Mating, Parenting, and the Evolution of Human Pair Bonds

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Human pair bonds are widely assumed to have arisen when ancient females began to rely on subsistence support from males (e.g., Leveque 1981; Lackey & Lackey 1983). The most influential versions of this argument is the "hunting hypothesis." Its elements have a long history in Western thought (Carter 1994, Augspurger Westermarck in his 1881 book, The History of Human Marriage, provided a nineteenth-century example:

When the human race passed beyond its foraging stage and spread over the earth living chiefly on animal food, the assistance of an adult male became still more necessary for the subsistence of the children. Everywhere the choice devolves on the adult, in the bearing a rare exception among savage peoples for a woman to engage in it. Under such conditions a family consisting of mother and young would probably, as a rule, have succumbed. (p. 19)

The hunting hypothesis was reiterated with especially wide influence by Sherwood Washburn in the mid twentieth century. Using what was then known of nonhuman primate behavior, modern hunter-gatherers, and the paleoanthropological record, Washburn linked tool use, bipedalism, brain expansion, nuclear families, and an array of other features that distinguish modern humans from our closest living primate relatives to the "hunting adaptation" (e.g., Washburn & Avis 1958; Washburn 1968, Washburn & DeVore 1961, Wash- burn & Lackey 1963). Building on Raymond Dart's arguments relying bipedality to hunting with weapons (Dart 1953), Washburn proposed that hunting large animals is evolved bipedalism, tool use, and bigger brains, which in turn created an observational dilemma for mothers. To be born at all, babies had to be born less well developed and so more dependent, longer, on maternal care. Maternal duties kept women from foraging, so they required provisioning by hunting males. Pair bonds and a sexual division of labor arose as reliance on large-
animal hunting made paternal provisioning essential. This need for biparental care was the foundation of the evolution of human pair bonds and nuclear families.

Paradoxically, the volume in which Wurzbach's most widely cited essay on this topic appeared (Wurzbach & Lasch 1969), Man the Hunter, also contained ethnographic reports of hunting and gathering societies in which subsistence was much more dependent on women's work and on plant foods than on big-game hunting. Ethnographers found that, although people claimed that big-game hunting was of primary importance, systematic observation of actual food consumption showed heavy reliance on plants—except at high latitudes where few plant foods are available. Richard Lee's (1979) chapter in that volume was especially important in challenging many assumptions about hunter-gatherers that were widespread at the time. Lee pointed out that speaking Bushmen in southern Africa and also summarized patterns from the ethnographic literature on foragers worldwide to show that aspects of the Kung way of life were nearly typical of modern foragers in temperate and tropical habitats.

Since the early 1960s, there have been important additions to the descriptive record of ethnology and primatology. The paleoanthropological evidence now shows bipedalism, brain expansion, and archaeological evidence for big-game hunting to be separated from each other by millions of years (Klein 1999). The theoretical perspective and methodological tools used to investigate evolutionary questions have also changed dramatically. Nevertheless, the hunting hypothesis, much as it was articulated by Wurzbach before these changes occurred, still continues to be favored (e.g., Tooby & DeVore 1987, Deacon 1997, Kaplan et al. 2000, Harrobi 2001, Cowan 2002).

Here I review concepts, models, and data in three domains that have implications for the hypothesis that human pair bonds evolved due to the dependence of mothers on subsistence support from hunting husbands. I begin with the history of ideas about links between parenthood and sexual selection. Starting with Darwin's theory, I consider George Williams' (1966) elaboration, Robert Trivers' (1972) definition of parental investment, and subsequent broadening of that definition (Kremer & Milom 1981, Clutton-Brock 1991). This broadening may be useful for some questions, but it obscures distinctions between mating and parenting effort that are central to the theory of sexual selection and were explicitly maintained by Trivers (1972). The errors that arise from the broader definition confuse evolutionary explanations for behavior, especially among primates—humans in particular.

The second domain of special relevance includes both theoretical and empirical work since the mid-1970s: distinguishing parenting from mating, primarily among nonhuman primates. As Darwin himself noted, the distinction between these things is not always straightforward. But it is fundamental to the theory of sexual selection. The recognition that females may seek copulations to improve their parenting prospects (Hrdy 1979, 1983, 1999), and that males may care for infants and juveniles to improve their mating success (Smuts 1983a, b, 1985, 1987), underlined the importance of distinguishing the form of behavior from its adaptive function. These and other findings about the ways that reproductive strategies of males and females can lead to relationships between them have implications for social patterns in many species. Their implications for the evolution of human pair bonds are of special interest.

The third domain I consider is the behavioral record for our own species, with particular emphasis on the ethnology and behavioral ecology of sexual division of labor among hunter-gatherers. Wurzbach and many others asserted that the basis for human pair bonds must be women's dependence for subsistence on a provisioning mate. This implies a "sex contract" (Fisher 1981), in which women trade increased probability of paternity to a man in exchange for his subsistence support (e.g., Beckerman & Valentine 2002). However, recent hunter-gatherer ethnography shows that family provisioning goals do not account for the work men usually do. Women and children often get most of the meat they eat from the hunting of men outside their own family, and the amount they get is generally unrelated to the hunting success of their own husbands or fathers. More recent quantitative data on this topic actually echo and elaborate qualitative claims that have long been made about household economics in foraging societies (Lee 1972, Shostal 1972, Manlin 1978, Kelly 1993).

This material underlines the basis of an argument that women make human pair bonds the consequence of increased paternal effort. A different suite of hypotheses based explicitly on sexual selection and dangers posed by male mating competition have been advanced to explain special relationships between mates and females in nonhuman species. These hypotheses apply to other primates that live in multimale social groups, making them particularly well suited on both phylogenetic and sociological grounds to identify the evolutionary foundation for pair bonds in humans.

Parenting and Sexual Selection

Darwin's theory of sexual selection depends on a distinction between characteristics that affect parenting success and those that affect success in competition for mates. Beginning with a review of Darwin's argument, I summarize some of the subsequent developments that both clarified implications and highlighted complications.

Darwin's Reasons for Sexual Selection

Many differences between the sexes, Darwin argued, can be explained by "ordinary" natural selection.

When the sexes differ in structure in relation to different habits of life . . . they have doubtless been modified through natural selection. . . . So again the primary sexual organs, and those for nourishing or protecting the young, come under this same head; for those individuals which preserved and transmitted their offspring best, would leave, ceteris paribus, the greatest number to inherit their superiority; whilst those which generated or nourished their offspring badly, would leave few to inherit their weakness. (1871: 185: 256)

Other differences between the sexes, such as male ornaments and ornaments, cannot be explained by "ordinary" natural selection, because

the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males. . . . Thse characters are the result of sexual selection and not of ordinary selection is clear, as untrained, untrained, or untrained males would succeed equally well in the battle for life and in leaving numerous progeny, if better endowed males were not present. (1871: 188: 257-258)

While Darwin noted that it was not always easy to separate the operations of sexual selection from other forms of natural selection, the distinction between parenting on one hand and competition for mates on the other was central to his theory. An important basis
for this distinction was the evident asymmetry in the operation of sexual selection on males and females. "On the whole," Darwin observed, "there can be no doubt that with almost all animals in which the sexes separate, there is a constantly recurrent struggle between the males for the possession of the females" (1871: 116). Because of this, "it is the males that fight together and boldly display their charms before the females" (p. 272). He recognized two components of sexual selection, male-male combat and female choice, each of which shapes the morphology, physiology, and behavior of males, so that "it is the male which, with care exceptions, has been chiefly modified" (p. 272).

Recognizing this asymmetry, "we are naturally led to enquire why the male in so many and such widely distinct classes has been rendered more eager than the female, so that he seeks for her and plays the more active part in courting... why should the male always be the seeker?" (Darwin 1871: 273). Male Andersson (1994) pointed out that Darwin came close to the antonymic explanation for stronger sexual selection on males. But it was not until A. J..bamman's (1984) experiments on sex differences in reproductive success among Drosophila, and then George Williams' (1966) use of this example, that the antonymic explanation was widely appreciated. Batesian's experiments showed that reproductive success varied more among males, each additional mating increasing the reproductive success of males but not females. The antonymic explanation for this result is based on differences in the two-game types. Since each zygote requires one gamete from each sex, and female gametes are fewer, produced more slowly, it is female gametes that limit offspring production. With more male gametes, produced at a faster rate, a male can increase his reproductive success by fertilizing more females than other males do. This makes parental competition a zero-sum game, as any male's gain subtracts from the paternity available for others. Williams (1966) stated with antonymy, and then moved beyond it to include additional kinds of parental contributions, extracting increased explanatory power from sexual selection by linking it to asymmetries in parental expenditure.

Jeffrey Blythe (1938) drew attention to one reason why Darwin himself did not make that link: patterns of ornamentation and parental care in silent fish. Darwin's survey of reproductive patterns was characteristically wide ranging. Summarizing observations of many species of fish, he concluded that it is "manifest that the fact of the eggs being protected or unprotected has little or no influence on the differences in color between the sexes. It is further manifest, that in many of the very cases where the males take exclusive charge of the nests and young...the males are more conspicuously colored than the females" (Darwin 1851: 21). Thus Darwin saw the greater adornment of males even though they appear to have little role in parental investment than females as evidence against any general dependence of sexual selection on relative parental expenditure.

Links between Parenting and Sexual Selection

Williams (1986), building on Darwin and of course Fisher (1930), was also characteristically wide ranging. He did not take up this middle of the fish, but, reviewing many other examples he showed that the evolutionary battle of the sexes arises from differences in the allocation of reproductive effort to parenting and mating. This conflict of interest was further clarified by Trivers (1972), who linked parental to sexual selection by defining parental investment so as to highlight a necessary interdependence among the trade-offs individuals face gives finite reproductive effort. Defining parental investment as the cost that a contribution to one offspring's fitness imposes on a "parent's ability to invest in other offspring" (Trivers 1972: 139), Trivers implied that the sum of all the parental investments in individual mates would equal its total parental effort (Lox 1975). If both sexes expend about the same average overall total reproductive effort (Williams 1986), and that total is composed of parental and mating effort, then differences in the sex ratio must imply in

verses differences in their mating effort. Members of the sex investing less in parenting compete with each other for the greater parental investment of the opposite sex.

The currency Trivers identified for males was parental investment clarified some basic trade-offs. But actually measuring the cost imposed on a parent's ability to invest in other offspring is not so easy. A measure of this cost for each sex is required for calculating the differences between them in species where both sexes contribute some parental care. An alternative index, more readily measured, is potential reproductive rate (Clutton-Brock 1981, Clutton-Brock & Parrot 1972). As recognized by R. A. Fisher, and maybe Darwin himself (Edwardes 1889), these factors have a mathematical and a father makes sex-rates likely to be even more of the time. Since overall reproductive rates depend on the lower sex, members of the faster sex, ready and waiting sooner, must compete for each reproductive opportunity. An alternative index, more readily measured, is potential reproductive rate (Clutton-Brock 1981, Clutton-Brock & Parrot 1972). As recognized by R. A. Fisher, and maybe Darwin himself (Edwardes 1889), these factors have a mathematical and a

Why Indirect Care May Not Be Parental Effort

Considering specifically the problem of identifying male parental effort in mammals, Debra Kleinman and James McIvor (1981: 348) developed a very broad alternative to Trivers' definition. They 'conceive male parental investment as any increase in a pre-reproductive
mammal’s fitness attributable to the presence or action of a mate” (original italics). This includes not only nonreproductive benefits, as defined above, but also “indirect care.”

Indirect male parental investment includes those acts a male may perform in the absence of the young which increase the latter’s survivability. These acts may have delayed effects on survivalship of young and include such behaviors as the acquisition, maintenance, and defense of critical resources within a home range or territory by the elimination of competitors, the construction of shelters, and actions which improve the condition of pregnant or lactating females. Many forms of male parental investment that are indirect are also incidental to the species’ breeding system, ecology, or social organization. These are activities which males would perform regardless of the presence of the young. For example,,” “scout marking and long distance vocalizations which aid in the spacing of individuals or groups, and thus may minimize critical resources for eventual use by young, should also be considered in indirect forms of male parental care. In short, these may be considered of great importance to the survivalship of young males, but they are not directly related to any specific behavior of the young male. In addition, they also require the expenditure of energy and time, which could be used for other purposes. Therefore, they are considered indirect forms of male parental care.

This very inclusive definition seems to simply, incorrectly, that parenting is the adaptive function of any male behavior that could affect the welfare of the young. While parenting could be the adaptive function of many of these behaviors, that depends not on whether the young benefit, but whether the net fitness benefits that maintain the behavior in the males have come through differential fitness gains of the parent’s offspring from the young. Thus, if a male is not performing any of these behaviors, he may still be considered a male parent if his offspring benefit from his behavior.

Not only does subordinate troop defense not change the relative fitness of dominant resident males, it also allows transient low-ranking males who father one or a few offspring in each of several troops to effectively parasitize the parental efforts of the resident males. The young of such “founding” “cheater” males would be defended and the males themselves would receive none of the attendant risks. Thus, an instances, nonparental males might reproducitively do as well, if not better than the resident males... (rendering the resident male’s parental behavior “evolutionarily unstable.”

On those grounds, parental benefits to the defending male (differential fitness for his own offspring) are poor candidates to explain troop defense by resident males. Kurland and Gaulin assert that the persistence of this behavior is more likely due to effects on the defending males’ mating success. The speculations about eye-pushing fish above parallel their suggestions: “Much of what often passes for male ‘parental care’ may, in primates and mammals, in general, be better interpreted as male mating effort rather than male parental investment” (Kurland & Gaulin 1984: 283).

Distinguishing Mating from Parenting, Especially in Primates

Boelens (1978: 200) pointed out that “Different apportionment of [reproductive effort] between mating and parental effort in the two sexes may occur even when the same structures or behavior is involved. For example, in any mammalian species in which males use home solely in dominance displays and fights to secure mates while females use theirs in de-
mates. If males are less likely to kill infants they may have fathered, a female might reduce the dangers to her own infants by selecting the possibility of paternity widely. This was known initially as the "mate-guarding" hypothesis, but self-defense might have been emphasized instead. As Holy observed more recently (1999: 123-24), "precautionary-sounding words like "promiscuous" only make sense from the perspective of the males. From the perspective of the female however her behavior is better understood as "absolutely maternal."

Holy's hypothesis was about relationships. She assumed that females might establish relationships with strange males and so reduce the danger these males otherwise posed. Increasing interest in exploring the character and consequences of relationships in primate social groups expanded from the late 1970s (Honale 1979; 1983; Harcourt 1989; 1992; Chupi 1992; 1995). One result was to draw further attention to the fact that more was going on between the sexes than copulation. As Barbara Smuts (1983a: 112) noted at about that time, "most studies of male-female interactions in nonhuman primates have focused on sexual behavior. Several recent studies, however, have shown that in savannah baboons and macaques, adult males and females may form long term friendly bonds that persist in the absence of any immediate sexual relationship."

Special Relationships

The importance of these friendships to both sexes is indicated by the effort they invest in them. "Both males and females compete for these relationships (e.g., both males and females sometimes threaten potential rivals away from their friends)" (Smuts 1987: 398). Males may interpret others' copulations and solicit the male themselves. The fitness related benefit of this "female mating competition" was proposed to be protection that male friends provide a female and her infant (Smuts 1985). In terms of the reproductive effort typology, the females gain parental benefits, so the effort they expend on these relationships is maternal effort.

What kind of reproductive effort are the males expending? Holy's infanticide protection hypothesis proposed that males behaved differently toward the offspring of potential copula
tion partners because of the possibility that they had fathered the infants. Some probability of paternity could have favored and maintained this strategic adjustment in males because of its net parenting benefits to them.

Other hypotheses are also worth entertaining. The problem of paternity confidence was highlighted by Trivers (1972) in his exploration of conflicts of interest between the sexes. He argued that a history of infanticide in a warring tribe might have selected males to be sensitive to paternity threats and to avoid "misdirecting" paternal effort to the offspring of other males. This "danger of cuckoldry" argument was a basis for selecting colonization by copulations as a "deceptive" or "manipulative." The proposition that males are generally in danger of being "cuckolded by deceptive females" resonates with long-held Western views (Buckman & Valentine 2002), including those among men's ownership rights over women (Wilson & Daly 1992) and about the basis of male sexual jealousy (Daly et al. 1982; Daly & Wilson 1987; Pinker 1997). But uncertain paternity arises from male mating competition. Male behavior in mammals generally, including other primates where little paternal effort is even dispensable, shows that the dangers males pose for each other provide sufficient reason for male jealousy. Both modelers (e.g., Mangel Smith 1977) and fieldworkers (e.g., Smuts 1985; Pau et al. 1992; reviews in Wrangham 1987, Wright 1990) have shown that paternity certainty is not necessarily a good predictor of male behavior toward infants. Smuts (1987: 393-394) summarized some findings of her own and others this way:

In a number of species in multiple groups, males appear to contribute to offspring survival through babysitting, protection, occasional carrying, and other affilia
tive behaviors. Male parental investment does not fully explain these behaviors because the infants are in many cases unlikely to be the male's own offspring. . . . [Observers have] suggested that, by developing an affiliative relationship with an infant, male savannah baboons might rekindle the bond with the mother in the future. If this hypothesis is correct, then male care of infants some
times represents mating effort rather than parental investment.

For olive baboons (Papio ursinus), Smuts (1985) showed that friendship with the mother was a better predictor of male care for the infants than likely fatherhood. Consistent with her hypothesis that female choice favored males who formed these relationships, she found that females preferred their friends as mothers. In a similar study, F. U. and Gubernick (1992) assembled data from a number of primate species that were consistent with this hypothesis.

Van Schaik and Paul (1996: 153), summarizing additional work in the variation in male care among many species of nonhuman primates, offered Smuts' assessment that this variation is not adequately explained by either paternity. Indeed, much of what has traditionally been considered paternal behavior may be better explained as mating effort in situations where females can exert control over their choice of mates.

Other Males Are a Problem for Both Males and Females

The picture is not, however, one of female choice favoring the evolution of ever greater guiltlessness and lackluster in males (Itch 1981). The advantage of these friendships for females is "an ally who because of his larger size and superior fighting ability, may make a significant contribution to the fitness of the female and her offspring" (Smuts 1983b: 263). Large size and fighting ability are especially valuable because an important source of danger to the welfare of infants and females themselves is posed by other males. Richard Wrang
gam (1979) hypothesized that females may establish and maintain relationships with aggressive males because of the protection this provides from other dangerous males (Wrang
gam & Rivstrom 1986).

The importance of this danger was chronicled by Smuts and Smuts (1993: 2) as male coercion: "the use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she would not otherwise be fertile, to decrease the chances that she will mate with other males, at some cost to the female." Chetnon Brock and Parker (1995) provided formal modeling to show how male coercion could play a large role in sexual selection in many species, including primates. Smuts (1987: 396) characterized the effects of female strategicizing in the context of male coercion this way: "by cooperating with some potential mates and resisting others, females alter the costs and benefits of competition among males and thus influence the form and frequency of male-male competition."

Reviewing primatology up to the early 1980s, Whyte and Whyte (1985: 3) pointed out that "while this trend toward field workers' focus on male behavior. However, only certain aspects of male behavior have received much attention. Smuts noted in her 1987 review that "the relationship between interest in male dominance and male nesting activity has probably received
more attention that any other aspect of primate social behavior" (p. 388). But other aspects of male social behavior were not studied much. More recently, Peter Kappeler (1999: 20) could justifyably conclude that "social relationships among males remain the most poorly studied aspect of primate socioculture." The same errors that Holly and Williams (1983: 5) blamed for insufficient attention to female social behavior biased the attention paid to males: "The futility of measuring reproductive success in both sexes by syringe production. Even worse is the assumption that it can be measured by mere copulatory performance, and that this will be the focus of selection on reproductive fitness."

Appreciation of the important effects of other behaviors on both parenting and mating success has steadily increased since then. Carol van Schaik (1986) saw that the dangers posed by infanticidal males might do more than stop females from seeking protection; this danger might be fundamental to the shape of primate social systems. Van Schaik and Peter Kappeler (1997) linked aspects of primate life history to the benefits for infanticidal males. They proposed that the extreme sexuality of our order, evident in the year-round associations of males and females results from the strategies used by both males and females to counter this danger. This provides a framework for understanding both adult social behavior and reproductive physiology (van Schaik et al. 1999). As well as the unusually high frequency and wide diversity in male-infant interactions that distinguish primates from most other mammals (Wuens 1987; Paul et al. 2000).

Ivy Palombi (1999) summarized observational and experimental data in several baboon and monteserron gorilla (Gorilla gorilla beringei) communities consistent with the hypothesis that females maintain social relationships with particular males, that is, pair bonds, to reduce the danger of infanticide by other males. As he noted, following Holly and Sinis, appreciation of family structure and observation of these patterns involves an important shift in thinking about the evolution of pair relationships. From the perspective of Tinbergen (1942) pair bonds are expected only with monogamy, which in turn is assumed to entail both sexes devoting substantial reproductive effort to parenting. Desa Klaiman (1977) had pointed out that it is contrast to this prediction, monogamy did not necessarily imply either pair bonds or kinship care. Work over the past two decades has shown that the converse is also true. Strong male-female attachments that persist outside pairs do not depend on monogamy. Long appreciation of these relationships in baboons, combined with the variation in social organization both within and among species, makes guppies (Poecilia reticulata) especially interesting for questions about pair bonds. While females benefit from the infanticide protection supplied by pairs (Palombi et al. 2000), the benefits males earn from these friendships may be more variable. Snufi (1985) found varied benefits among olive baboons, but data on other savannah populations challenges the mating effort hypothesis (Palombi 2000). Observations and playback experiments among chacma baboons (Papio 1 (pseudotrichopsis erson) (Palombi et al. 1997) showed that males responded differently to the screams of their friends only when infants were threatened by infanticidal males. The males, who were possible fathers in 68% of the friendships in this study, stopped responding to their (former) friend’s screams after the death of an infant. Just when the females would be returning to estrus and so presenting a mating opportunity, the friends responded even less to the playback than controls did.

It could be that infant loss brings on end to friendships. During this study, infant mortality was 76%. At least half of this loss was due to infanticides committed by a recently inseminated alpha male with whom the mothers of the victims subsequently mated. As the researchers note (Palombi et al. 1997: 611), females may have ended friendships under these circumstances because their friends were unable to protect them.

The variation among and within baboon populations over time in an invitation to test sociocological hypotheses about the interplay of male and female strategies. Robert Barton (2000; Barton et al. 1996) proposed a model for some of the variation that includes characteristics of the food resources which shape feeding competition among females, the dangers posed by infanticidal males, and the mixture of coercion and affiliation that males use to keep females from associating with other males.

Changing Views of Monogamy

Coincident with these developments in understanding the importance of pair relationships in nonmonogamous primates, the 1980s and 1990s saw radical changes in the understanding of monogamy as a "mating system." David Rubenstein (1994) listed attributes of monogamy and noted that they all involved various combinations of pair bonds, mating exclusivity, and mate care, each of which might, in principle, evolve independently. The most dramatic impetus to a revised perspective on monogamy came first in ethology, where the traditional view was "mated on its head" (Black 1996) with the discovery that "social monogamy" persisted in the absence of "genetic monogamy." In his definitive review of avian breeding patterns, David Lack (1988) explained the extremely high frequency of monogamy in birds as the result of the importance of parental provisioning. Pairs usually persisted through a breeding season, sometimes longer, he explained, because genetic paternal effort increased the reproductive success of the family. Lack was not the only influential figure to favor relationships about pair bonds. As Patricia Gowaty (1996: 23) noted, "almost everyone’s (Darwin 1871, Williams 1966, Lack 1968, Orns 1969, Thomas 1972) ideas about selective pressures accounting for the evolution of mating systems pivot around the necessity (or not) of male parental care."

Lack’s hypothesis was challenged initially by a combination of theoretical developments that highlighted conflict of interest between the sexes (Williams 1966, Trivers 1972, Maynard Smith 1977), and later by technological developments that allowed investigators to discover that extra-pair paternities were much more frequent than observers had previously guessed (Birkhead & Moller 1992). New questions arose about the fitness-related benefits for each partner in mating a pair. Investigators found that while male care sometimes varied with female paternity, more often it did not (Wright 1990; Hoekstra 1995). With experimental manipulation of pairs, investigators measured the effect of male care on female parenting success. Reviewing the data from removal experiments (Birk & Trivers 1989, Gowaty 1996: 489) concluded that while "for some females there exist important advantages for male care... for many females male parental care has small or negligible effects on female reproductive success, suggesting that in a general prediction for social monogamy, the Male Care Effect is Essentially Hypothesis is inadequate."

The discoveries that avian pair bonds were not necessarily based on mating exclusivity, that a male’s care for infants often did not go to his offspring, and that females sometimes fledged more offspring with a male partner than were mated to one means that long-favored hypotheses did not explain partnerships in birds (Black 1996). Male-female relationships that persisted over a breeding season had been assumed to imply monogamous and so require sexual exclusivity. But, in fact they did not. Combined with the work on male-
female relationships in primates, this has provided the basis for revisions in assumptions about the character and evolution of pair bonds generally, and about the evolution of human pair bonds in particular.

Pair Bonds, Marriage, and Human Evolution

It is widely assumed that, among modern hunter-gatherers, men's hunting is potent effort. This is the major source of support for the claim that substantial paternal investment is the key to human pairing relationships and major transitions in human evolution. The assumption persists even though other widely accepted claims about men's reproductive strategies contradict it. I review some of these claims, noting that they have generally incapacitated the contradictions severely. They often provide better justification for the alternative hypothesis that hunting like many other male occupations, is largely shaped by mating competition. The discussion clears the ground to return to hypotheses about the evolution of human pair bonds that arise from work on other primates.

Before tackling these issues, some concerns about placing human pair bonds in a comparative perspective require attention. We all have firsthand knowledge about emotional dimensions and behavioral patterns associated with human pair bonds. As noted in the preceding section, our ideas about them shape hypotheses about other species. They may, however, be wrong for other species. They may not even apply generally to our own. Revisiting the human variation recorded in both history and ethnography, Sarah Hidy (1999: 232) concluded that "earlier commentators failed to consider how unusual are the particular cultural, mental and demographic conditions that make long term monogamy advantageous for both sexes." Urban BELL (1997: 241) recently noted that "contemporary Westerners' marriage is a poor vantage point from which to consider the ethnographic universe of marriage." Donald Symons (1979: 141) more than 20 years ago, also warned behavioral biologists against relying too much on their own personal experience: "intuitions about marriage based on the extremely artificial environments of modern industrial societies may be somewhat misleading, since in industrial societies, unlike face-to-face, kin based societies in which the overwhelming majority of human evolution occurred, one's mate is often one's only hope for establishing an intimate, durable relationship with another adult."

Social anthropologists, from the beginning of the discipline (Morgan 1878), have struggled with both describing and explaining the wide variation observed in human marriage practices. Disputes over the definition of pair bonds in behavioral biology are but a whisper compared to the loud volume of debate devoted to the definition of marriage in sociocultural anthropology (e.g., summary in Goodenough 1970). Often, these attitudes the ethnographic variation have been more important than the data: they may have any relevance to understanding the wide variability in our own.

Edmond Leach (1988: 91) memorably claimed that "marriage and mating are totally different concepts, and differing as far as from each other. His definition of marriage focused on inheritance of relatively impersonal property. "Marriage provides a set of legal rules under which a man's property is handed down from generation to generation" (p. 93). This notion of marriage is contrary to our conceptions of marriage at all. Questions of the universality of marriage in human societies continue to be debated in social anthropology (e.g., Bell 1997). In many cultural settings, the legitimate inheritance of property is of great importance, and sometimes it explicitly depends on a special kind of legally recognized union in combination with other ties among potential claimants. But sometimes, especially among mobile foragers, people do not hold much marital property and little, if any, of that is transferable enough to pass to descendants. Property concepts, as argued below, have many important uses, including the help they provide for distinguishing parenting from mating effort. They can also be useful for analyzing strategies of mate defense. But these were not the property issues Leach had in mind. He focused on marriage to the explicit disregard of mating, assuming that mating involved little variation of interest since the "prevailing mating system is a free-for-all caital in the dark" (Leach 1988: 107).

Others, prepared to see a relationship between mating and marriage, might still second Leach's view that the differences between them and as other animals are greater than the similarities. Symons (1979: 108) made this observation:

The lexicon of English is usefully inadequate. . . for describing the thoughts, feelings, and behaviors associated with marriage and with other relations among men and women. . . . The complexity and subtlety of thought, feeling, and action invariably must be sacrificed if the written record is to be made at all . . . to sketch the present vocabulary to one phrase—a pair bond—and to imagine if that is done so is so it is scientific—submerging humans under principles that account for data on non-human animals—is simply to delude oneself.

The danger could be even greater. We may underestimate the experience of other animals especially our primate cousins as well as our own.

But along with costs some benefits from simplification. While language reveals aspects of experience that can only be appreciated in humans, other dimensions can be studied in comparable ways in both human and nonhuman animals. Some of the human behavioral variations may be due to the same processes that govern the variation in other species and the wider cross-species differences. The many physiological and specifically neuroendocrine processes we share with other primates are a foundation for the emotional architectures that shapes behavior in us all (Darwin 1872) 1965, Hidy 1999). Similarities between us and other animals can correct erroneous conclusions about the uniqueness of human patterns. The similarities are especially important for any investigation of human evolution.

Sex Differences and the "Sexual Division of Labor"

Symons (1979) assembled a wide range of ethnographic and sociological data showing marked differences in the sexual preferences and behavior of men and women. He persuasively linked the differences to the much greater importance of mating competitions among men, concluding, "Humans then are typical mammals in this selection has favored greater male-male reproductive competition" (p. 144) and "The evidence suggests that in hunting, as in fighting, human males are effectively in competition with each other for females and that there are substantial differences among males in competitive abilities" (p. 162).

Yet this conclusion presented him with a serious problem. Recognizing that the importance of mating competitions among men is consistent with Darwin's predictions from sexual selection, Symons also recognized the links that had been made between parenting and sexual selection. He cited Trivers (1972) for the expectation that structures and behaviors...
associated with mating competition are favored in members of the sex that expends less in parenting. The problem was that Symons, following Wachtel, also "knew" that high parental effort was characteristic of humans under ethnocultural circumstances most like those of deepest antiquity:

The basic social unit of human forager-gatherers is the nuclear family in which men hunt and women gather vegetable foods, and the sexes are divided and given to their offspring. (p. 130)

Obligations and rights entailed by marriage vary among societies, but marriage is fundamentally a political, economic, and child raising institution, based on a division of labor by sex and on economic cooperation between the spouses. (p. 123)

Symons assumed the hunting hypothesis to be generally correct. However, according to theory (Williams 1966, Trivers 1972), one sex has more to spend on mating competition only if it spends less on parenting. The problem, then, is that substantial parental effort from men cannot be isolated from male mate preference and sex-specific males are in need of our evolutionary, should meagre reduced mating effort compared to our close primate relatives. Symons dealt with this problem in the following way:

It is not then a simple question of high female parental investment and male competition for female mates. Males invest in different ways. Not only did males hunt while females gathered, but if warfare was often over land and other scarce resources from which the winning males’ offspring benefitted, male fighting was in part parental investment; that is, like hunting and gathering, fighting and nurturing were part of the human division of labor by sex. (Symons 1979: 167)

The cost-off assumptions of reproductive effort models are thus suspended for men. Symons had assembled evidence to support the claim that “throughout most of human evolutionary history, hunting, fighting, and that elusive activity, ‘politics,’ were highly competitive, largely male domains” (p. 163). Then, following widespread usage, he classified these activities as parental effort. Instead of more parental effort resulting in less mating effort, the activities of human males are more of both.

It does sometimes happen that a single activity maximizes two things at once, but that is rare in a finite world. Optimality models have promised to be powerful tools for explaining the diversity of life because most of the trade-offs are encodable (Maynard Smith 1978, 1982; Seger & Rostblad 1996). In the case at hand, the adaptive function of men’s hunting, a trick of language draws attention away from the trade-offs faced by individuals. Characterizing many activity differences between men and women as a “sexual division of labor” is the legacy of a long history of talking about human behavior from a societal point of view. As Symons (1979: 147) himself noted, there is a tendency to see the passive voice when talking of the sexual division of labor, as for example, in the claim, “In all known societies the ‘defensive role’ is assigned to adult males.” . . . The passive construction conveys the subject, the agent who did the assigning. When the subject does not materialize in such statements, almost invariably it turns out to be “society.” The implication is that this work is divided to serve the productive goals of some larger entity, the family, domestic group, or household, which assigns tasks by sex and age. If females are assumed to be sexes of common interest, the conflicts of interest between and within the sexes (in theory the heart of the story) become, at best, secondary complications.

In spite of noting this problem, Symons still talked of a “sexual division of labor,” but he also considered some likely reproductive benefits to the individuals involved. He followed others, however, in claiming that “if warfare was often over land and other scarce resources from which the winning males’ offspring benefitted, male fighting was in part paternal investment because the offspring of the winning males benefitted.” The objection raised by Kirkland and Gaulin to a similar explanation for troop defense in baboons applies here. Resource benefits that go to the winner also go to all on the winning side, including the offspring of males who did not pay the cost of the fight.

Public Goods and Collective Action Problems

Parental benefits are insufficient to explain community defense because it is a public good, consumed by all group members whether or not they pay to supply it. Public goods are distinguished from private goods by two features: nonexcludability, and nonrivalry (Ostrom & Ostrom 1977). Consumers cannot be excluded from use of a public good, and its use is nonrival; consumption by one does not reduce the benefits available to others. With private goods, on the other hand, owners incur no cost in excluding other users, and any benefits consumed subtract from those remaining. Few goods or services are perfectly public or perfectly private, but some are more like public goods than private. The cost of exclusion is higher for some goods, and consumption of a unit subtracts less from the remaining benefits of some things than others. In the language used earlier, goods and services can be more or less depreciable.

The most public a good, the more likely that the value it has for consumers will not motivate consumer supply. Eliciting financial support from public goods listeners exemplifies the undersupply problem long recognized by economists (Samuelson 1954): Why pay for what you get free? An array of collective action problems (Oskin 1965) that arise around these issues have engaged political philosophers for centuries (Hardin 1982). Some of the same problems have been recognized by evolutionary biologists under the heading of individual versus group selection (Williams 1966). Free-rider problems, game theoretic (Axelrod 1984) payoff structures like the prisoners dilemma (e.g., Schelling 1978) and Garrett Hardin’s (1968) well known “tragedy of the commons” have come to be free illustrations of collective action problems (Hauke 1992). These arise whenever the potential or the cost of an individual interest does not promote the welfare of the collective. As Russell Hardin (1982) notes, Adam Smith extolled the beneficial effects of the natural invisible hand, but the back of that hand is just as ubiquitous—and paradoxically both coincident and contrary. When individuals can operate to relieve all and in Collective action with economic power (Hardin 1982, Hardin 1982, Rehnfeldt 2001).

The collective action problem with troop defense that Kirkland and Gaulin highlighted is one of two. On one hand, since all the troop infants and juveniles get protection, there is no differential benefit for the defenders’ own offspring. Parental benefits are thus unlikely to explain the continuing expenditure any male pairs into defense. On the other hand, males are observed to “defend the troop.” A corollary thing that begins to be explained. Other fitness-related benefits that, unlike offspring protection, are private gains for the defenders may be important in the explanation. Kirkland and Gaulin hypothesized that instead of parenting, the defending males earn mating benefits. A parallel argument applies to the human case. As noted above, Symons (1979: 162) makes it: “the evidence suggests that in hunting,
as in fighting, human males are effectively in competition for females, and that there are substantial differences among males in competitive abilities."

Collective action problems around communal defense can also arise with hunting large prey. Although food is the classic illustration of a private good, some food resources are much more like public goods. While a nomad of food goes into only one stomach, and each bite subtracts from the total quantity available to all, those with access to large packages, tens or even hundreds of kilos of meat at a time. Acquired by anyone, a large carcass can then be consumed by many. If the prey is taken unpredictably, one hunter may benefit when others fail to make a capture. The potential for exclusion for excluding other hunger may be substantial. If the hungry claimants are armed with lethal weapons, the cost of defense can be especially high and the wisdom of hospitality especially clear. The bigger the prey, the higher the cost of not sharing, and the less the additional consumer subtracts from available consumption benefits. As costs go up and benefits go down, marginal gains for trying to exclude other claimants disappear altogether (Blauner 1964; Blumberg 1964). Hunters may face problems which whatever hunters resources are like public goods (Hawks 1991, Hawkins 1992a, 1993).

Symons (1979: 158) concluded that "among all hunter-gatherers as well as among many other peoples, the primary economic activity of adult males is hunting, and nowhere do men hunt only for themselves, the fruits of the hunt are always shared with women and children." A long and rich ethnographic record confirms that food, especially meat, is often widely shared (e.g. Litvack 1972; Nunn 1990). The sharing is usually labeled exchange and/or reciprocity by social anthropologists, a usage that leads biologically trained males to assume that something like "Tvers's" (1973) "reciprocal altruism" might explain the sharing—hunters allegedly get a share of meat in return for shares in future hunts when hunting fortunes are reversed. But the sharing that is common in hunter-gatherer societies (Sahlins 1972) is not what Karl Polanyi (1957) called "market exchange." As two-disciplines studying social behavior, sociobiology and social anthropology are "divided by a common language." Tvers' model is essentially a market model of private goods and services exchanged that it is, of no effect external to the exchanging party. Individuals can benefit from this kind of reciprocity as long as they "keep accounts" and terminate transfers in any who fail to repay. They benefit as long as sharing is contingent on repayment.

The goods and services required accounting for such exchange strategies to be evolutionarily stable (Axelrod & Hamilton 1981) is explicitly denied in a multitude of ethnographies that detail food-sharing in kinship societies (Lienhardt 1969; Liénard 1972; Kelly 1996). Indeed, the threat of meat by large prey is not the hunter's private property is repeatedly confirmed (e.g., Marshall 1976; Barrand & Woodburn 1988, Wiessner 1990, 1994). It is possible, of course, that there is no position to direct shares according to his personal account (e.g., Hill & Kaplan 1988).

Ethnographers have also used observations of actual distribution to investigate whether food sharing is contingent on food repayments. In a few cases. We know of some (Boehm et al. 2000), but not many, and especially for large game animals, there is little indication that the distribution of shares depends on meat repayments to the hunter (e.g., Marchand 1977, 1979, Kaplan & Hill 1985a, Bliege Bird & Bird 1997, Woodburn 1998, Hawkins et al. 2004). The quantitative investigations add to the evidence against the view that meat is the hunter's private property (Hawkes 2003). The more often large prey are like public goods, the more likely that is that paternal benefits do not provide a general explanation for why men hunt them (Hawkes 1990, 1991, 1993, Hawkins et al. 2001). The same collective action problems that underlie Garrett hard core explanations for community defense applies to hunting big animals: the food benefits for the hunter's effort go not only to his wife and offspring but to the wives and offspring of less successful and less hardworking hunters as well. This is one reason the hunter can anticipate. Knowing that most of the meat will be claimed by others, he still sets out to hunt.

These observations recall an old idea in cultural anthropology that emphasized women's lack of economic dependence on husbands among hunter-gatherers. Weinstock's near contemporary Lewis Henry Morgan (1870) speculated that monogamy was actually a late development in the evolution of human society. Fredrick Engels (1884; 1972) elaborated on Morgan's in his scenario of The Origin of the Family, Private Property and the State. In the mid-twentieth century, Elster Leacock and his elaborations of the North American Montagnais, agreed with Engels. Other cultural anthropologists have developed and defended similar views (e.g., Collier & Rinaldi 1981, Leacock 1972: 29) summed that civilization transformed the "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33). Like other anthropologists, Leacock hypothesized, that in "primitive communal society... the economy did not involve the dependence of the wife and children on the husband. All major food supplies, like meat, produce and game, derive from the fields, were shared among a group of people" (p. 33).
but about the empirical assessment of the costs and benefits to the individual actors. Brodie (1999b: 236) notes that "among many mobile hunter-gatherers the most able hunters willingly acquire game for the entire group, and this meat is widely distributed with a minimum of bickering even though unrelated families are sharing it." I agree with this ethological generalization, but Brodie (1999b: 236) surmises that "if band members are disposed to associate with and to be associated by the band, this is likely to engender a group selection argument." His empirical evidence is that sharing imposes a net cost on shares compared to nonshares, and that the "able hunters" do not get differential fitness benefits for their effort. There is evidence to the contrary.

Ethnography shows a considerable cost to not sharing in these communities (Blumstein Jones & Jones 1984, 1987; Peterson 1990). If the prey shared are like public goods, then those claiming shares are appropriating a public good. Under these circumstances, any one trying to exclude clanmates is interfering with their "rights" and is likely to pay a cost for that interference. As we have invested in provisions the prey in the first place, the point I underline here is that the hunter gains benefits other than the meat. The magnitude and character of both his costs and his benefits should be assessed empirically. Getting the correct estimate of the costs and benefits for both sharing and hunting is just as important under the banner of multifunctional selection as it is within a standard evolutionary paradigm.

Why Do Men Hunt?

A collective action framework directs attention to benefits that go only to the individual hunters. What Olson (1965) called "collective interest," private gains that go only to the suppliers of public goods, are the thing to look for. If men in hunter-gatherer communities are often choosing to specialize in resources that go mostly to others, this should not obscure the benefits for this effort that go only to hunters themselves.

Like egg gathering or troop defense, the meat of large prey is consumed by many, not just the supplier's own family. But the hunter is the one who gets credit for supplying it. Distinctions between the credits and the meat are important. Examining hunter-gatherer ethnology, Fried (1967: 34) concluded that conventions for assigning "ownership" of the prey are "all techniques by which credit for bringing game to camp is randomized." He, and others, see these as "bequest mechanisms," with bequest further reflected in the famously self-effacing style of hunters (Lee 1969, Sah林1972, Harris 1977, Hawkes 1992b). But neither practice interferes with widespread interest in the eventual events of a hunt.

Among foragers, behavior of this sort is more common. Among the Kung bushmen of the Kalahari Desert, the division of meat among hunters is not based on the relative size of their hunts. Rather, it is based on the relative size of the kill and the size of the group (Lee 1979). Among the !Kung, the meat from a large kill is divided among all the hunters, regardless of whether they contributed to bringing the kill down or not. This is done so that all hunters can share in the same meat, regardless of their individual contribution.

Since everyone pays attention to hunters' successes, credit to successful hunters develops into reputation. Like other costly signals of quality (Zahavi 1975, 1977, 1995; Zahavi & Zahavi 1997; Grafen 1990), hunting reputations benefit hunters. The foundations for such social standing can be sustained by others. People already interested in the meat, hunting large animals can be a particularly effective way for men to display their skills and be noticed by others in the many decisions of social life. Because people are already interested in the meat, hunting large animals can be a particularly effective way for men to display their skills and be noticed by others in the many decisions of social life.

Hunting behavior is an example of a social norm, which is a set of expectations that are generally accepted by members of a society. These norms can be divided into two categories: formal norms and informal norms. Formal norms are rules that are explicitly stated and enforced, such as laws and regulations. Informal norms, on the other hand, are unwritten rules that are learned through social interaction and are generally followed by members of a society. Hunting behavior is an example of an informal norm because it is not explicitly stated, but rather is learned through social interaction. For example, a group of hunters might decide to hunt a certain type of animal, such as a deer, and then everyone in the group will follow this norm.

In conclusion, hunting behavior is an example of a social norm, which is a set of expectations that are generally accepted by members of a society. These norms can be divided into two categories: formal norms and informal norms. Formal norms are rules that are explicitly stated and enforced, such as laws and regulations. Informal norms, on the other hand, are unwritten rules that are learned through social interaction and are generally followed by members of a society. Hunting behavior is an example of an informal norm because it is not explicitly stated, but rather is learned through social interaction.
likely to hunt. Raising levels of meat procurement can be high enough that meat becomes a substantial component of the average diets of women and children.

Frank Marlowe (2000) has linked cross-cultural variation in men’s average division to variation in women’s average reproductive success. Using a worldwide sample of foraging societies, Marlowe found that increases in men’s relative contribution to the diet are associated with increased well-being of surviving children per woman. While the reasons for variation in male economic production between societies are not clear, Marlowe’s result may imply that increased production from men more means more food available to women, allowing them to increase fertility without commensurate losses in offspring survival. If so, this is an especially interesting instance of a general principle of life in which more food—from wherever sources means more surviving offspring.

Large effects on the number of children women can rear are to translate to classify the economic production from men as parental effort (or indirect parental investment, e.g., Kaplan et al. 2000; Marlowe 2000). Of course men can and sometimes do expend parental effort. But even if men do not in fact take on the cost of parental effort in actual food consumption, it is still parental effort if the usual hunter-gatherer patterns hold. As long as the wives and children of other men get about the same amount of meat from a hunter’s kills in his own children do, his fitness payoff cannot be differential nutrition for his offspring (Kaplan & Hill 1983b; Hawkes et al. 1991, 2001a, b). If the differential benefit to the hunter herself, the private benefit that only he gets for his work, is the credit for his kills, then his payoff depends on the effects of his hunting reputation. High status could bring differential treat ment of his children by others (Kaplan & Hill 1985b, Hawkes 1990). But the evidence available shows that hunting reputations affect men’s fitness largely through mating advantages. Both female choice (Kaplan and Hill 1985b) and mate competition are implicated (Hill & Hurtado 1996, Hawkes et al. 2001b).

What About Pair Bonds?

The tenor of the argument that men’s contribution to subsistence is parental effort turns partly on the ubiquity of human pair bonds. Disagreements about definitions of marriage continue, but in all ethnographic reports of human communities, men and women form special relationships with mating partners that involve more than copulation. People may not mate for life and partnerships may not be sexually exclusive (Beckerman & Valentine 2002), but men and women do form persistent emotional attachments. The hunting hypothesis has long been the favored explanation for this human trait. The contrary hypothesis that hunting is driven by male status competition, cancels the provisioning reason for women to pair with hunters. If women can consume food procured by men whether or not are married to them, why marry?

Special relationships in other primates where males supply us provisioning indicate that females can gain other things from partners, especially protection from other males. Benefits for males are initially less clear. But modeling results show that male mating competition alone can make pair bonds advantageous to males. One set of models (Hawkes et al. 1995) focused only on male strategies, with mating effort and parental effort assumed to be mutually exclusive to clarify the relative strengths of their fitness effects. In these simulations, paternity was the vital outcome, but not because males specialized in parenting. Under a wide array of parameter conditions, including potentially large effects on offspring survival, the model males earned higher fitness payoffs from more guarding than from parental effort. No female choice was included, yet pair bonds—each male pairing all his reproductive effort into guarding a female—were the usual result of the simulations.

Pairing patterns among hunter-gatherers show some parallels with these results. Nicholas Blomley Jones and colleagues (2004) examined variation in pair bonds among four hunter-gatherer societies for which both operational sex ratios and the effects of father’s presence on child survival could be estimated. In this sample, the stability of pair bonds varied directly with the intensity of male competition and was unrelated to variation in “father effects.” Divorce rates were lower where there were fewer paternity opportunities per male, highlighting the mate-guarding advantages that men can earn from marriage. Among the Hadza, foragers in East Africa and one of the cases in this sample, differences in father’s hunting success had no direct effect on children’s nutritional welfare, as expected given the wide sharing of meat. Better hunters were, however, found to be married to harder working wives whose children’s nutrition reflected the differential work of their mothers and grandmothers. These results highlighted the advantage that marriage may provide to both males and any advantages to their wives (Hawkes et al. 2004b).

That analysis may underestimate the value of a protector (Wurmsbam et al. 1999). Because human children are more dependent, longer on provisioning by mothers and grandmothers (Hawkes et al. 1998, 2003), harassment by males may impose higher costs on women than it does on other female primates (Blomley Jones et al. 2004). Hypotheses about patterns in prionws have been more fully developed by those investigating pair bonds in other primates. These hypotheses, already relevant on phylogenetic grounds, become more likely on grounds of sociocultural as well. Smuts (1992: 9–10) said:

'Most reconstructions of human evolution have assumed that pair bonds resolved to facilitate the exchange of resources between the sexes... often with a particular emphasis on the need for increased male parental investment in the form of meat. .. These scenarios assume that females benefited from pair bonds because they gained meat from males. Given the importance of male sexual coercion among nonhuman primates, and especially among one closely related species (chimpanzees, gorillas, and orangutans) however, we should carefully consider the alternative hypothesis that pair bonds benefited females initially because of the protection provided against other males (including protection from male-female interactions).

Smuts developed a hypothetical scenario that reflects the importance of conditions in male mating competition in many other primate species. I suggest that, among hominids, the kind of tolerance we see among male allies in nonhuman primates became formalized in each male began to develop a long-term mating association with a particular female or females (a trend formalized in the human lineage). .. Viewed in this light, human pair bonds, and therefore human marriage, can be considered a means by which cooperating males agree about mating rights, respect (at least in principle) one another’s possession of particular females, protect their mates and their mates’ children from aggression by other men, and gain rights to correct their own females with robust interference by other men. (Smuts 1992: 10–11)
Sarah Messick (1997) assenbled data on a wide array of taxa, including her own on elephant seals, to further document the high costs that male aggression can impose on female. She formulated the "bodyguards hypothesis," in which protection is a primary crite-

rion of female choice. Agreeing with Simms, she showed that "alliances with protective males can be an effective female behavior that reduces vulnerability to aggression from other, conspecific males. It is also a factor to consider in explaining ... human patriline," (Messick 1997: 207). Wilson and Messick (1997) tested predictions of the bodyguard hy-

pothesis for humans on Canadian records of sexual assault homicides and reported nonfatal sexual assault. They found, as predicted, that married women were less at risk from other men. 

Helen Fisher (1992) suggested a scenario for the evolution of human pair bonds that deserves special attention for its use of some of these ideas. She argued that while pair bonds are "the hallmark of the animal species" (p. 66), these relationships are often erratic lifelong or fully exclusive. While assuming that the hunting hypothesis in which ancestral males were paternal provisioners was generally correct, Fisher proposed that "our ancestors only needed to form pair bonds long enough to rear their young through infancy" (p. 153). Assembling data from a wide array of sources, she showed that marriages most frequently break up after about four years, and examined an ancient tendency to pair just long enough "to raise a single dependent child through infancy." (p. 154) This "four-year itch," however, would make fathers an unreliable source of help at just the time that human mothers need it most. One of the salient ways that human offspring differ from other primates is that our children are unable to feed themselves at weaning. It is when a mother shifts her effort to the next baby that help in caring for the still-dependent toddler is so crucial.

Others have evaluated the evolution of our extended infantile dependence to help from provisioning fathers. But the general primate patterns, and the data and arguments about hunting and sharing among modern hunter-gatherers are evidence against that scenario. An alternative hypothesis links our overlapping dependents to life history shifts resulting from changes in female foraging strategies that include increased longevity and delayed menopause (Flaxel et al. 1998, 2000; O'Connell et al. 1999, 2002; Alvarez 2000; Flaxel 2003). The general health and vigor of peripartum and premenopausal women and the late maturity of human adolescents distinguishes us from other apes. Both grandmothers and older sibings provide a source of help to weanlings when mothers bear newsworns. This means our pattern of cooperative breeding (Holly 1999, 2001) does not depend on fathers. Though they may sometimes be enlisted, other help is available when fathers trade-off parenting for mating.

Human mothers are well equipped to deal with the daily care and feeding of infants, so much so that, as with other primates, an infant's death advances the possible time of a next conception. This means we share a vulnerability to infantilic males, since, under some circumstances, that could increase the paternity chances for a man unlikely to be the infant's father. Helen Fisher observed the dangers of infantilization to primates but made less of this than have others cited here. Nevertheless she recognized that special relationships between males and females in other primates are the likely evolutionary foundation for human pair bonds. "Olive baboons provide, in effect, a model for pair bonding, the nuclear family, and divorce could have evolved" (Fisher 1992: 154).

We know that the hormonal induction included gesture unlike any now living, that modern humans are a very recent species, and that other members of our own genus were different from us. Since all extinct hominids not only differed from modern humans but also from each other in ways largely unknown, their mating arrangements may have been quite di-

verse. But that does not make all possibilities equally likely. Like us, they were all large-

bodied primates. We know that primates have bigger brains and slower life histories for body size than other mammals; and that married society, with continuous year-round mixed-sex groups is a (related) hallmark of our order. Individuals interact repeatedly over long time periods with the same others, who can be their most important competitors as well as potential allies. Consequently, capacities and strategies for managing social relation-

ships are especially well developed in primates (Hauser 1992). Conflicts of interest be-

tween (and within) the sexes have especially complex repercussions in the context of these life histories and this society (van Schaik and Janson 2000).

In light of what we now know about other primates, and our own species—especially, but not only—in hunting and gathering communities—the hypothesis that human pair bonds developed as a consequence of paternal provision or ancestral males should be viewed with extreme skepticism. Numerous lines of theory and evidence stand against it. At the same time, the special relationships between males and females is other primates and their links to dangers posed by male mating competition are increasingly well described. On phylogenetic grounds alone, these patterns should be the first place to look for hypotheses about the evolution of our emotional attachments. Increasing understanding of the sociolo-

gy of those relationships makes them an even more promising foundation for hypotheses about the evolution of human pair bonds.

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Note 1. Excludability and subtractability are seen as independent dimensions, so that their inter-

section defines four classes of goods (Ostrom & Ostrom 1977). The two remaining are common pool resources, which are subtractable but not excludable, and toll (or club) goods, which are excludable but not subtractable. The consequences and the interplay of these dimensions are topics of a large and diverse literature in public choice and property rights economics.

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