male) involvement from investment. Contributors in the first section of the book utilize the term male or father investment, while contributors in the second section tend to use the term involvement. The term investment comes from evolutionary biology and refers to a broad range of activities that the father engages in that contributes to the survival of his offspring, and ultimately to the father's own reproductive success. Generally, two types are recognized—direct and indirect (Kleinman and Malcolm 1981). Direct investment refers to male activities and behaviors that have an

immediate physical influence on the child's survival. Direct investment may include holding, grooming, providing food, actively transmitting cultural knowledge, giving gifts, property, or access to resources. Indirect forms of investment are the father's activities and behaviors that benefit the child, but the father would do regardless of the presence of the child. Defending and maintaining access to important food resources, providing the mother with economic or emotional support, or providing the child with an extensive kin network are but a few forms of indirect investment.

Father involvement, on the other hand, is essentially one type of father investment. Involvement refers to interaction with or proximity to the child. Again, there are generally two types of involvement—active and passive. Active involvement refers to holding, feeding, cleaning, or talking to the child, while passive involvement refers to touching, sleeping with, or being near the child. The term involvement is usually used by psychologists or those interested in cross-cultural human development because they are interested in how the father's presence/absence or level of involvement influences the child's emotional, cognitive, personality, or moral development.

Development of the Volume

I began a study of Aka Pygmy father–infant relations in 1984 because of the paucity of data on fathers in non-Western cultures that has been described above. Hundreds of articles and papers existed on white middle-class European and American fathers, but it is near impossible to locate data on fathers in the rest of the world.

While it was very difficult to find published data on fathers in non-Western settings, I knew that many anthropologists and psychologists who were working with non-Western populations must have some data on fathers because the quantitative (behavioral observations) and qualitative (interviews, participant-observation) methods I used in the Aka father study were similar to those used in other anthropological and psychological studies. The idea for the volume emerged several years ago, but it was not possible to start this comparative study of fathers until the Aka study was completed. Shortly after writing up the Aka material I invited anthropologists and psychologists working with non-Western populations to analyze and publish their data on fathers. Preliminary versions of most chapters were first presented at the 1989 Annual Meeting of the American Anthropological Association in Washington, D.C.

THE FATHER'S ROLE IN BIOSOCIAL CONTEXT

The chapters in the first section of the book utilize evolutionary biology to evaluate the nature of the father's role in human populations. This theoretical perspective is often called "biosocial" because it is interested in how biological or evolutionary factors influence and interact with social-cultural factors. Evolutionary biologists are concerned with how individuals in any species adapt to a particular environment. The ability of an individual to adapt to an environment is generally measured by its reproductive success—how many offspring or genes it was able to leave behind in subsequent generations. Consequently, the chapters in the first section focus on the father's reproductive interests—having children, raising children to reproductive maturity, and finding and keeping a spouse.

The biosocial perspective contributes to a better understanding of the father's role in several ways. First, it recognizes a biological dimension to paternal behavior. Anthropologists characterize their discipline as holistic, in part, because it recognizes biological-cultural interactions, but are generally reluctant to utilize evolutionary biology to explain human behavior because it is said to be "reductionist." Daly and Wilson (1988) describe the nature of this biophobia in the social sciences. Evolutionary biology provides the theoretical framework and the analytical tools for investigating biological constraints on human behavior. Second, the evolutionary perspective provides a conceptual framework that contributes to a broad understanding of the father's role. Evolutionary biologists prefer the term male parental investment to father involvement. Investment refers to the multitude of ways in which males can contribute directly and indirectly to their children—providing, caregiving, training, inheritance, etc. The term involvement focuses on active caregiving and interaction and neglects the various other ways that fathers can contribute. The term male rather than father also indicates that men can and do invest in children who are not their own. Finally, the evolutionary approach emphasizes the unity or commonalities of humankind. The assumption of an evolved biological basis for human paternal behavior suggests that fathers worldwide will have common interests, concerns, and emotions. Fathers from all parts of the world are likely to have similar concerns about the safety, health, and development of their children, the paternity of their children, and tradeoffs between spending time with their children and doing things that attract and keep women (e.g., working to increase status, prestige or wealth).

Figure 1 places the father's reproductive interests in the life effort model utilized by evolutionary theorists (Williams 1975; Low 1978). The

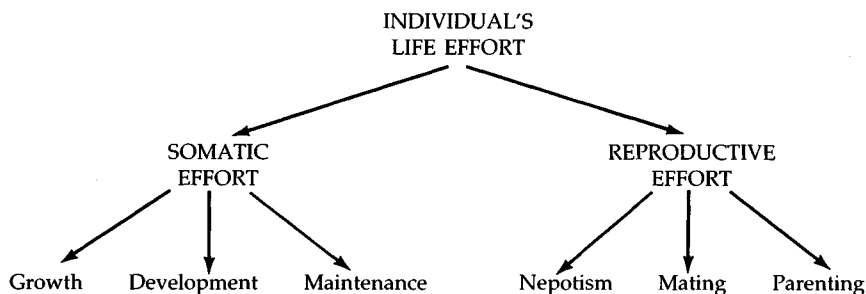


Figure 1. The father's reproductive interests in the life effort model.

model identifies two conceptually distinct categories—somatic and reproductive effort—that an individual engages in if it is to be biologically successful. Somatic effort refers to the risks and costs involved to ensure the physical survival of the individual—having shelter, protection from predators and conspecifics, obtaining food, keeping healthy, and so forth. Reproductive effort has to do with getting copies of one's self into subsequent generations. It is divided into three broad categories—parental effort (rearing children), mating effort (attracting, keeping, and guarding a spouse), and nepotistic effort (helping relatives besides one's own children). Several of the chapters indicate that there are problems with this model (Chapters 1, 7, and 8), especially with the mating effort-parenting effort dichotomy, and discuss the tradeoffs (costs and risks versus benefits) between survival and reproduction, growth and reproduction, and providing parental care and having several children. Fathers that expend more parental effort than mating effort are sometimes said to practice a "dad" reproductive strategy, while fathers with the reverse pattern are characterized as utilizing a "cad" reproductive strategy (Dawkins 1976; Draper and Harpending 1982).

Human males can generally enhance their reproductive success by spending more time in mating effort than in parental effort because males invest less in production than do females. A male's sperm is much smaller than the female's egg and males do not carry the fetus to term or lactate and nurse the infant. Since there is a higher cost to female reproduction, females are predicted to invest more in parental effort than are males. Males on the other hand tend to invest more time in mating effort and therefore compete with other males over available females. The intrasexual competition leads to considerable variance in males' reproductive success—some males gain status and prestige through competition and may attract several wives while other males may never have a wife because they do not have any resources. Chap-

ters 3, 4, and 5 examine how intrasexual competition and father's wealth and status influence paternal caregiving.

Degree of genetic relatedness is also an important factor for evolutionary biologists. A father is predicted to be concerned about the paternity of his children and the degree of relatedness of children that he nurtures, supports, trains, and protects. Several of the chapters (1–4) discuss how paternity certainty or degree of relatedness influences intracultural variability in paternal care.

There is some ordering to the chapters in this section. Chapter 1 is the only chapter in the book that provides a cross-species perspective to male caregiving, and demonstrates that we can better understand human paternal behavior by examining nonhuman primate paternal behavior. It is also a major theoretical contribution to evolutionary biology. Chapters 2–5 identify several evolutionary factors that influence intracultural variability, while Chapters 6–8 move slowly away from a biosocial analysis of the father's role and move into conceptual frameworks of the next section of the book—the cultural context of the father's roles. Chapters 6–8 are especially nice transitions to the second section of the book because both biosocial and cultural paradigms are described and evaluated.

THE CULTURAL CONTEXT OF THE FATHER'S ROLE

The chapters in the second section of the book to a greater or lesser degree take biology for granted and focus on how cultural factors influence fathers' roles. To understand this theoretical perspective it is necessary to understand the concept of culture. Culture is knowledge that is transmitted generation to generation and has several distinguishing features: it is by nature ethnocentric, it influences an individual's physical and affective reality, and patterns how an individual classifies and organizes the world. Culture, of course, manifests itself in infinite ways. Super and Harkness (1986) describe three major aspects of culture as experienced by an individual at various life stages: (1) the physical and social setting of everyday life, (2) culturally regulated customs of care and rearing, and (3) the cognitive and affective orientations of parents and other caregivers (i.e., caregivers ideology and beliefs). A researcher interested in understanding the cultural factors that influence the father's role would have to know the place the father sleeps, eats, works in relation to his children, the availability of other caregivers, contexts in which fathers are expected to care for children, and the beliefs fathers have about children and their role as fathers. According to Super and

Harkness these three aspects of culture—demographic context, cultural practices, and ideology—can help to explain intracultural and intercultural diversity in fathers' roles.

The chapters in this section emphasize different components of the Super and Harkness model. Chapters 10 and 11 identify factors in the physical and social setting that contribute to the level and nature of father-child relations, Chapters 13 and 14 describe cultural practices that influence father-child relations, and Chapters 12, 15, and 16 emphasize how ideology or symbolic systems influence fathers' roles.

There are of course other cross-cultural human development models that identify important features of cultural context (Whiting and Whiting 1975; Whiting and Edwards 1988; LeVine 1977), but the Super and Harkness model is the most recent contribution and covers many of aspects of culture context identified in other models. Harkness and Super discuss some of these other models in Chapter 9.

The cultural perspective contributes to a better understanding of father's roles in several ways. First, it demonstrates how the father's role is often relative to culture context. Culture is by nature ethnocentric; individuals raised in a particular culture generally come to view their customs and ideology about the father's role as universal and natural. As previously described, Europeans and Americans perceive active participation in childbirth and vigorous interaction with children as not only highly desirable but as natural and universal aspects of the father's role. These are not necessarily universal or natural aspects of the father's role if non-Western cultural contexts are considered. Second, the cultural perspective demonstrates that ideology influences the father's actions. For instance, Chapter 9 by Harkness and Super indicates that U.S. and Kipsigis fathers are around their children about the same amount of time, but U.S. fathers are much more engaging with their children than are the Kipsigis fathers. U.S. fathers are more interactive because they feel that stimulating interaction with their children is an important part of their role.

The first three chapters of the second section use cross-cultural comparisons to examine the diversity and cultural context of fatherhood. The last of these three chapters that uses a comparative approach (Chapter 11) is exceptional in that both cultures live in the same tropical forest environment. Chapters 12–16 are ethnographic case studies of father-child relations. Chapters 12–14 explore the cultural context of father's role among three Asian tropical forest hunter-gatherer societies, while Chapters 15 and 16 describe how the father's role in Cameroon and Inner Mongolia is influenced by modernization and urbanization.

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PART I

***Dad and Cad Reproductive Strategies:
Biosocial Context of Father's Role***



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Chapter 1

Male–Infant Relationships in Nonhuman Primates: Paternal Investment or Mating Effort?

Barbara B. Smuts and David J. Gubernick

Since natural selection favors behaviors that promote individual reproductive success, both males and females should be expected to direct caregiving to their own offspring rather than the offspring of other individuals. Because female mammals gestate and give birth, they can normally be certain which offspring are theirs. In contrast, males can never be absolutely certain of paternity, because their mates could have copulated with other males. This has led to the prediction that male care of offspring is most likely to evolve in species in which males can achieve high paternity certainty and thus increase the chances that their investment is directed toward their own young (Alexander et al. 1979; Barash 1982; Kurland and Gaulin 1984).

Although male care of infants is uncommon in mammals in general, it occurs in about 40% of primate genera (Kleiman and Malcolm 1981). High paternity certainty is the most common explanation given for the occurrence of male–infant care in nonhuman primates (Alexander and Noonan 1979; Bales 1980; Busse 1984; Kurland 1977; Redican 1976; but see Snowdon and Suomi 1982 for a different view). In this chapter, we evaluate several predictions derived from the paternity certainty hypothesis by examining differences between nonhuman primate species in the prevalence of male–infant care. As a further test of the paternity certainty hypothesis, we investigate differences between individuals within polygynous species in the extent of male care of young. We argue that the paternity certainty hypothesis does not provide an adequate explanation for patterns of male–infant care in nonhuman primates, and we present an alternative hypothesis to account for these patterns. We

conclude with some possible implications for the evolution of male-infant care in humans.

A careful formulation of the paternity certainty hypothesis states that high paternity certainty is a necessary, but not sufficient, condition for the evolution of male parental care; in addition, infants must also benefit from male care. Thus, interspecific variation in the importance of male care to infant survival (and, ultimately, to the infant's own reproductive success) could in theory account for some of the variation across species in patterns of male care. However, since almost no information is available on the effects of male care on infant survival in the wild, we cannot presently determine the role this variable plays in the evolution of male parental care in primates. In evaluating the paternity certainty hypothesis, therefore, we assume that interspecific variations in the benefits infants derive from male care do not obscure the expected relationships between paternity certainty and male care described below.

Paternity Certainty Hypothesis: Predictions

Several predictions follow from the paternity certainty hypothesis:

1. Male care of infants should be more prevalent in monogamous species because a single male typically monopolizes matings, and paternity certainty is therefore high.
2. Male care of infants should be more prevalent in species that live in one-male groups because a single male typically monopolizes matings, and paternity certainty is therefore high.
3. Male care of infants should be relatively rare in species that live in multimale groups because females typically mate with more than one male, and paternity certainty is therefore low.
4. In those multimale groups in which male care is observed, it should involve those infants most likely to be the male caregiver's offspring.

Below, we first evaluate predictions 1–3, which concern interspecific variation in the prevalence of male-infant care. We then evaluate the fourth prediction, which concerns variation in male care within particular species.

MALE CARE OF INFANTS: INTERSPECIFIC COMPARISONS

We evaluate the first three predictions listed above using data primarily from wild and free-ranging (provisioned) primates. Information from captive groups is included when it is especially relevant. These compari-

sons are necessarily based on qualitative information, since few studies provide quantitative information on rates of male-infant interactions that can be compared across species.

Male care of infants can be divided into two types: (1) direct care, where the male directs caregiving behaviors (such as carrying, holding, grooming, protection) toward particular infants, and (2) indirect care, where the male performs behaviors that could benefit infants (such as defending the group's territory or chasing away predators), but these behaviors are not directed toward any particular infant(s) (Kleiman and Malcolm 1981). Although indirect care may sometimes be important, it is in practice difficult to determine when male behavior such as territorial defense is designed to benefit infants and when such potential benefits are simply an incidental byproduct of behavior performed for other reasons, such as to exclude male rivals. Because of this difficulty, we focus our analysis on instances of direct male care.

To simplify comparison between species, we have used a dichotomous classification: presence or absence of male care (see Table 1 for details). We categorize species as *male care present* when adult males typically show either "intensive caretaking" or "affiliation," as defined by Whitten (1987). We categorize species as *male care absent* when males show either no care of infants or only "occasional affiliation" or "tolerance" (Whitten 1987). Male caretaking and affiliative behaviors include carry, protect, share food, co-feed (allow infant to feed in close proximity), groom, hold, and frequent close proximity.

Table 1 lists the presence or absence of male care in monogamous, one-male, and multimale groups of nonhuman primates. Table 1 is not exhaustive but includes all species in which it is known that male care is present, except for some marmosets and tamarins (see below).

Prediction 1: Male Care Is More Prevalent in Monogamous Species

In general, prediction one is supported: most monogamous species show male care of infants (Table 1). In fact, in the monogamous species listed as having male care (such as owl monkeys and titi monkeys), all paired males show infant care, and they provide more extensive care than males in any other primate species except tamarins and marmosets, which are discussed further below. However, the gibbons represent a striking exception to this general pattern; within this family, only siamangs show direct male care. Several gibbon species have been well studied in the wild, and no evidence indicates that paternity certainty is lower for gibbon males than for males of the other monogamous species listed here (Robbins Leighton 1987). Thus, although male care is most

Table 1. Presence or Absence of Male-Infant Care in Relation to Mating System in Selected Nonhuman Primates^a

| | <i>Male care present</i> | <i>Male care absent</i> |
|------------------|--|--|
| Monogamy | Owl monkey ¹ Dusky titi monkey ² Yellow-handed titi monkey ³ Siamang ⁴ Black howler monkey ⁵ | All gibbons (8 species) ¹⁵ |
| One-male groups | Mountain gorilla ⁶ | Gelada baboon ¹⁶ Hamadryas baboon ¹⁷ Hanuman langur ¹⁸ Banded leaf monkey ¹⁹ Dusky leaf monkey ²⁰ Mentawai langur ²¹ Capped langur ²² Campbell's guenon ²³ Lowe's guenon ²⁴ Patas monkey ²⁵ |
| Multimale groups | Saddle-back tamarin ⁷ Black-capped capuchin ⁸ Olive baboon ⁹ Yellow baboon ¹⁰ Chacma baboon ¹¹ Babary macaque ¹² Stumptail macaque ¹³ Japanese macaque ¹⁴ | Sifaka ²⁶ Red howler monkey ²⁷ Common squirrel monkey ²⁸ Rhesus macaque ²⁹ Bonnet macaque ³⁰ Long-tailed macaque ³¹ Vervet monkey ³² Chimpanzee ³³ |

Note: Species are classified as "male care present" when they show "intensive caretaking" or "affiliation"; species are classified as "male care absent" when they show "occasional affiliation" or "tolerance." Whitten (1987) defines these terms as follows: "Intensive caretaking: males spend a large part of the day engaged in infant caretaking; although the actual extent of male participation varies, males predictably perform some parental duties for all infants"; "Affiliation: males spend part of the day engaged in affiliative interactions with one or more specific infants; most males interact affiliatively with at least one infant"; "Occasional affiliation: males occasionally interact affiliatively with one or more infants, but these associations are not characteristic of all males nor of any single male all of the time"; "Tolerance: males permit infants to be near them but otherwise interact rarely with infants" (p. 343). This table is not exhaustive, but it includes all species in which it is known that male care is present, except for some tamarins and marmosets (discussed in text). For many additional species living in one-male and multimale groups, no evidence of male care, as defined here, exists.

^aReferences: ¹Wright (1984); ²Wright (1984); ³Kinzey (1981); Kinzey et al. (1977); Starin (1978); ⁴Chivers (1974); Chivers and Raemakers (1980); ⁵Bolin (1981); ⁶Fossey (1979, 1983); Harcourt (1979); Harcourt and Stewart (1981); some groups have more than one adult male; additional males usually do not breed; ⁷Goldizen (1987, 1988); Terborgh and Goldizen (1985); ⁸Escobar-Paramo (1989); Janson (1984, 1986); van Schaik and van Noordwijk (1989); ⁹Packer (1980); Ransom and Ransom (1971); Smuts (1985); Strum (1984, 1987); ¹⁰Altmann (1980); Stein (1984a,b); ¹¹Busse (1984); Busse and Hamilton (1981); ¹²Burton (1972); Deag (1974, 1980); MacRoberts (1970); Taub (1980b, 1984); ¹³Estrada (1984); Estrada and Sandoval (1977); Smith and Peffer-Smith (1984); ¹⁴Itani (1959); Hasegawa and Hiraiwa

common and most intensive among monogamous primates, the paternity certainty hypothesis leaves unexplained some notable exceptions.

Prediction 2: Male Care Is More Prevalent in Species Living in One-Male Groups

The evidence in Table 1 does not support this prediction. With the exception of mountain gorillas, in none of these species does the breeding male show frequent caregiving or affiliative behavior toward infants, and in some species, males virtually never interact with infants at all (e.g., capped langurs, patas monkeys). Thus, the paternity certainty hypothesis does not explain patterns of male-infant relations in species breeding in one-male groups.

One possible objection to this conclusion is that, despite the one-male group structure, females in these species actually mate frequently with other males and hence paternity certainty is thereby reduced (cf. Alexander and Noonan 1979). In some cases, copulations with outside males do occur (e.g., patas monkeys: Chism and Rowell 1986; Harding and Olson 1986; redbtail monkeys: Cords 1984; blue monkeys: Tsingalia and Rowell 1984; hanuman langurs: Hrdy 1977; Sommer 1988). In patas monkeys, for example, multimale influxes during the breeding season occur regularly, females mate promiscuously with several different males, and paternity certainty for the "resident" male is probably consistently quite low (Chism and Rowell 1986; Harding and Olson 1986). The situation for other "one-male" species appears to be more ambiguous. In blue monkeys and redbtails, multimale influxes accompanied by promiscuous mating sometimes occur (Cords 1984; Henzi and Lawes 1988; Tsingalia and Rowell 1984), but their likelihood varies from year to year, depending on factors such as the number of females that are simultaneously sexually receptive and the local population density of extra-group males (Butynski 1982; Cords 1987; Henzi and Laws 1988).

(1980); Hiraiwa (1981); Takahata (1982a); the extent of male care varies considerably between different troops in this species, but in at least some troops, males show frequent affiliation (Itani, 1959); ¹⁵Robbins-Leighton (1987); Wittenberger and Tilson (1980); ¹⁶Dunbar (1984a); Mori (1979a); ¹⁷Kummer (1968); ¹⁸Hrdy (1976, 1977); in some habitats found in multimale groups; ¹⁹Curtin (1980); in some habitats, found in multimale groups; ²⁰Curtin (1980); in some habitats, found in multimale groups; ²¹Wittenberger and Tilson (1980); ²²Stanford (1989); ²³Galat-Luong and Galat (1979); ²⁴Bourliere et al. (1970); ²⁵Hall (1967); Loy and Loy (1987); ²⁶Jolly (1966); ²⁷Sekulic (1983); ²⁸Vogt (1984); ²⁹Breuggeman (1973); Taylor et al. (1978); Vessey and Meikle (1984); ³⁰Simonds (1965, 1974); Sugiyama (1971); ³¹van Noordwijk and van Schaik (1988); Mitchell and Brandt (1972); ³²Struhsaker (1967); Whitten (1987); ³³Goodall (1986); Nishida (1983).

Observations to date indicate that in both blue monkeys and redtails, several years may pass in which the resident male monopolizes most matings (Butynski 1982; Cords 1987; Rudran 1978; Struhsaker and Leland 1979). Speaking of blue monkeys, Rowell (1988, p. 192) carefully concludes, "It is quite likely that resident males sire most of the offspring conceived in their group during their tenure, but it is by no means sure." A similar conclusion may apply to hanuman langur populations characterized by one-male groups. During most of the tenure of a given male, he monopolizes matings with the females in his group, but females do occasionally mate with outside males, especially during takeover attempts when an all-male band may invade the troop (Hrdy 1977; Sommer 1988). It is important to note that, contrary to the paternity certainty hypothesis, male care is consistently absent in the species mentioned above, even during those times when paternity certainty appears to be quite high.

In still other species that live in one-male groups, female copulation with males other than the adult breeding male appears to be extremely rare. For example, observers studying wild hamadryas baboons for several years saw no instances of adulterous mating (Sigg et al. 1982). Similarly, in gelada baboons, mating is usually restricted to a single male (Dunbar 1984b). Yet, in neither of these species does the breeding male show frequent affiliative interactions with his infants.

Until paternity is determined through genetic analysis, the frequency with which infants are fathered by nonresident males cannot be known with certainty, but our current knowledge of mating behavior indicates that, in many species that live in one-male groups, the resident male is usually the father of infants born in those groups. The virtual absence of male-infant care in these species does not support the paternity certainty hypothesis.

Prediction 3: Male Care is Relatively Rare in Species Living in Multimale Groups

The presence of male care/affiliation in a number of species living in multimale groups is inconsistent with this prediction. Table 1 shows that patterns of male-infant relationships vary considerably in primates living in multimale groups characterized by female promiscuity (i.e., females typically mate with more than one male around the time of conception). In some species, such as rhesus macaques or vervet monkeys, males rarely interact with infants, which would appear to conform to the paternity certainty hypothesis. However, other species living in multimale groups, such as Barbary macaques and savanna baboons, show frequent affiliative male-infant interactions, despite low certainty

of paternity. The paternity certainty hypothesis might account for instances of male care in these species if only one or two males monopolized matings. There is no evidence that this is the case; for example, in savanna baboons, which show male care, females typically mate with several males during the week of peak fertility (Hausfater 1975; Scott 1984; Smuts 1985). In addition, behavioral evidence indicates that Barbary macaques are more promiscuous than any other species listed in Table 1 (Small 1990; Taub 1980a). While in estrus, female Barbary macaques initiate and terminate a series of brief consortships that allow them to copulate, at least once, with virtually every sexually mature male in the group. Yet the males of this species frequently carry, hold, and protect infants, and they are, in fact, the only nonmonogamous species classified by Whitten (1987) as showing "intensive caretaking."

The saddle-back tamarins listed in Table 1 deserve special mention. The callitrichid primates (the tamarins and marmosets) all show elaborate male care of infants (Box 1975; Epple 1975; Hoage 1978; Terborgh and Goldizen 1985; Vogt et al. 1978), including extensive infant carrying, comparable to the male care shown by monogamous New World monkeys like owl monkeys and titi monkeys (Wright 1984). Until recently, callitrichids were considered monogamous, because all wild groups that had been observed contained only one breeding female, and captive animals appeared to breed most successfully when caged in pairs (Goldizen 1988). However, a detailed field study of individually recognized saddle-back tamarins showed that many groups included two males and one breeding female, and behavioral observations indicated that both males copulated and both males cared for the infants (Goldizen 1987; Terborgh and Goldizen 1985). Few data are available on the mating patterns of other callitrichids, but in both moustached tamarins (Garber et al. 1984) and emperor tamarins (Goldizen 1988), many groups contain more than one adult male, suggesting that polyandry may occur. Saddle-back tamarins are the only callitrichids included in Table 1, because, until more field data are available, we cannot reliably classify the breeding systems of the other species. The data available for saddle-back tamarins do not support the paternity certainty hypothesis, since extensive male care is shown by males even though paternity certainty is considerably reduced.

In summary, the paternity certainty hypothesis does not provide an adequate explanation for *interspecific* differences in the prevalence of male care of infants in nonhuman primates (see also Smuts 1985; Snowdon and Suomi 1982; Whitten 1987). This conclusion is supported, in particular, by the fact that several highly promiscuous species show considerably more frequent male care of infants than do any of the species breeding in one-male groups.

MALE-INFANT RELATIONSHIPS IN PROMISCUOUS SPECIES

Olive Baboons: A Case Study

The fourth prediction states that, within multimale groups, male care should reflect the degree of paternity certainty. In other words, males should care primarily for those infants they are most likely to have sired. This prediction is evaluated below, first, through a detailed case study of olive baboons and, second, by reviewing patterns of male care in several other species living in multimale groups.

Affiliative relationships between particular adult males and particular infants were a notable feature of the Eburru Cliffs group, a savanna baboon society studied between 1977 and 1983 near Gilgil, Kenya (Nicolson 1982; Smuts 1983a,b, 1985). These male-infant relationships were characterized by frequent close proximity, affiliative interactions such as greeting and grooming, and intimate physical contact including carrying, holding, and cuddling (Figure 1). Affiliative and care-giving interactions between males and infants were almost entirely restricted to these particular relationships. Infants showed fear toward, and avoided, all other males.

Males provided numerous, important benefits to the infants with whom they associated (Smuts 1985). They protected the infants against predation and potential infanticide by other baboon males (see also Packer 1980; Stein 1984b). They also allowed the infants to feed with them. Since adult males monopolized the best feeding sites, this association may have provided important nutritional benefits to rapidly growing infants (see also Altmann 1980; Stein 1984b). Males encouraged the infants to rest near them by engaging in spirited grunting duets, and they were very tolerant of infant proximity and physical contact during rest or play sessions.

In the Eburru Cliffs group, the male's relationship with the infant was closely tied to the male's relationship with the infant's mother (Figure 2). Quantitative analysis of data on male-female interactions showed that each female in the troop formed a long-term, special relationship, or "friendship," with one or two of the 18 adult males; different females had different males as friends. Friends groomed each other much more than other male-female dyads, had many more affiliative interactions, and spent a great deal of time in proximity, especially when the female was nursing a young infant. As a result of the male's friendship with the mother, he developed a long-term, protective relationship with her infant. Although only 12% of all possible adult male-adult female dyads in the troop were considered "friends," virtually all male-infant affiliative interactions involved males who were friends with the infant's



Figure 1. An adult male olive baboon from Eburru Cliffs troop holding the hand of an infant female with whom he has developed an affiliative relationship.

mother (Smuts 1985). With few exceptions, friendships involved males who had transferred from other groups and who were therefore unrelated to their female friends.

Friendship with the mother appeared to be a better predictor of male-infant relationships than was probability of paternity (Smuts 1985). Evidence for possible paternity was based on detailed observations of female mating behavior during the estrous cycle in which she conceived. At this time, females typically form a series of temporary but exclusive mating relationships, called consortships, with several different males. Males observed in consort with the female during the 7 days of peak fertility of her conception cycle were labeled "possible fathers." Using this criterion, most infants had two or three possible fathers. In 55% of the friendships, the male was a possible father of the female's current



Figure 2. Adult male (left) and adult female olive baboon “friends” asleep together.

infant, but in the remaining 45%, he had never been observed mating with the mother, and, in several cases, had not even been in the group when the infant was conceived.

Table 2 shows that friendship was a better predictor of male–infant relationships than was possible paternity. In 80% of the male–infant dyads where the male was a friend of the mother, the male showed affiliative behavior toward her infant, and this probability remained the same whether or not he was a possible father. Males who were possible fathers but who were not friends with the mother showed affiliative behavior toward the infant in only 25% of the dyads, while males who

Table 2. Effect of Possible Paternity and Friendship with the Infant’s Mother on Male–Infant Affiliation in Eburru Cliffs Baboons

| <i>Male was friend</i> | <i>Male was possible father</i> | <i>Number of dyads</i> | <i>Percent of dyads affiliative</i> |
|------------------------|---------------------------------|------------------------|-------------------------------------|
| Yes | Yes | 12 | 83.3 |
| Yes | No | 10 | 80.0 |
| No | Yes | 12 | 25.0 |
| No | No | 192 | 3.0 |

Note: Data from Smuts (1985).

were neither friends nor possible fathers showed affiliative behavior in only 3% of the dyads. These results indicate that (1) for a male, the existence of a prior friendship with the mother was both a necessary and sufficient condition for the development of an affiliative relationship with her infant and (2) being a probable father was likely to result in an affiliative relationship with the infant only if the male also had a friendship with the mother.

Thus, in the Eburru Cliffs group males sometimes formed close bonds with infants who were not their own offspring. Why did they do so? Data on consortships during the second-half of the study showed that adult males who had formed a prior friendship with the female had a significantly increased probability of mating with her in the future. Smuts (1985) argued that, in these baboons, males invested in infants not because those infants were likely to be their own (i.e., they had high paternity certainty), but because caring for infants increased the probability that the male would be chosen by the mother as a mate in the future (see also Seyfarth 1978). In other words, male-infant caregiving can be viewed as a form of "mating effort" rather than as "paternal investment." This hypothesis is developed further, below. First, however, we ask whether observations of other species living in multimale groups are consistent with the results presented above for Eburru Cliffs.

Male-Infant Relationships in Savanna Baboons and Macaques

Affiliative relationships between particular adult males and infants, similar to those described above for Eburru Cliffs, have been observed in a number of baboon troops and in several species of macaques. However, quantitative data relating male-infant interactions to probability of paternity and to the males' social relationships with the infants' mothers are available in only a few cases, which are summarized in Table 3. We can use these data to test further the prediction that male care is related to a high probability of paternity.

In three of the six cases listed in Table 3, males developed affiliative relationships with infants significantly more often when they were likely fathers than when they were not, but in the other three cases, probability of paternity had no effect on male-infant relationships. Information is available on the males' relationships with the infants' mothers in four of the six cases. In all of these instances, affiliative bonds with mothers were significantly associated with the development of male-infant relationships. Most importantly, in the three cases that showed a positive relationship between probability of paternity and male-infant affiliation, researchers concluded from the evidence that the male's

Table 3. Male-Infant Affiliation, Paternity, and Male-Female Relationships in Savanna Baboons and Macaques

| Species ^a | Male-Infant Affiliation Related to: | | Method of assessing paternity ^b | References |
|----------------------|---|-----------------------------|--|---|
| | Special relationship with mother | Probability of paternity | | |
| Olive baboon (w) | Yes | Yes | CC | Smuts (1983b, 1985) |
| Olive baboon (w) | — | No | CC | Packer (1980) |
| Yellow baboon (w) | Yes | Yes | CC | Altmann (1980); Stein (1984a,b) |
| Barbary macaque (p) | ? | No | MC | Kuester and Paul (1986) |
| Japanese macaque (p) | Yes | No | CB | Takahata (1982a); Gouzoules (1984) |
| Rhesus macaque (c) | Yes | Yes | G | Berenstain et al. (1981); Kaufman (1967) |

Note: Even though rhesus males show only occasional affiliation with infants (Table 1), they are included here because this study provides information highly relevant to the paternity certainty hypothesis. Berenstain et al. (1981) define male-infant affiliation in terms of amount of time spent in close proximity.

^aw, wild; p, free-ranging, provisioned; c, captive.

^bCC, quantitative analysis of consort activity around the time the infant was conceived; MC, quantitative analysis of mating around the time the infant was conceived; CB, quantitative analysis of consort activity throughout the breeding season; G, genetic determination of paternity.

^cOf seven studies on Barbary macaques, only two provide information on male-female relationships. MacRoberts (1970) reported that two subadult males who developed strong affiliative bonds with infants had special relationships with the infants' mothers. Small (1990) claimed that Barbary macaque males and females do not form special relationships but did not present data on proximity or social interactions of particular male-female dyads.

relationship with the mother was an even more important determinant of male-infant affiliation than was paternity (Berenstain et al. 1981; Smuts 1985; Stein 1984b). The research by Berenstain et al. (1981) is particularly noteworthy, because it is the only study that determined paternity through biochemical analysis. In a large, captive group of rhesus macaques, fathers and offspring were found in close proximity to one another more often than other male-infant dyads. However, "the

effect of paternity disappeared when maternal association with males was controlled. . . . This result accords with the hypothesis that selective father-offspring association depends on the mother's relationship with males" (p. 1061).

Several other studies provide information that supplements the data summarized in Table 3. Strum argued that the male-infant affiliative relationships she observed in olive baboons were related to the males' social bonds with the infants' mothers (Strum 1987) and were unrelated to paternity (Strum 1984). Busse (1984) and Busse and Hamilton (1981) reported that instances of male-infant carrying in chacma baboons in the presence of other males ("triadic interactions") were related to both male-female bonds and to paternity. However, because their assessment of paternity was based on male dominance rank rather than mating activity, the role of paternity in male-infant carrying remains unclear. In a review of all published studies of triadic interactions in savanna baboons, Smith and Whitten (1988) concluded that "the most common denominator of triadic interactions is a close affiliative relationship of the carrier male, whether related or not, with the infant and its mother . . . [which] suggests that the cultivation and/or maintenance of special relationships with females may be central to triadic interactions" (p. 422). van Noordwijk and van Schaik (1988) reported increased proximity between probable fathers and infants in wild long-tailed macaques, but, like Busse and Hamilton (1981), they used male dominance rank to estimate probability of paternity. They did not provide a measure of male-female affiliation. In stumptailed macaques, in which males frequently interact in affiliative ways with infants, no data are available on the effect of paternity, but several studies suggest that the males' social relationships with mothers may influence male-infant affiliation (Estrada and Sandoval 1977; Estrada 1984; Smith and Peffer-Smith 1984).

In summary, in savanna baboons and macaques, the relationship between probable paternity (as assessed from mating activity) and male-infant affiliative relationships explains some, but by no means all, or even a major part, of the data. Although several studies report a link between probable paternity and male-infant affiliation, no studies have shown that probability of paternity influences male-infant affiliation independent of male-female bonds. When researchers have systematically examined both the male's social relationship with the infant's mother and paternity, they have concluded that the former is a more important determinant of male-infant affiliation. Below, we explore the implications of this finding in more detail. First, however, we briefly review data from two other primates relevant to the paternity certainty hypothesis.

Male-Infant Relationships in Vervets and Capuchins

Vervets are small African monkeys related to baboons and macaques that live in small groups with several adult males and females. Males typically show neither caretaking nor affiliative behaviors toward infants. Hauser (1986), however, examined the potential for male protection of infants by playing back tape recordings of infant distress calls to adult males in five groups of wild vervets. He found that some males attended to the call (measured by the duration of looking toward the speaker) significantly more than did other males. Paternity was estimated by frequencies of copulations with the infants' mothers during the season when the infants were conceived. Paternity certainty correlated positively and significantly with male response to infant distress calls.

It is possible, however, that a male's response to infant distress calls reflects the male's social relationship with the mother; if sexual and social relationships overlap extensively, as they do in baboons, this could account for the correlation Hauser (1986) found between mating behavior and male response. There is no evidence that male vervets form obvious friendships with females as male baboons and macaques do, but further study might reveal more subtle social preferences.

Laboratory data indicate, however, that the male vervet's response to infants is mediated by the mother's presence (Keddy Hector et al. 1989). Individual males and infants were removed from the group and allowed to interact briefly. The infant's mother was either present and visible behind a plexiglass partition, present behind a one-way mirror (so that she could see the male and infant but they could not see her), or absent. When they knew mothers were watching, alpha males directed significantly less agonistic behavior toward infants. Under these same conditions subordinate males (all unlikely fathers) showed significantly more affiliative behavior toward infants. When the mothers were subsequently given access to the males, the degree of agonism they showed toward the males correlated negatively and almost perfectly with the degree of affiliative behavior the males had shown toward their infants; in other words, females punished males who were not nice to their infants.

Whether or not the mother was present, alpha males who were likely fathers showed significantly more affiliative behavior toward infants than alpha males who were not likely fathers. However, subordinate males (unlikely fathers), contrary to the paternity certainty hypothesis, showed as much affiliative behavior toward infants as did alpha males, but only when they could see that the mothers were watching.

These data suggest that males behaved affiliatively toward infants to influence their relationships with the mothers—specifically, to reduce female aggression and perhaps also to increase the likelihood of future cooperative relations with particular females. Field data suggest that such reductions in female aggression could be important for males, since vervet females reject male suitors aggressively (Andelman 1985) and form aggressive coalitions to prevent males from joining their troops (Cheney 1983a,b). More data are needed to clarify the effects of paternity and male–female relationships on male–infant interactions in vervets.

Black-capped capuchins are the only nonmonogamous New World primates in which extensive male–infant affiliation has been described (Escobar-Paramo 1989; Janson 1984). Like vervets, they live in fairly small, multimale, multifemale groups. Janson (1984) found that all estrous females initiated copulations and showed strong and active preferences for mating with the alpha male around the time of conception. The alpha male was therefore the likely father of all infants in the group. He allowed these infants to feed near him, although he threatened other subordinate animals away. Since the alpha male monopolized the best feeding sites, his tolerance at food sources provided nutritional benefits to infants. In addition, he was observed defending infants against aggression from other troop members. Escobar-Paramo (1989) describes similar alpha male tolerance of infants during feeding, and she also reports that infants congregate around the alpha male during rest and play sessions. However, other males have been observed behaving affiliatively toward infants. van Schaik and van Noordwijk (1989) reported that during times of fruit scarcity, not only the alpha male, but other troop males as well, attracted females and their young by food calls and allowed them to eat the males' leftovers.

Janson argued that the alpha male's tolerance and protection of infants reflected paternity. In support, he cited one instance in which a newly dominant male was intolerant toward a juvenile sired before the male took over, but was later tolerant toward juveniles of similar age that he probably fathered (1984, p. 196). Although paternity certainty may influence male–infant relationships in black-capped capuchins, male–female relationships may also be important, as discussed further below.

Summary of Results within Species Living in Multimale Groups

Contrary to the paternity certainty hypothesis, in all promiscuous species that show regular male–infant caregiving, males often care for

infants they probably did not father. The relationship between likelihood of paternity and male-infant care varies. Male-infant care is not associated with paternity (as measured by mating behavior) in Barbary macaques (Kuester and Paul 1986), Japanese macaques (Gouzoules 1984), and some baboon groups (e.g., Packer 1980). In other baboon groups (e.g., Smuts 1985; Stein 1984a,b), paternity and male care are positively correlated, but paternity appears to be a less important determinant of male-infant relationships than the male's social relationship with the infant's mother. Vervet data suggest a possible role for paternity certainty, but they also show that male behavior toward infants is influenced by the mother's presence, independent of paternity certainty.

In all of these studies, paternity was estimated on the basis of sexual behavior; such estimates may not always reflect actual paternity (Stern and Smith 1984). Only one study (Berenstein et al. 1981) has combined biochemical analysis of paternity and data on male-infant relationships, and it clearly showed that the male's relationship with the mother influenced male-infant proximity, while paternity alone did not.

Taken together, these data suggest that patterns of male-infant relationships in species living in multimale groups often reflect the males' social relationships with the infants' mothers more than the males' genetic relationships to the infants. Below, we discuss this finding and develop further the mating effort hypothesis.

MALE-INFANT CAREGIVING AS MATING EFFORT

Males normally maximize reproductive success by mating with multiple females. Female reproductive success, in contrast, is limited primarily by time and energy demands, which can sometimes be reduced through male paternal assistance (Trivers 1972; Wittenberger and Tilson 1980). However, male investment in one female's offspring often reduces the male's chances of inseminating other females (Trivers 1972). For this reason, evolutionary theorists usually regard male efforts to obtain mates (i.e., mating effort) and male care of infants as alternative and opposing male reproductive strategies (see Hurtado and Hill, this volume). However, male care of young is not always an alternative to mating effort; it can sometimes represent a means by which males increase their mating success. Indeed, male care of infants represents mating effort rather than parental investment whenever selection favors male care because of the benefits males receive *in exchange* for this care rather than because of enhanced survivorship of their own infants. This does not mean that females or infants do not benefit from male care; in fact, they must do so, or else females would not be selected to engage in

an exchange of benefits with males. We propose that male primates sometimes care for infants in response to female mate preferences for such caring males, or in exchange for other benefits provided by females (or occasionally by the infants themselves) that contribute to male mating success.

The mating effort hypothesis predicts that male care of and affiliation toward infants will be most likely when (1) infants can benefit from male care, (2) females (or infants) can control and offer important benefits to males, and (3) females (or infants) have opportunities to compare the behavior of different males and then, on the basis of this comparison, distribute benefits to some males but not others.

The benefits females provide males in exchange for male care, affiliation, or protection of their infants can vary within and between species. In olive baboons, males gain increased mating opportunities with the mothers of affiliated infants (Seyfarth 1978; Smuts 1985). Males can also gain benefits directly from affiliated infants who cooperate with the males during tense interactions with other males, thereby reducing the males' vulnerability to attack (Collins 1986a,b; Packer 1980; Stein 1984a,b; Strum 1984).

In rhesus and Japanese macaques, friendship with females and their infants generally does not increase a male's mating opportunities with those females (Chapais 1981, 1983a; Takahata 1982a,b). However, male macaques appear to receive substantial benefits from agonistic alliances with affiliated females. Among rhesus macaques, female intervention in male-male disputes can strongly influence male-male dominance relationships (Chapais 1983b). Female interventions also appear to affect male status in Japanese macaques (Koyama 1970), and female aggression—or lack of it—can determine the fate of a new male attempting to enter a group (Fedigan 1976; Packer and Pusey 1979). In 10 captive groups of vervet monkeys in which the alpha males were experimentally removed, bonds with high-ranking females predicted the identity of the new alpha males while male rank did not (Raleigh and McGuire 1989). In macaques as well, bonds with high-ranking females can be especially important in helping a male to achieve and/or maintain high rank (Chapais 1983b; de Waal 1989). The importance of developing ties with influential females may explain why male macaques (Auerbach and Taub 1979; Gouzoules 1975; Hendy-Neely and Rhine 1977) and vervets (Keddy Hector et al. 1989) sometimes bias their affiliative interactions toward the infants of high-ranking females.

The third condition listed above suggests that male care for infants as a form of mating effort should be more common when females are in a position to dispense benefits among more than one male on the basis of the males' behavior toward infants. In species that live in one-male

groups, such as hamadryas baboons, mountain gorillas, or hanuman langurs, such opportunities for female choice are probably normally more limited than in species that live in multimale troops, where females can routinely interact with, and compare, several different males. The mating effort hypothesis is thus entirely consistent with the fact that male-infant caregiving is more common in polygamous primates living in multimale groups than it is in those living in one-male groups.

However, even in species living in one-male groups, females sometimes have opportunities to choose between different males. Such female choice may help to explain several findings that are not consistent with the paternity certainty hypothesis. For example, in gelada baboons, young male "followers" sometimes attempt to join one-male breeding units. If successful, the follower may eventually succeed in luring a few females away to form a unit of his own. Followers cultivate special relationships with females and infants of the unit, even though those infants are not their own. Mori (1979b) has suggested that follower males attempting to join a breeding unit care for infants to develop intimate bonds with the infants' mothers. In addition, Dunbar (1984a) suggested that the infants themselves may provide benefits to the male, by either buffering aggression from the breeding male or soliciting agonistic support from the mother. If such bonds with infants facilitate group membership, and group membership, in turn, facilitates future breeding, then the follower's treatment of infants represents a form of mating effort.

Similarly, in one-male groups, even though the male is probably the father of all of the infants, he may develop special relationships with particular infants. This appears to be the case for gorillas, at least in captivity (Tilford and Nadler 1978). In this instance, the male's special relationship with an infant mirrored his special relationship with the infant's mother. In the wild, the breeding male might cultivate such preferential relationships to reduce the chances that one of his females will transfer to another male, a hypothesis currently under investigation (Sicotte 1989).

*Mating Effort versus Paternity Certainty:
Future Directions*

Evaluating the mating-effort versus paternity-certainty hypotheses will often be difficult, because, under certain conditions, both selective forces can produce a strong positive correlation between male care and high paternity certainty for very different reasons. Suppose, for a moment, that paternity certainty is driving male-infant caregiving in a multimale primate species, such as savanna baboons. The result will be