

Kinship and Behavior in Primates

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- Murdock, G. P. 1962. Ethnographic atlas. *Ethnology*, 1, 113–134.
- Murdock, G. P. 1967. *Ethnographic Atlas*. Pittsburgh: University of Pittsburgh Press.
- Murdock, G. P. 1981. *Atlas of World Cultures*. Pittsburgh: University of Pittsburgh Press.
- Myers, F. 1986. *Pintubi Country, Pintupi Self*. Washington, DC: Smithsonian Institution.
- O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.*, 36, 461–485.
- Palombit, R. A. 1994. Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. *Behaviour*, 128, 65–101.
- Pusey, A. & Packer, C. 1997. The ecology of relationships. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 254–283. Oxford: Blackwell Science.
- Pusey, A., Williams, J., & Goodall, J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277, 828–831.
- Radcliffe-Brown, A. R. 1930. The social organization of Australian tribes. *Oceania*, 1, 34–63, 322–341, 426–456.
- Ray, V. F. 1933. The Sanpoil and Nespelem: Salishan peoples of north eastern Washington. *Univ. Washington Pub. Anthropol.*, 5, 1–237.
- Riddell, F. A. 1978. Maidu and Konkow. In: *Handbook of North American Indians, Vol. 8*, (Ed. by W. C. Sturtevant), pp. 370–386. Washington, DC: Smithsonian Institution.
- Rodseth, L., Wrangham, R., Harrington, A., & Smuts, B. 1991. The human community as a primate society. *Curr. Anthropol.*, 32, 221–254.
- Schebesta, P. 1929. *Among the Forest Dwarfs of Malay*. London: Hutchinson and Co.
- Schrire, C. 1984. Wild surmises on savage thoughts. In: *Past and Present in Hunter Gatherer Studies* (Ed. by C. Schrire), pp. 1–21. New York: Academic Press.
- Service, E. A. 1962. *Primitive Social Organization: An Evolutionary Perspective*. New York: Random House.
- Smith, E. A. & Winterhalder, B. 1992. Natural selection and decision-making: some fundamental principles. In: *Evolutionary Ecology and Human Behavior* (Ed. by E. A. Smith & B. Winterhalder), pp. 25–60. New York: Aldine de Gruyter.
- Steward, J. H. 1936. The economic and social basis of primitive bands. In: *Essays in Anthropology* (Ed. by R. H. Lowie), pp. 321–347. Berkeley, CA: University of California Press.
- Steward, J. H. 1977. The foundations of Basin-Plateau Shoshonean society. In: *Evolution and Ecology: Essays on Social Transformations* (Ed. by J. C. Steward & R. F. Murphy), pp. 366–406. Urbana, IL: University of Illinois Press.
- Sugiyama, Y. 1999. Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates*, 40, 61–68.
- Turnbull, C. M. 1961. *The Forest People*. New York: Simon and Schuster.
- Turnbull, C. M. 1965. The Mbuti pygmies: an ethnographic survey. *Anthropol. Pap. Am. Mus. Nat. Hist.*, 50, 145–281.
- Turney-High, H. H. 1941. Ethnography of the Kutenai. *Am. Anthropol. Suppl.*, 43, 1–202.
- van Schaik, C. P. 1999. The socioecology of fission-fusion sociality in orangutans. *Primates*, 40, 69–86.
- Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. 2001. Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci. USA*, 98, 12890–12895.
- Williams, B. J. 1974. A model of band society. *Men. Soc. Am. Archaeol.*, No. 29.
- Wilmsen, E. N. & Denbow, J. R. 1990. Paradigmatic history of San-speaking peoples and current attempts at revision. *Curr. Anthropol.*, 31, 489–524.
- Wrangham, R. 1987. The significance of African apes for reconstructing human social evolution. In: *The Evolution of Human Behavior: Primate Models* (Ed. by W. Kinzey), pp. 55–71. Albany, NY: SUNY Press.

Mating, Parenting, and the Evolution of Human Pair Bonds

Kristen Hawkes

Human pair bonds are widely assumed to have arisen when ancestral females began to rely on subsistence support from mates (e.g., Lovejoy 1981; Lancaster & Lancaster 1983, 1987). The most influential version of this argument is the “hunting hypothesis.” Its elements have a long history in Western thought (Cartmill 1994). August Westermarck in his 1891 book, *The History of Human Marriage*, provided a nineteenth-century example:

When the human race passed beyond its frugivorous 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 chase devolves on the man, it being a rare exception among savage peoples for a woman to engage on it. Under such conditions a family consisting of mother and young only would probably, as a rule, have succumbed. (p. 39)

The hunting hypothesis was elaborated 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 1960, Washburn & DeVore 1961, Washburn & Lancaster 1968). Building on Raymond Dart’s arguments tying bipedality to hunting with weapons (Dart 1953), Washburn proposed that hunting large animals favored bipedalism, tool use, and bigger brains, which in turn created an obstetrical 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 hunting, so they required provisioning by hunting mates. 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 Washburn's most widely cited essay on this topic appeared (Washburn & Lancaster 1968), *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 meat. 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 (1968) chapter in that volume was especially important in challenging many assumptions about hunter-gatherers that were widespread at the time. Lee reported his observations of !Kung-speaking Bushmen in southern Africa and also summarized patterns from the ethnographic literature on foragers worldwide to show that aspects of the !Kung case were broadly 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 primate socioecology. 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 modeling tools used to investigate evolutionary questions have also changed dramatically. Nevertheless, the hunting hypothesis, much as it was articulated by Washburn before these changes occurred, still continues to be favored (e.g., Tooby & DeVore 1987, Deacon 1997, Kaplan et al. 2000, Horrobin 2001, Calvin 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 parenting 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 (Kleiman & Malcom 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 success (Hrdy 1979, 1981, 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 here.

The third domain I consider is the behavioral record for our own species, with particular emphasis on the ethnology and behavioral ecology of sexual divisions of labor among hunter-gatherers. Washburn and many others assumed 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 (cf. 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 and 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 (Leacock 1972, Sahlins 1972, Marshall 1976, Kelly 1995).

This material undermines the basis for scenarios that 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 males 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 socioecological 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 two sexes differ in structure in relation to different habits of life . . . they have no doubt 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 generated and nourished 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 but few to inherit their weaker powers. ([1871] 1981: 256)

Other differences between the sexes, such as male armaments 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. . . . That these characters are the result of sexual selection and not of ordinary selection is clear, as unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving numerous progeny, if better endowed males were not present. (Darwin [1871] 1981: 257–258)

While Darwin noted that it was not always easy to tease apart the operation 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 are separate, there is a constantly recurrent struggle between the males for the possession of the females" ([1871] 1981 ii: 260). Because of this "it is the males that fight together and sedulously display their charms before the females" (p. 272). He recognized two components of sexual selection, male-male combat and female choice, both of which shape the morphology, physiology, and behavior of males, so that "it is the male which, with rare 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 searches for her and plays the more active part in courtship . . . why should the male almost always be the seeker?" (Darwin [1871] 1981 ii: 273). Malte Andersson (1994) pointed out that Darwin came close to the anisogamy explanation for stronger sexual selection on males. But it was not until A. J. Bateman's (1948) experiments on sex differences in reproductive success among *Drosophila*, and then George Williams' (1966) use of this example, that the anisogamy explanation was widely appreciated. Bateman's experiments showed that reproductive success varied more among males, each additional mating increasing the reproductive success of males but not females. The anisogamy explanation for this result is based on differences in the two-gamete 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 paternity competition a zero-sum game, as any male's gain subtracts from the paternity available for others. Williams (1966) started with anisogamy, 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 Baylis (1981) drew attention to one reason why Darwin himself did not make that link: patterns of ornamentation and parental care in teleost 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 had 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 [1871] 1981 ii: 21). Thus Darwin saw the greater adornment of males even though they appeared to be more actively engaged in parenting than females as evidence against any general dependence of sexual selection on relative parental expenditure.

Links Between Parenting and Sexual Selection

Williams (1966), building on Darwin and of course Fisher (1930), was also characteristically wide ranging. He did not take up this riddle 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 parenting to sexual selection by defining parental investment so as to highlight a necessary interdependence among the trade-offs individuals must face given 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 an individual makes would equal its total parental effort (Low 1978). If both sexes expend about the same average overall total reproductive effort (Williams 1966), and that total is composed of parental and mating effort, then differences in the parental investment of the sexes must imply inverse 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 measuring 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 1991, Clutton Brock & Parker 1992). As recognized by R. A. Fisher, and maybe Darwin himself (Edwards 1998), the fact that (among most sexual reproducers) everybody has a mother and a father makes sex ratios likely to be even most of the time. Since overall reproductive rates depend on the rate of the slower sex, members of the faster sex, ready and waiting sooner, must compete for each reproductive opportunity.

Another issue here, also partly one of measurement, can involve the fundamental question of distinguishing parenting from mating. Trivers focused on the costs to a parent's ability to invest in other offspring. Some contributions that improve offspring welfare may benefit multiple recipients jointly. For example, a nest may cost the nest builder the same amount of effort and benefit each offspring the same whether it is used by one or several. This collective aspect of certain goods has been recognized with various labels, depreciable and nondepreciable care among them (Clutton Brock 1991). All goods and services are not the private property of individual parents and offspring.

In the case of the egg-guarding fish that may have kept Darwin from linking relative parental effort to sexual selection, the collective nature of the benefits to eggs has fundamental consequences for the fitness-related benefits to the guarding males. If a unit of guarding provided to one egg or nest does not reduce the guarding benefits available to another egg, a male can guard many clutches of eggs with the same effort with which he could guard a few. If females gain parental advantages by leaving eggs where they are safer, females may prefer to leave their eggs in the presence of many other eggs. Moreover, conspecific males may release sperm to compete with the sperm of the bright defending male, so the guarding male's probability of paternity for the eggs laid at his site can be substantially less than 100% (Gross & Sargent 1985). Guarding may thus have little effect on relative parenting success of the guarding male, that is, the relative welfare of his eggs versus those of other males. Under these circumstances, selection could maintain brightness and guarding because of its relative effects on male mating success. Whether an aspect of reproductive effort affects fitness through parenting or mating is of great importance in explaining both its origin and maintenance.

Why Indirect Care May Not Be Parental Effort

Considering specifically the problem of identifying male parental effort in mammals, Devra Kleiman and James Malcom (1981: 348) developed a very broad alternative to Trivers' definition. They "conceive male parental investment as *any increase in a prereproductive*

mammal's fitness attributable to the presence or action of a male" (original italics). This includes not only nondepreciable 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 survivorship. These acts may have delayed effects on survivorship 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 young . . . behaviors such as scent marking and long distance vocalizations which aid in the spacing of individuals or groups, and thus may maintain critical resources for eventual use by young, should also be considered as indirect forms of male parental investment. (Kleiman & Malcom 1981: 348-349)

This very inclusive definition seems to imply, incorrectly, that parenting is the adaptive function of any male behavior that could affect the welfare of 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 come through differential welfare of the performer's offspring compared to the young of males who act otherwise. Many of the activities in this list supply collective goods. Once supplied, they could benefit not only the male's offspring, but also others besides. Jeffrey Kurland and Steven Gaulin (1984: 285) pointed out one of the problems this presents for the specific case of troop defense in baboons (*Papio* spp.) or macaques (*Macaca* spp.).

Not only does indiscriminate 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 "floating," "cheater" males would be defended and the males themselves would incur none of the attendant risks. Thus, transient, nonparental males might reproductively do as well as, 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 welfare for his own offspring) are poor candidates to explain troop defense by resident males. Kurland and Gaulin surmise that the persistence of this behavior is more likely due to effects on the defending males' mating success. The speculations about egg-guarding fish above parallel their suggestion: "Much of what often passes for male 'parental care' may, in primates and mammals in general, in fact be more parsimoniously interpreted as male mating effort rather than male parental investment" (Kurland & Gaulin 1984: 285).

Distinguishing Mating from Parenting, Especially in Primates

Bobbi Low (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 structure or behavior is involved. For example, in any mammalian species in which males use horns solely in dominance displays and fights to secure matings while females use theirs in de-

fense of young, horns represent mating effort for males and parental effort for females." The lesson applies generally. Care for eggs or infants may be parenting, and copulation may be mating effort, but not necessarily. Whether the adaptive function of a behavior is mating or parenting depends on the character of the net fitness effects on the performer compared to a nonperformer. This includes strategies that result in pair bonds.

Darwin's cross-species review of reproductive behavior supported his conclusion that males are generally more eager to mate than females. He linked this to sexual selection and so to the benefits of mating effort for males. Pointing to the usual difference in parental expenditure of the sexes, Williams (1966: 183) said "the traditional coyness of the female is thus easily attributed to adaptive mechanisms by which she can discriminate the ideal moment and circumstances for assuming the burdens of motherhood." Trivers (1972) elaborated this argument with illustrative examples of ardent males and coy females. Paralleling Williams (1966), Trivers (1972) noted that "sex role reversed" species provide a test of whether the sex investing less in parenting spends more effort competing for the greater parental investment of the opposite sex. His examples were species where males contribute more parental effort than females, and where, as predicted, males are coy and females compete ardently for matings.

But What About Primate Females Who Are Not Coy?

Our own order, however, presents clear challenges to the generalization that the more parental sex is coy. Like other mammals, primate females do the bulk of parenting. Yet there are numerous examples in which females are anything but shy (Rowell 1988, Berkovitch 1995). Smuts (1987: 392) went so far as to say, "Females have been observed soliciting copulations in virtually every primate species that has been studied, and in the majority of species, females initiate the majority of copulations."

Sarah Hrdy faced the puzzle of libidinous females initially with hanuman langurs (*Presbytis entellus*). Having shown that sexual selection could favor the infanticidal behavior of langur males, she turned to the question of female counterstrategies. Exploring the role that reproductive competition among females plays in the evolutionary battle of the sexes (Hrdy 1979, 1981), she documented the eagerness of primate females to copulate with strange males.

At issue here are behaviors exhibited by the majority of species in the order primates, the best studied order of animals in the world, and the order specifically included by Bateman in his extrapolation from coyness in arthropods to coyness in anthropoids. Furthermore, females engaged in such "promiscuous matings" entail obvious risks, ranging from retaliatory attacks by males, venereal disease, the energetic costs of multiple solicitations, predation risks from leaving the troop, all the way to the risk of lost investment by a male consort who has been selected to avoid investing in other males' offspring (Trivers 1972). In retrospect one really does wonder why it was nearly 1980 before promiscuity among females attracted more than cursory theoretical interest. (Hrdy 1986: 126-127)

Once researchers began to investigate the patterns, an array of hypotheses were suggested to explain them. Most nominate benefits in offspring welfare that females may earn by copulating with many males. Hrdy developed the hypothesis that primate females solicited stranger males in response to the danger that males pose to the infants fathered by other

males. If males are less likely to kill infants they may have fathered, a female might reduce the dangers to her own infants by spreading the possibility of paternity widely. This was known initially as the "manipulation" hypothesis, but self-defense might have been emphasized instead. As Hrdy observed more recently (1999: 87–88), "pejorative-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 'assiduously maternal.'"

Hrdy's hypothesis was about relationships. She surmised that females might establish relationships with strange males and so reduce the danger those males otherwise posed. Increasing interest in exploring the character and consequences of relationships in primate social groups expanded from the late 1970s (Hinde 1979, 1983; Harcourt 1989, 1992; Chais 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). Females may interrupt 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? Hrdy's infanticide protection hypothesis proposed that males behaved differently toward the offspring of previous copulation partners because of the possibility 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 selection should design males to be sensitive to probable paternities and to avoid "misdirecting" paternal effort to the offspring of other males. This "danger of cuckoldry" argument was a basis for labeling solicitation of copulations by females as "deceptive" or "manipulative." The proposition that males are generally in danger of being "cuckolded by deceptive females" resonates with long-held Western views (Beckerman & Valentine 2002), including those about 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 ever dispensed, shows that the dangers males pose for each other provide sufficient reason for male jealousy.

Both modelers (e.g., Maynard Smith 1977) and fieldworkers (e.g., Smuts 1985, Paul et al. 1992; reviews in Whitten 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 living in multimale groups, males appear to contribute to offspring survival through babysitting, protection, occasional carrying, and other affiliative 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 be able to improve their chances of mating with the mother in the future. If this hypothesis is correct, then male care of infants sometimes represents mating effort rather than parental investment.

For olive baboons (*Papio anubis*), 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 mating partners. Smuts 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 on the variation in male care among many species of nonhuman primates, affirmed Smuts' assessment that this variation "is not adequately explained by parentage. 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 gentleness and affability in males (Hrdy 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 Wrangham (1979) hypothesized that females may establish and maintain relationships with aggressive males because of the protection this provides from other dangerous males (Wrangham & Rubenstein 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 is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female." Clutton 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 strategizing 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, Hrdy and Williams (1983: 5) pointed out "a strong tendency among field workers to focus on male behavior." However, only certain aspects of male behavior had received much attention. Smuts noted in her 1987 review that "the relationship between male dominance and male mating activity has probably received

more attention than 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: 26) could justifiably conclude that "social relationships among males remain the most poorly studied aspect of primate socioecology." The same errors that Hrdy and Williams (1983: 8) blamed for insufficient attention to female social behavior biased the attention paid to males: "The fallacy of measuring reproductive success in both sexes by zygote 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. Carel van Schaik (1996) saw that the dangers posed by infanticidal males might do more than spur females to seek protectors: 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 sociality 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, 2000), as well as the unusually high frequency and wide diversity in male-infant interactions that distinguish primates from most other mammals (Whitten 1987, Paul et al. 2000).

Ryne Palombit (1999) summarized observational and experimental data in savannah baboons and mountain gorillas (*Gorilla gorilla beringei*) consistent with the hypothesis that females maintain special relationships with particular males, that is, pair bonds, to reduce the danger of infanticide by other males. As he noted, following Hrdy and Smuts, appreciation of these patterns involves an important shift in thinking about the evolution of pair bonds. From the perspective of Trivers (1972), pair bonds are expected only with monogamy, which in turn is assumed to entail both sexes devoting substantial reproductive effort to parenting. Devra Kleiman (1977) had pointed out that in contrast to this prediction, monogamy did not necessarily imply either pair bonds or biparental care. Work over the past two decades has shown that the converse is also true. Strong male-female attachments that persist outside estrus 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 genus *Papio* especially interesting for questions about pair bonds. While females benefit from the infanticide protection supplied by friends (Palombit et al. 2000), the benefits males earn from these friendships may be more variable. Smuts (1985) found mating benefits among olive baboons, but data on other savannah populations challenges the mating effort hypothesis (Palombit 2000). Observations and playback experiments among chacma baboons (*Papio cynocephalus ursinus*) (Palombit et al. 1997) showed that males responded differentially 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 playbacks than control males did.

It could be that infant loss brings an end to friendships. During this study, infant mortality was 76%. At least half of this loss was due to infanticides committed by a recently immigrated alpha male with whom the mothers of the victims subsequently mated. As the

researchers note (Palombit 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 is an invitation to test socioecological 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 Gubernick (1994) listed 17 hypotheses for the evolution of monogamy and noted that they all involved various combinations of pair bonds, mating exclusivity, and male care, each of which might, in principle, evolve independently. The most dramatic impetus to a revised perspective on monogamy came first in ornithology, where the traditional view was "turned 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 (1968) explained the extremely high frequency of monogamy in birds as the result of the importance of paternal provisioning. Pairs usually persisted through a breeding season, sometimes longer, he explained, because male parental effort increased the reproductive success of the family. Lack was not the only influential figure to favor this hypothesis about pair bonds. As Patricia Gowaty (1996a: 23) noted, "almost everyone's (Darwin 1871, Williams 1966, Lack 1968, Orians 1969, Trivers 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 conflicts 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 to each partner for maintaining a pair bond. Investigators found that while male care sometimes varied with probable paternity, more often it did not (Wright 1990, Houston 1995). With experimental manipulation of pairs, investigators measured the effects of male care on female parenting success. Reviewing the data from removal experiments (Bart & Tornes 1989), Gowaty (1996b: 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 as a general explanation for social monogamy, the Male Care is Essential 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 own offspring, and that females sometimes fledged no more offspring with a male partner than without one meant 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 mutual parenting 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 paternal 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 incorporated the contradictions uncritically. 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. Reviewing the human variation recorded in both history and ethnography, Sarah Hrdy (1999: 232) concluded that "earlier commentators failed to consider how unusual are the particular environmental and demographic conditions that make long term monogamy advantageous for both sexes." Duran Bell (1997: 241) recently noted that "contemporary Western '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 circumstances 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 1870), 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, those studying the ethnographic variation have been skeptical that studies of other species could have any relevance to understanding the wide variability in our own.

Edmund Leach (1988: 91) memorably claimed that "mating and marriage are totally different concepts, as different as chalk from cheese." His definition of marriage focused on inheritance of relatively imperishable property. "Marriage provides a set of legal rules under which such items of property are handed down from generation to generation" (p. 93). This made marriage "exclusively a feature of human societies and not all human societies at that." 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 material property and little, if any, of that is imperishable 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 cuddle 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 us and other animals are greater than the similarities. Symons (1979: 108) made this observation:

The lexicon of English is woefully inadequate . . . [for] describing the thoughts, feelings, and behaviors associated with marriage and with other relations among men and women. . . . No doubt complexity and subtlety of thought, feeling, and action inevitably must be sacrificed if the written record is to be made at all . . . but to shrink the present vocabulary to one phrase—pair bond—and to imagine that in doing so one is being scientific—subsuming 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 come 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 variation 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 neurological and endochronological processes we share with other primates are a foundation for the emotional architecture that shapes behavior in us all (Darwin [1872] 1965, Hrdy 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 competition among men, concluding, "Humans then are typical mammals in that 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 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 competition 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 Washburn, also “knew” that high paternal effort was characteristic of humans under ethnographic circumstances most like those of deepest antiquity:

The basic social unit of human hunter-gatherers is the nuclear family in which men hunt, women gather vegetable foods, and the results are shared 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. 121)

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 parenting effort from men, supposed to characterize our species and to be key to our evolution, should mean 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 females: males and females invested 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 benefited, male fighting was in part paternal investment; that is, like hunting and gathering, fighting and nurturing were part of the human division of labor by sex. (Symons 1979: 163)

The trade-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 paternal 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 proven to be powerful tools for explaining the diversity of life because most of the time trade-offs are inescapable (Maynard Smith 1978, 1982; Seger & Stubblefield 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 use 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 conceals the subject, the agent who did the assigning. When the subject does materialize in such statements, almost invariably it turns out to be ‘society.’” The implication is that work is divided to serve the production goals of some larger entity, the family, domestic group, or household, which assigns tasks by sex and age. If families are assumed to be units 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 benefited, male fighting was in part paternal investment because the offspring of the winning males benefit.” The objection raised by Kurland 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 usefully labeled excludability and subtractability (Ostrom & Ostrom 1977). Consumers cannot be excluded from using a public good; and consumption by one does not subtract from 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.¹ Few goods or services are perfectly public or perfectly private, but some are more like public goods than others. 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 cited earlier, goods and services can be more or less depreciable.

The more public a good, the more likely that the value it has for consumers will not motivate commensurate supply. Eliciting financial support from public radio listeners exemplifies the undersupply problem long recognized by economists (Samuelson 1954): Why pay for what you get free? An array of collective action problems (Olson 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 payoff structures like the prisoner’s dilemma (e.g., Schelling 1978), and Garrett Hardin’s (1968) well known “tragedy of the commons” have come to be frequent illustrations of collective action problems (Hawkes 1992a). These arise whenever the pursuit of individual interests does not promote the welfare of the collective. As Russell Hardin (1982) notes, Adam Smith extolled the beneficial effects of the famous invisible hand, but the back of that hand is just as ubiquitous—and paradoxically both coincidence and conflicts of interest can operate to elevate as well as to depress economic productivity (Hardin 1982, Hirshleifer 2001).

The collective action problem with troop defense that Kurland and Gaulin flagged has two implications. 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 puts into defense. On the other hand, males are observed to “defend the troop,” a costly behavior that begs to be explained. Other fitness-related benefits that, unlike offspring protection, are private gains for the defenders may be important in the explanation. Kurland 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 community 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 than private goods. While a morsel of food goes into only one stomach, and each bite subtracts from the remainder available, large prey come only in big 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 are taken unpredictably, one hunter may succeed when all others fail to make a capture. Then the cost to the hunter (or anyone else) for excluding other hungry users 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 any 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 (Blurton Jones 1984, 1987). Hunting creates a collective action problem whenever hunted resources are like public goods (Hawkes et al. 1991, Hawkes 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., Sahlins 1972, Kelly 1995, Wiessner 1996). The sharing is usually labeled exchange and/or reciprocity by social anthropologists, a usage that leads biologically trained readers to assume that something like Trivers’ (1971) “reciprocal altruism” might explain the sharing—hunters doling out shares of meat in return for shares repaid in future 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.” Trivers’ model is essentially a market model of private goods and services exchanged by owners with negligible externalities, that is, no effects external to the exchanging parties. Individuals can benefit from this kind of reciprocity as long as they “keep score” and terminate transfers to any who fail to repay. They benefit as long as sharing is contingent on repayment.

The quid pro quo accounting required for such exchange strategies to be evolutionarily stable (Axlerod & Hamilton 1981) is explicitly denied in a multitude of ethnographies that detail food sharing in kinship societies (e.g., compilations in Dowling 1968, Lévi-Strauss 1969, Sahlins 1972, Kelly 1995). Insistence that the meat of large prey is not the hunter’s private property is repeatedly confirmed (e.g., Marshall 1976, Barnard & Woodburn 1988, Wiessner 1996, Woodburn 1998). It is possible, of course, that ethnographers have been mistaken, or that their subjects’ descriptions of their own norms do not reflect actual behavior. Sometimes, however, ethnographers see and report that the successful hunter plays no part in the distribution, so is in no position to direct shares according to his personal accounts (e.g., Hill & Kaplan 1988).

Ethnographers have also used observations of actual distributions to investigate whether food sharing is contingent on food repayments. In a few cases, for some foods, researchers report contingency (Gurven et al. 2000, Hames 2000). But more frequently, and especially for large game animals, there is little indication that the distribution of shares depends on

meat repayments to the hunter (e.g., Marshall 1976, Lee 1979, Kaplan & Hill 1985a, Bliege Bird & Bird 1997, Woodburn 1998, Hawkes et al. 2001a). The quantitative investigations add to the evidence against the view that meat is the hunter’s private property (Hawkes 2001). The more often large prey are like public goods, the more likely it is that parenting benefits do not provide a general explanation for why men hunt them (Hawkes 1990, 1991, 1993; Hawkes et al. 2001b). The same collective action problem that undercuts parenting 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 of course an outcome 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. Westermarck’s near contemporary Lewis Henry Morgan (1870) speculated that monogamy was actually a late development in the evolution of human society. Frederick Engels ([1884] 1972) relied on Morgan in his scenario of *The Origin of the Family, Private Property and the State*. In the mid-twentieth century, Eleanor Leacock, an ethnographer and ethnohistorian of the North American Montagnais, agreed with Engels. Other cultural anthropologists have developed and defended similar views (e.g., Collier & Rosaldo 1981). Leacock (1972: 29) surmised that civilization transformed “the nuclear family into the basic economic unit of society, within which a woman and her children became dependent on an individual man.” 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, large game and produce from the fields, were shared among a group of families” (p. 33). Like other hunter-gatherer ethnographers, Leacock was especially impressed with the constant sharing and egalitarian character of hunter-gatherer social life.

Morton Fried (1967: 33) classically defined an egalitarian society as one in which “there are as many positions of prestige in any given age-sex grade as there are persons capable of filling them.” Arguments long favored in cultural anthropology to explain such patterns pointed to the group benefits of wide sharing which leveled differences and prevented wealth accumulation (e.g., Fried 1967, Sahlins 1972, Wiessner 1996). By contrast, most behavioral ecologists ever since Williams (1966), and some social scientists ever since Schelling (1960) and Olson (1965), have seen fatal flaws in explanations for social behavior that ignore payoffs to individuals and rely only on group-level functions. David S. Wilson and colleagues (e.g., Wilson 1983, 1998; Sober & Wilson 1998) argue that these critiques of group selection led to premature rejection by sociobiologists of explanations for human social behavior in terms of group benefits. Emphasizing that selection is a multilevel process, the “new group selectionists” argue that well-known patterns of human cooperation remain inexplicable when the focus is improperly restricted to within-group effects on individuals. Christopher Boehm (1993, 1999a, b) agrees with this criticism. He has revived the group benefit explanations for egalitarian societies previously advanced by an earlier generation of cultural anthropologists, concluding that patterns of distinctly cooperative human behavior defy the “standard evolutionary paradigm” (Boehm 1999b: 209).

The counterargument is central to the issues of this chapter: It turns on a full tally of the fitness-related costs and benefits to individuals for both meat sharing and hunting. My disagreement with Wilson and Boehm is not about the logic of multilevel selection models,

but about the empirical assessment of the costs and benefits to the individual actors. Boehm (1999b: 209) 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 ethnological generalization, but Boehm (1999b: 210) surmises that “if band members are disposed to assist nonkin in the band, this is likely to require a group selection argument”. His explicit inference is that sharing imposes a net cost on sharers compared to nonsharers, 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 (Blurton Jones 1984, 1987; Petersen 1993). If the prey shared are like public goods, then those claiming shares are appropriating from the public domain. Under these circumstances, anyone trying to exclude claimants is interfering with their “rights” and is likely to pay a cost for that interference. As to the work invested in procuring the prey in the first place, the point I underline here is that the hunter gets 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 multilevel 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 “selective incentives,” 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 guarding 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 credit 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, saw these as “leveling mechanisms,” with leveling further reflected in the famously self-effacing style of hunters (Lee 1969, Sahlins 1972, Harris 1977, Hawkes 1992b). But neither practice interferes with widespread interest in the actual events of a hunt.

Among foragers, the behavior of hunters and their prey and the circumstances of the death of particular animals are usually topics of endless interest (Blurton Jones & Konner 1976, Marshall 1976, Lee 1979, Hawkes 2000). In contrast to Fried’s claim about “randomizing credit,” the evidence indicates that repeated storytelling assures that details of each hunt are widely known and well remembered. Ethnographers can collect lifetime tallies of the large prey killed by each hunter (Lee 1979), and rankings of hunters’ success rates that closely correlate with records of kills that the ethnographers observed (Kaplan & Hill 1985a, Blurton Jones et al. 1997). Conventions that assign “ownership” of prey animals delegate duties associated with distributing the meat (Marshall 1976), but the carcass is no more this “owner’s” private property than it is the hunter’s (Marshall 1976, Barnard & Woodburn 1988, Woodburn 1998, Hawkes 2001). And such conventions do not interfere with eager interest in who killed the animal.

Since everyone pays attention to hunters’ successes, credit to successful hunters develops into reputations. Like other costly signals of quality (Zahavi 1975, 1977, 1995; Zahavi & Zahavi 1997; Grafen 1990), hunting reputations benefit hunters as this information is used 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 how desirable as allies and dangerous as competitors they are. Everyone has two reasons to be pay attention to hunters’ successes: they get meat and they get information about the hunter’s qualities (Hawkes & Bliege Bird 2002).

The nonfood benefits for the hunters themselves can be substantial. By hunting, a man maintains or improves his social standing among other men. His social position affects whether and how much other men defer to him, and that affects his value as an ally to both men and women—with consequences for his mating success (Kaplan & Hill 1985b; Hawkes 1993; Hill & Hurtado 1996; Blurton Jones et al. 1997, 2000; Bliege Bird et al. 2001; Hawkes et al. 2001b). Costly signaling models can help highlight mating benefits that explain why men hunt while women gather, as well as other aspects of foraging differences between the sexes (Bliege Bird 1999, Bliege Bird et al. 2001). The same framework applies, as Thorstein Veblen ([1899] 1922) proposed more than a century ago, to many other puzzles of human behavior in which social benefits can explain what is mysterious on more “utilitarian” grounds (e.g., Boone 1998, Neiman 1998, Roberts 1998, Frank 1999, Miller 2000, Smith & Bliege Bird 2000, Gintis et al. 2001).

Arguments about the nonfood benefits men earn from hunting make the emerging evidence about hunting among chimpanzees (*Pan troglodytes*) of special interest. When Washburn elaborated his version of the hunting hypothesis, chimpanzees were not known to hunt. Now evidence from a wide array of study sites shows chimpanzees to be active and effective hunters (summaries in Stanford 1996, 1999; Mitani et al. 2002). As among humans, chimpanzee hunting is a male specialty and prey are more widely shared than other foods, although little is eaten by females and juveniles. Several lines of evidence now indicate that hunting and meat sharing are costly, with little nutritional gain for the time spent. Instead of a feeding strategy, chimpanzee hunting appears to be motivated by male status competition (Mitani & Watts 2001).

In chimpanzees and in other primates, male activities have large effects on females. As Smuts (1992: 5) noted, “when we look closely, we find that in many primates, hardly an aspect of female existence is not constrained in some way by the presence of aggressive males.” Yet there is no temptation with nonhuman species to describe these aspects of male behavior as part of a “sexual division of labor.” In humans, lethal weapons change the cost of aggressive encounters, making the potential effects of male behavior even greater. Armed opponents, whatever their relative physical strength, can be much more dangerous. Models that include contest costs predict a tendency to adopt conventional solutions to contests more quickly as those costs increase (Maynard Smith 1982, Blurton Jones 1987, Clutton Brock & Parker 1995). This line of argument points toward the greater use of conventional solutions to contests among men than among chimpanzees (Hawkes 2000). But it does not make the male competition less important.

In addition to the use of lethal weapons, men also differ from chimpanzees by often hunting prey larger than their own body size. Large prey also mean more meat with each kill. More meat means more consumers and more general interest in the success of hunters. The more important hunting reputations are to a man’s social standing, the more men are

likely to hunt. Resulting levels of meat procurement can be high enough that meat becomes a substantial component of the average diets of women and children.

Frank Marlowe (2001) has linked cross-cultural variation in men's average subsistence contribution 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 increases in the average number 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 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 primate pattern in which more food—from whatever sources—means more surviving offspring.

Large effects on the number of children that women can rear are temptation to classify the economic production from men as parental effort (or indirect paternal investment, e.g., Kaplan et al. 2000, Marlowe 2000). Of course men can and sometimes do expend parental effort. But even when hunting has large effects on average food consumption, it is not paternal 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 as his own children do, his fitness payoffs cannot be differential nutrition for his offspring (Kaplan & Hill 1985a; Hawkes et al. 1991, 2001a, b). If the differential benefit to the hunter himself, 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 treatment 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 male competition are implicated (Hill & Hurtado 1996, Hawkes et al. 2001b).

What About Pair Bonds?

The tenacity of the assumption that men's contribution to subsistence is paternal 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 tendency. 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 they are married to them, why marry?

Special relationships in other primates where males supply no 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 strength of their fitness effects. In these simulations, pairing was the usual 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 for mate guarding than for parental effort. No female choice was included, yet pair bonds—each male putting 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 Blurton Jones and colleagues (2000) examined variation in pair bond stability among four hunter-gatherer societies for which both operational sex ratio 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 mating 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 may 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 advantages that marriage may provide to husbands more than any advantages to their wives (Hawkes et al. 2001b).

That analysis may underestimate the value of a protector (Wrangham 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 (Blurton Jones et al. 2000). Hypotheses about partners as protectors 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 socioecology as well. Smuts (1992: 9–10) said:

Most reconstructions of human evolution have assumed that pair bonds evolved 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 non-human primates, and especially among our closest living relatives (chimpanzees, gorillas, and orangutans) however, we should carefully consider the alternative hypothesis that pair bonds benefited females initially because of the protection mates provided against other males (including protection from infanticide).

Smuts developed a hypothetical scenario that reflects the importance of coalitions 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 as each male began to develop a long term mating association with a particular female or females (a trend foreshadowed in savanna baboons).

. . . 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 coerce their own females with reduced interference by other men. (Smuts 1992: 10–11)

Sarah Mesnick (1997) assembled 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 females. She formulated the “bodyguard hypothesis,” in which protection is a primary criterion of female choice. Agreeing with Smuts, 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 pairbonding” (Mesnick 1997: 207). Wilson and Mesnick (1997) tested predictions of the bodyguard hypothesis for humans on Canadian records of sexual assault homicides and reported nonlethal sexual aggression. 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 human animal” (p. 66), these relationships are often neither lifelong nor 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 surmised 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 attributed the evolution of our extended juvenile 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 maturity (Hawkes et al. 1998, 2003; O’Connell et al. 1999, 2002; Alvarez 2000; Hawkes 2003). The general health and vigor of peri- and postmenopausal women and the late maturity of human adolescents distinguishes us from other apes. Both grandmothers and older siblings provide a source of help to weanlings when mothers bear newborns. This means our pattern of cooperative breeding (Hrdy 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 infanticidal males, since, under some circumstances, that could increase the paternity chances for a man unlikely to be the infant’s father. Helen Fisher recognized the dangers of infanticide 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 a . . . model . . . for how pairbonding, the nuclear family, and divorce could have evolved” (Fisher 1992: 154).

We know that the hominid radiation included genera 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 diverse. 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 marked sociality, 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 relationships are especially well developed in primates (Harcourt 1992). Conflicts of interest between (and within) the sexes have especially complex repercussions in the context of these life histories and this sociality (van Schaik & 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 provisioning by ancestral males should be viewed with serious skepticism. Numerous lines of theory and evidence stand against it. At the same time, the special relationships between males and females in other primates and their links to dangers posed by male mating competition are increasingly well described. On phylogenetic grounds alone, those patterns should be the first place to look for hypotheses about the evolution of our emotional attachments. Increasing understanding of the socioecology 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 their intersection 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.

References

- Alvarez, H. P. 2000. Grandmother hypothesis and primate life histories. *Am. J. Phys. Anthropol.*, 113, 435–450.
- Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, 211, 1390–1396.
- Barnard, A. & Woodburn, J. 1988. Property power and ideology in hunting and gathering societies: an introduction. In: *Hunters and Gatherers 2: Property, Power and Ideology* (Ed. by T. Ingold, D. Riches, & J. Woodburn), pp. 4–31. New York: Berg.
- Bart, J. & Tornes, A. 1989. Importance of monogamous male birds in determining reproductive success: evidence for house wrens and review of male-removal experiments. *Behav. Ecol. Sociobiol.*, 24, 109–116.

- Barton, R. A. 2000. Socioecology of baboons: the interaction of male and female strategies. In: *Primate Males: Causes and Consequences of Variation in Group Composition* (Ed. by P. M. Kappeler), pp. 97–107. Cambridge: Cambridge University Press.
- Barton, R. A., Byrne, R. W., & Whitten, A. 1996. Ecology, feeding competition and social structure in baboons. *Behav. Ecol. Sociobiol.*, 38, 321–329.
- Bateman, A. J. 1948. Intrasexual selection in *Drosophila*. *Heredity*, 2, 349–368.
- Baylis, J. R. 1981. The evolution of paternal care in fishes, with reference to Darwin's rule of male sexual selection. *Environ. Biol. Fishes*, 6, 223–251.
- Beckerman, S. & Valentine, P. 2002. Introduction: the concept of partible paternity among native South Americans. In: *Cultures of Multiple Fathers: The Theory and Practice of Partible Paternity in Lowland South America* (Ed. by S. Beckerman & P. Valentine), pp. 1–13. Gainesville, FL: University Press of Florida.
- Bell, D. 1997. Defining marriage and legitimacy. *Curr. Anthropol.*, 38, 237–253.
- Berkovitch, F. 1995. Female cooperation, consortship maintenance, and male mating success in savanna baboons. *Anim. Behav.*, 50, 137–149.
- Birkhead, T. & Moller, A. 1992. *Sperm Competition in Birds: Its Evolutionary Causes and Consequences*. London: Academic Press.
- Black, J. M. 1996. *Partnerships in Birds*. Oxford: Oxford University Press.
- Bliege Bird, R. B. 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. *Evol. Anthropol.*, 8, 65–75.
- Bliege Bird, R. & Bird, D. 1997. Delayed reciprocity and tolerated theft: the behavioral ecology of food sharing strategies. *Curr. Anthropol.*, 38, 49–78.
- Bliege Bird, R., Smith, E. A., & Bird, D. 2001. The hunting handicap: costly signaling in male foraging strategies. *Behav. Ecol. Sociobiol.*, 50, 9–19.
- Blurton Jones, N. G. 1984. A selfish origin for food sharing: tolerated theft. *Ethol. Sociobiol.*, 5, 1–3.
- Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding, and scrounging. *Soc. Sci. Info.*, 26(1), 31–54.
- Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. 1997. Why do Hadza children forage? In: *Uniting Psychology and Biology: Integrative Perspectives on Human Development* (Ed. by N. Segal, G. E. Weisfeld, & C. C. Weisfeld), pp. 279–313. Washington, DC: American Psychological Association.
- Blurton Jones, N. G. & Konner, M. J. 1976. !Kung knowledge of animal behavior (or: the proper study of mankind is animals). In: *Kalahari Hunters: Studies of the !Kung San and Their Neighbors* (Ed. by R. B. Lee & I. DeVore), pp. 325–348. Cambridge, MA: Harvard University Press.
- Blurton Jones, N. G., Marlowe, F., Hawkes, K., & O'Connell, J. F. 2000. Paternal investment and hunter-gatherer divorce. In: *Adaptation and Human Behavior: An Anthropological Perspective* (Ed. by L. Cronk, N. Chagnon, & W. Irons), pp. 61–90. New York: Aldine de Gruyter.
- Boehm, C. 1993. Egalitarian society and reverse dominance hierarchy. *Curr. Anthropol.*, 35, 178–180.
- Boehm, C. 1999a. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge, MA: Harvard University Press.
- Boehm, C. 1999b. The natural selection of altruistic traits. *Hum. Nat.*, 10, 205–252.
- Boone, J. L. 1998. The evolution of magnanimity: when is it better to give than to receive? *Hum. Nat.*, 9, 1–21.
- Calvin, W. H. 2002. *A Brain for All Seasons: Human Evolution and Abrupt Climate Change*. Chicago: University of Chicago Press.
- Cartmill, M. 1994. *A View to Death in the Morning: Hunting and Nature Through History*. Cambridge, MA: Harvard University Press.
- Chapais, B. 1992. The role of alliances in the social inheritance of rank among female primates. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 29–60. Oxford: Oxford University Press.
- Chapais, B. 1995. Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. *Ybk. Phys. Anthropol.*, 38, 115–136.
- Clutton Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.
- Clutton Brock, T. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.*, 67, 437–456.
- Clutton Brock, T. & Parker, G. 1995. Sexual coercion in animal societies. *Anim. Behav.*, 49, 1345–1365.
- Collier, J. F. & Rosaldo, M. Z. 1981. Politics and gender in simple societies. In: *Sexual Meanings* (Ed. by S. Ortner & H. Whitehead), pp. 275–329. New York: Cambridge University Press.
- Daly, M. & Wilson, M. 1987. The Darwinian psychology of discriminative parental solicitude. *Nebr. Symp. Motivation*, 35, 91–144.
- Daly, M., Wilson, M., & Weghorst, S. 1982. Male sexual jealousy. *Ethol. Sociobiol.*, 3, 11–27.
- Darwin, C. [1871] 1981. *The Descent of Man and Selection in Relation to Sex*. Reprint, Princeton, NJ: Princeton University Press.
- Darwin, C. [1872] 1965. *The Expression of the Emotions in Man and Animals*. Reprint, Chicago: University of Chicago Press.
- Dart, R. A. 1953. The predatory transition from ape to man. *Int. Anthropol. Ling. Rev.*, 1, 201–217.
- Deacon, T. W. 1997. *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: Norton.
- Dowling, J. H. 1968. Individual ownership and the sharing of game in hunting societies. *Am. Anthropol.*, 70, 502–507.
- Edwards, A. W. F. 1998. Natural selection and the sex ratio: Fisher's sources. *Am. Nat.*, 151, 564–569.
- Engels, F. [1884] 1972. *Origin of the Family, Private Property and the State*. Reprint, with an introduction by Eleanor Burke Leacock, New York: International Publishers.
- Fisher, H. E. 1981. *The Sex Contract: The Evolution of Human Behavior*. New York: William Morrow.
- Fisher, H. E. 1992. *Anatomy of Love: The Natural History of Monogamy, Adultery, and Divorce*. New York: Norton.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.
- Frank, R. 1999. *Luxury Fever: Why Money Fails to Satisfy in an Era of Excess*. New York: Free Press.
- Fried, M. H. 1967. *The Evolution of Political Society: An Essay in Political Anthropology*. New York: Random House.
- Gintis, H., Smith, E. A., & Bowles, S. 2001. Costly signaling and cooperation. *J. Theor. Biol.*, 213, 103–119.
- Goodenough, W. H. 1970. *Description and Comparison in Cultural Anthropology*. Chicago: Aldine.
- Gowaty, P. A. 1966a. Battle of the sexes and the origins of monogamy. In: *Partnerships in Birds* (Ed. by J. M. Black), pp. 21–52. Oxford: Oxford University Press.

- Gowaty, P. A. 1996b. Field studies of parental care in birds: new data focus questions on variation among females. *Adv. Study Behav.*, 25, 477–531.
- Grafen, A. 1990. Biological signals as handicaps. *J. Theor. Biol.*, 144, 517–46.
- Gross, M. & Sargent, R. 1985. The evolution of male and female parental care in fishes. *Am. Zool.*, 25, 807–822.
- Gubernick, D. J. 1994. Biparental care and male-female relations in mammals. In: *Infanticide and Parental Care* (Ed. by S. Parmigiani & F. S. vom Saal), pp. 427–463. Chur, Switzerland: Harwood Academic.
- Curven, M., Hill, K., Hurtado, A., & Lyles, R. 2000. Food transfers among Hiwi foragers of Venezuela: tests of reciprocity. *Hum. Ecol.*, 28, 171–214.
- Hames, R. 2000. Reciprocal altruism in Yanomamo food exchange. In: *Adaptation and Human Behavior: An Anthropological Perspective* (Ed. by L. Cronk, N. Chagnon, & W. Irons), pp. 397–416. New York: Aldine de Gruyter.
- Harcourt, A. H. 1989. Social influences on competitive ability: alliances and their consequences. In: *Comparative Socioecology of Mammals and Man* (Ed. by V. Standon & R. Foley), pp. 223–242. London: Blackwell.
- Harcourt, A. H. 1992. Coalitions and alliances: are primates more complex than non-primates? In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 445–472. Oxford: Oxford University Press.
- Hardin, G. 1968. The tragedy of the commons. *Science*, 162, 1243–1248.
- Hardin, R. 1982. *Collective Action*. Baltimore, MD: Johns Hopkins University Press.
- Harris, M. 1977. *Cannibals and Kings: The Origins of Cultures*. New York: Random House.
- Hawkes, K. 1990. Why do men hunt? Some benefits for risky strategies. In: *Risk and Uncertainty in Tribal and Peasant Economies* (Ed. by E. Cashdan), pp. 145–166. Boulder, CO: Westview Press.
- Hawkes, K. 1991. Showing off: tests of an hypothesis about men's foraging goals. *Ethol. Sociobiol.*, 12, 29–54.
- Hawkes, K. 1992a. Sharing and collective action. In: *Evolutionary Ecology and Human Behavior* (Ed. by E. Smith & B. Winterhalder), pp. 269–300. New York: Aldine de Gruyter.
- Hawkes, K. 1992b. On sharing and work (a comment on Bird-David). *Curr. Anthropol.*, 33(4), 404–407.
- Hawkes, K. 1993. Why hunter-gatherers work: an ancient version of the problem of public goods. *Curr. Anthropol.*, 34(4), 341–361.
- Hawkes, K. 2000. Big game hunting and the evolution of egalitarian societies. In: *Hierarchies in Action: Cui Bono?* (Ed. by M. Deihl), pp. 59–83. Carbondale, IL: Southern Illinois University. Center for Archaeological Investigations, Occasional Paper No. 27.
- Hawkes, K. 2001. Is meat the hunter's property? Ownership and explanations of hunting and sharing. In: *Meat-Eating and Human Evolution* (Ed. by C. Stanford & H. Bunn), pp. 219–236. Oxford: Oxford University Press.
- Hawkes, K. 2003. Grandmothers and the evolution of human longevity. *Am. J. Hum. Biol.*, 15, 380–400.
- Hawkes, K. & Bliege Bird, R. 2002. Showing-off, handicap signaling, and the evolution of men's work. *Evol. Anthropol.*, 11, 58–67.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. 1991. Hunting income patterns among the Hadza: big game, common goods, foraging goals, and the evolution of the human diet. *Phil. Trans. Royal Soc. Lond., B*, 334, 243–251.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. 2001a. Hadza meat sharing. *Evol. Hum. Behav.*, 22, 1–30.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. 2001b. Hunting and nuclear families: some lessons from the Hadza about men's work. *Curr. Anthropol.*, 42, 681–709.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. 2003. Human life histories: primate tradeoffs, grandmothering socioecology, and the fossil record. In: *The Role of Life Histories in Primate Socioecology* (Ed. by P. Kappeler & M. Pereira), pp. 204–227. Chicago: University of Chicago Press.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. L. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. USA*, 95(3), 1336–1339.
- Hawkes, K., Rogers, A. R., & Charnov, E. L. 1995. The male's dilemma: increased offspring production is more paternity to steal. *Evol. Ecol.*, 9, 662–677.
- Hill, K. & Hurtado, A. M. 1996. *Ach \ddot{e} Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.
- Hill, K. & Kaplan, H. 1988. Tradeoffs in male and female reproductive strategies among Ache foragers. In: *Human Reproductive Effort* (Ed. by L. Betzig, M. Borgerhoff-Mulder, & P. Turke), pp. 277–306. Cambridge: Cambridge University Press.
- Hinde, R. A. 1979. *Towards Understanding Relationships*. London: Academic Press.
- Hinde, R. A. ed. 1983. *Primate Social Relationships: An Integrated Approach*. Sunderland, MA: Sinauer Associates.
- Hirshleifer, J. 2001. *The Dark Side of the Force: Economic Foundations of Conflict Theory*. Cambridge: Cambridge University Press.
- Horrobin, D. 2001. *The Madness of Adam and Eve: How Schizophrenia Shaped Humanity*. London: Bantam Press.
- Houston, A. I. 1995. Parental effort and paternity. *Anim. Behav.*, 50, 1635–1644.
- Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.*, 1, 13–40.
- Hrdy, S. B. 1981. *The Woman That Never Evolved*. Cambridge, MA: Harvard University Press.
- Hrdy, S. B. 1986. Empathy, polyandry, and the myth of the coy female. In: *Feminist Approaches to Science* (Ed. by R. Bleier), pp. 119–146. New York: Pergamon Press.
- Hrdy, S. B. 1999. *Mother Nature: A History of Mother's Infants and Natural Selection*. New York: Pantheon Books.
- Hrdy, S. B. 2001. Mothers and others. *Nat. Hist.*, 110(4), 50–64.
- Hrdy, S. B. & Williams, G. C. 1983. Behavioral biology and the double standard. In: *Social Behavior of Female Vertebrates* (Ed. by S. K. Wasser), pp. 1–17. New York: Academic Press.
- Kaplan, H. & Hill, K. 1985a. Hunting ability and reproductive success among male Ache foragers: preliminary results. *Curr. Anthropol.*, 26, 131–133.
- Kaplan, H. & Hill, K. 1985b. Food sharing among Ache foragers: tests of explanatory hypotheses. *Curr. Anthropol.*, 26, 223–246.
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.*, 9, 156–185.
- Kappeler, P. M. 1999. Primate socioecology: new insights from males. *Naturwissenschaften*, 85, 18–29.
- Kelly, R. L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.
- Kleiman, D. G. 1977. Monogamy in mammals. *Q. Rev. Biol.*, 5, 39–69.
- Kleiman, D. G. & Malcolm, J. R. 1981. The evolution of male parental investment in mammals. In: *Parental Care in Mammals* (Ed. by D. J. Gubernick & P. H. Klopfer), pp. 347–387. New York: Plenum Press.

- Klein, R. G. 1999. *The Human Career: Human Biological and Cultural Origins*, 2nd ed. Chicago: University of Chicago Press.
- Kurland, J. & Gaulin, S. 1984. The evolution of male parental investment: effects of genetic relatedness and feeding ecology on the allocation of reproductive effort. In: *Primate Paternalism* (Ed. by D. M. Taub), pp. 259–308. New York: Van Nostrand Reinhold.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Lancaster, J. B. & Lancaster, C. 1983. Parental investment: the hominid adaptation. In: *How Humans Adapt: Biocultural Odyssey* (Ed. by D. J. Ortner), pp. 33–56. Washington, DC: Smithsonian Institution Press.
- Lancaster, J. B. & Lancaster, C. 1987. The watershed: change in parental-investment and family formation strategies in the course of human evolution. In: *Parenting Across the Life Span: Biosocial Dimensions* (Ed. by J. B. Lancaster, J. Altmann, A. S. Rossi, & L. R. Sherrod), pp. 187–205. Hawthorne, NY: Aldine de Gruyter.
- Leach, E. 1988. The social anthropology of marriage and mating. In: *Mating and Marriage* (Ed. by V. Reynolds & J. Kellett), pp. 91–110. Oxford: Oxford University Press.
- Leacock, E. B. 1972. Introduction and notes. In: *The Origins of the Family, Private Property and the State* (By Frederick Engels), pp. 7–67. New York: International Publishers.
- Lee, R. B. 1968. What hunters do for a living, or how to make out on scarce resources. In: *Man the Hunter* (Ed. by R. B. Lee & I. DeVore), pp. 30–48. Chicago: Aldine.
- Lee, R. B. 1969. Eating Christmas in the Kalahari. *Nat. Hist.*, 14–22, 60–63.
- Lee, R. B. 1979. *The !Kung San: Men, Women and Work in a Foraging Society*. Cambridge: Cambridge University Press.
- Lévi-Strauss, C. 1969. *The Elementary Structures of Kinship*. Revised and translated from the French edition (1949). New York: Beacon Press.
- Lovejoy, C. O. 1981. The origin of man. *Science*, 211, 341–350.
- Low, B. S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.*, 112(983), 197–213.
- Marlowe, F. 2000. Paternal investment and the human mating system. *Behav. Proc.*, 51, 45–61.
- Marlowe, F. 2001. Male contribution to diet and female reproductive success. *Curr. Anthropol.*, 42, 755–760.
- Marshall, L. 1976. *The !Kung of Nyae Nyae*. Cambridge, MA: Harvard University Press.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, 25, 1–9.
- Maynard Smith, J. 1978. Optimization theory in evolution. *Annu. Rev. Ecol. Sys.*, 9, 31–56.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Mesnick, S. L. 1997. Sexual alliances: evidence and evolutionary implications. In: *Feminism and Evolutionary Biology: Boundaries, Intersections, and Frontiers* (Ed. by P. A. Gowaty), pp. 207–257. New York: Chapman Hall.
- Miller, G. F. 2000. *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. New York: Doubleday.
- Mitani, J. D. & Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Anim. Behav.*, 61, 915–924.
- Mitani, J. C., Watts, D. P., & Muller, M. N. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol. Anthropol.*, 11, 9–25.
- Morgan, L. H. 1870. *Systems of Consanguinity and Affinity of the Human Family*. Washington, DC: Smithsonian Institution Press.
- Neiman, F. D. 1998. Conspicuous consumption as wasteful advertising: a Darwinian perspective on spatial patterns in the Classic Maya terminal monument dates. In: *Rediscovering Darwin: Evolutionary Theory and Archaeological Explanation* (Ed. by C. M. Barton & G. A. Clark), pp. 267–290. Washington, DC: Archaeological Papers of the American Anthropological Association.
- O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.*, 36, 461–485.
- O'Connell, J. F., Hawkes, K., Lupo, K. D., & Blurton Jones, N. G. 2002. Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.*, 43, 831–872.
- Olson, M. 1965. *The Logic of Collective Action: Public Goods and the Theory of Groups*. Cambridge, MA: Harvard University Press.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.*, 103, 589–603.
- Ostrom, V. & Ostrom, E. 1977. Public goods and public choices. In: *Alternatives for Delivering Public Services: Toward Improved Performance* (Ed. by E. S. Savas), pp. 7–49. Boulder, CO: Westview Press.
- Palombit, R. A. 1999. Infanticide and the evolution of pair bonds in nonhuman primates. *Evol. Anthropol.*, 7, 117–129.
- Palombit, R. A. 2000. Infanticide and the evolution of male-female bonds in animals. In: *Infanticide by Males and Its Implications* (Ed. by C. P. van Schaik & C. H. Janson), pp. 239–268. Cambridge: Cambridge University Press.
- Palombit, R. A., Cheney, D. L., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R. M., & Silk, J. B. 2000. Male infanticide and defense of infants in chacma baboons. In: *Infanticide by Males and Its Implications* (Ed. by C. P. van Schaik & C. H. Janson), pp. 123–152. Cambridge: Cambridge University Press.
- Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. 1997. The adaptive value of “friendships” to female baboons: experimental and observational evidence. *Anim. Behav.*, 54, 599–614.
- Paul, A., Kuester, J., & Arnemann, J. 1992. DNA fingerprinting reveals that infant care by male Barbary macaques (*Macaca sylvanus*) is not parental investment. *Folia Primatol.*, 58, 93–98.
- Paul, A., Preuschoft, S., & van Schaik, C. P. 2000. The other side of the coin: infanticide and the evolution of affiliative male-infant interactions in Old World primates. In: *Infanticide by Males and Its Implications* (Ed. by C. P. van Schaik & C. H. Janson), pp. 269–292. Cambridge: Cambridge University Press.
- Peterson, N. 1993. Demand sharing: reciprocity and the pressure for generosity among foragers. *Am. Anthropol.*, 95, 860–874.
- Pinker, S. 1997. *How the Mind Works*. New York: Norton.
- Polanyi, K. 1957. The economy as instituted process. In: *Trade and Market in the Early Empires: Economies in History and Theory* (Ed. by K. Polanyi, C. Arensberg, & H. Pearson), pp. 243–270. Chicago: Henry Regnery.
- Roberts, G. 1998. Competitive altruism: from reciprocity to the handicap principle. *Proc. Royal Soc. Lond., B*, 265, 427–431.
- Rowell, T. E. 1988. The social system of guenons, compared with baboons, macaques, and mangabeys. In: *A Primate Radiation: Evolutionary Biology of the African Guenons* (Ed. by F. Gautier-Hion, H. Bourlier, J. P. Gautier, & J. Kingdon), pp. 347–351. Cambridge: Cambridge University Press.
- Sahlins, M. D. 1972. *Stone Age Economics*. Chicago: Aldine.
- Samuelson, P. A. 1954. The pure theory of public expenditure. *Rev. Econ. Stat.*, 36, 387–389.
- Schelling, T. C. 1960. *The Strategy of Conflict*. Cambridge, MA: Harvard University Press.
- Schelling, T. C. 1978. *Micromotives and Macrobehavior*. New York: Norton.
- Seger, J. & Stubblefield, J. W. 1996. Optimization and adaptation. In: *Adaptation* (Ed. by G. Lauder & M. R. Rose), pp. 93–123. New York: Academic Press.

- Smith, E. A. & Bliege Bird, R. 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. *Evol. Hum. Behav.*, 21, 245–261.
- Smuts, B. B. 1983a. Dynamics of special relationships between adult male and female olive baboons. In: *Primate Social Relationships: An Integrated Approach* (Ed. by R. A. Hinde), pp. 112–120. Sunderland, MA: Sinauer Associates.
- Smuts, B. B. 1983b. Special relationships between adult male and female olive baboons: selective advantages. In: *Primate Social Relationships: An Integrated Approach* (Ed. by R. A. Hinde), pp. 262–266. Sunderland, MA: Sinauer Associates.
- Smuts, B. B. 1985. *Sex and Friendship in Baboons*. New York: Aldine.
- Smuts, B. B. 1987. Sexual competition and mate choice. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. Seyfarth, R. W. Wrangham, & T. T. Struhsaker), pp. 385–399. Chicago: University of Chicago Press.
- Smuts, B. B. 1992. Male aggression against women: an evolutionary perspective. *Hum. Nat.*, 3, 1–44.
- Smuts, B. B. & Gubernick, D. 1992. Male-infant relationships in nonhuman primates: paternal investment or mating effort? In: *Father-Child Relations: Cultural and Biosocial Contexts* (Ed. by B. Hewlett), pp. 1–30. New York: Aldine de Gruyter.
- Smuts, B. B. & Smuts, R. T. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.*, 22, 1–63.
- Sober, E. & Wilson, D. S. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.
- Stanford, C. B. 1996. Hunting ecology of chimpanzees. *Am. Anthropol.*, 98, 96–113.
- Stanford, C. B. 1999. *The Hunting Apes*. Princeton, NJ: Princeton University Press.
- Symons, D. 1979. *The Evolution of Human Sexuality*. Oxford: Oxford University Press.
- Tooby, J. & DeVore, I. 1987. The reconstruction of human behavioral evolution through strategic modeling. In: *Primate Models of Human Behavior* (Ed. by W. Kinzey), pp. 183–237. Albany, NY: SUNY Press.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.*, 46, 35–57.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 139–179. Chicago: Aldine.
- van Schaik, C. P. 1996. Social evolution in primates: the role of ecological factors and male behavior. *Proc. Br. Acad.*, 88, 9–31.
- van Schaik, C. P., Hodges, J. K., & Nunn, C. L. 2000. Paternity confusion and the ovarian cycles of female primates. In: *Infanticide by Males and Its Implications* (Ed. by C. P. van Schaik & C. Janson), pp. 361–387. Cambridge: Cambridge University Press.
- van Schaik, C. P. & Janson, C. 2000. *Infanticide by Males and Its Implications*. Cambridge: Cambridge University Press.
- van Schaik, C. P. & Kappeler, P. M. 1997. Infanticide risk and the evolution of male-female associations in primates. *Proc. Royal Soc. Lond., B*, 64, 1687–1694.
- van Schaik, C. P. & Paul, A. 1996. Male care in primates: does it ever reflect paternity? *Evol. Anthropol.*, 5, 152–156.
- van Schaik, C. P., van Noordwijk, M. A., & Nunn, C. L. 1999. Sex and social evolution in primates. In: *Comparative Primate Socioecology* (Ed. by P. C. Lee), pp. 204–240. Cambridge: Cambridge University Press.
- Veblen, T. [1899] 1992. *The Theory of the Leisure Class* (Ed. by C. W. Mills). Reprint, New Brunswick, NJ: Transaction Publishers.
- Washburn, S. 1960. Tools and human evolution. *Sci. Am.*, 203, 63–75.
- Washburn, S. & Avis, V. 1958. Evolution and human behavior. In: *Behavior and Evolution* (Ed. by A. Koe & G. G. Simpson), pp. 421–436. New Haven, CT: Yale University Press.
- Washburn, S. & DeVore, I. 1961. Social behavior of baboons and early man. In: *Social Life of Early Man* (Ed. by S. Washburn), pp. 91–105. Chicago: Aldine.
- Washburn, S. L. & Lancaster, C. S. 1968. The evolution of hunting. In: *Man the Hunter* (Ed. by R. B. Lee & I. DeVore), pp. 293–303. Chicago: Aldine.
- Westermarck, E. 1891. *The History of Human Marriage*. London: Macmillan.
- Whitten, P. 1987. Males and infants. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. Seyfarth, R. W. Wrangham, & T. T. Struhsaker), pp. 343–357. Chicago: University of Chicago Press.
- Wiessner, P. 1996. Leveling the hunter: constraints on the status quest in foraging societies. In: *Food and the Status Quest: An Interdisciplinary Perspective* (Ed. by P. Wiessner & W. Schiefelhoevel), pp. 171–191. Providence: Berghahn Books.
- Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wilson, D. S. 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.*, 14, 159–87.
- Wilson, D. S. 1998. Hunting, sharing, and multilevel selection: the tolerated theft model revisited. *Curr. Anthropol.*, 39, 73–97.
- Wilson, M. & Daly, M. 1992. The man who mistook his wife for a chattel. In: *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Ed. by J. H. Barkow, L. Cosmides, & J. Tooby), pp. 289–322. New York: Oxford University Press.
- Wilson, M. & Mesnick, S. 1997. An empirical test of the bodyguard hypothesis. In: *Feminism and Evolutionary Biology: Boundaries, Intersections, and Frontiers* (Ed. by P. A. Gowaty), pp. 505–511. New York: Chapman Hall.
- Woodburn, J. 1998. Sharing is not a form of exchange: an analysis of property sharing in immediate return hunter-gatherer societies. In: *Property Relations: Renewing the Anthropological Tradition* (Ed. by C. M. Hann), pp. 48–63. Cambridge: Cambridge University Press.
- Wrangham, R. W. 1979. On the evolution of ape social systems. *Soc. Sci. Info.*, 18, 334–368.
- Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. L. 1999. The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.*, 40, 567–594.
- Wrangham, R. W. & Rubenstein, D. I. 1986. Social evolution in birds and mammals. In: *Ecological Aspects of Social Evolution: Birds and Mammals* (Ed. by R. W. Wrangham & D. I. Rubenstein), pp. 452–470. Princeton, NJ: Princeton University Press.
- Wright, P. 1990. Patterns of paternal care in primates. *Int. J. Primatol.*, 11, 89–102.
- Zahavi, A. 1975. Mate selection: selection for a handicap. *J. Theor. Biol.*, 53, 205–214.
- Zahavi, A. 1977. The cost of honesty: further remarks on the handicap principle. *J. Theor. Biol.*, 67, 603–605.
- Zahavi, A. 1995. Altruism as a handicap: the limitations of kin selection and reciprocity. *Avian Biol.*, 26, 1–3.
- Zahavi, A. & Zahavi, A. 1997. *The Handicap Principle*. Oxford: Oxford University Press.