Perspectives on human attachment (pair bonding): Eve's unique legacy of a canine analogue

Ronald S. Immerman, Department of Psychiatry, Case Western University, Cleveland, Ohio 44106, USA.

*Wade C. Mackey, 7103 Oakwood Glen Boulevard, Apartment 19, Spring, Texas 77379, USA. Email: WADDMAC@aol.com. *Corresponding author.

Abstract: The mother-child bond is undoubtedly homologous with that of other primates (and mammals). However, the man-woman pair bond and man(to)child pair bond are not paralleled by any terrestrial primate nor many mammals. Hence, knowledge of primate behavior would not be predictive of the pan-human (i) social father and (ii) the extended pair bond between a man and woman (with the cultural overlay of marriage). It is suggested that female choice of mating partner shifted in the direction of a canid analogue in which men's motivations to share resources with the female and to exhibit paternalistic behaviors were positively selected. Accordingly, it would be predicted that, compared to other terrestrial primates, the neuro-hormonal bases for the mother-child affiliative bond would be similar, but the bases of man-woman affiliative bond and the man(to)child affiliative bond would be dissimilar.

Keywords: Human evolution, convergent evolution, pair-bonding, father-child relations.

Introduction

While "love" has been a favorite fodder for poets and playwrights, scientific efforts have been less prolific. Nonetheless, in a series of investigations, Fisher et al. (2002), *inter alios*, have attempted to isolate neural circuitry and brain chemistry which profiles three types of "love" (at least in adults): (i) lust or sexual

passion (independent of personality of a partner) (ii) romance or limerence (Tennov 1979) (dependent upon a particular personality), and (iii) attachment (pair-bonding over extended time). To complement others' work on (i) lust and (ii) romance, this effort focuses on (iii) adult human attachment (extended pair-bonding between a man and a woman and the man[to]child bond).

It seems self-evident that any and all emotions must have neuro-hormonal correlates. There is no reason to presume any emotional facet of "love" would be distinct or transcendent. By extension, there must be appropriate genetic material to properly construct the circuits and to govern the chemistry that, in turn, activates the circuits and lends motivation to affiliative behavior.

Candidates from the neuro-endocrine systems which have been suggested to affect affiliative behaviors include (i) neuro-peptides and hormones, e.g. oxytocin, vasopressin, and prolactin [1] (Insel 1997, Insel, Gingrich and Young 2001, Insel and Young 2000, Kendrick 2000, McCarthy and Altemus 1997, Porges 1998, Uvnas-Moberg 1998, Wang, Moody, Newman and Insel 1997, Wynne-Edwards and Reburn 2000, Young, Lim, Gingrich and Insel 2001, Ziegler 2000); (ii) nuclei, e. g. ventral pallidum, nucleus accumbens, medial nucleus of the amygdala, lateral septum, medial preoptic area, medial bed nucleus of the stria terminalis, nucleus reuniens and paraventricular nucleus of the thalamus (Berridge 2003, Insel 1997, Kirkpatrick, Kim and Insel 1994, Pitkow, Sharer, Ren, Insel, Terwilliger and Young 2001, Wang, Moody, Newman, and Insel 1997, Young, Lim, Gingrich and Insel 2001), ventral tegmental area, mediobasal hypothalamus, (Insel and Young 2001), (iii) the hypothalamic-pituitary adrenal axis (Carter 1998), (iv) steroids, e. g. estradiol, estrogen, testosterone, and cortisol (Berg and Wynne-Edwards 2001, Rosenblatt 1994, Storey, Walsh, Quinton and Wynne-Edwards 2000, Wynne-Edwards 2001), plus, (v) endogenous opioids, catecholamines, and serotonin (Gerald et al. 2002, Insel and Winslow 1998, Nelson and Panksepp 1998).

It is generally agreed that the female is the more selective gender in choosing a sexual partner (Buss 1989, 1994, Buss and Schmitt 1993; Cashdan 1993, Symons 1979). This partner would impregnate her and, thus, contribute his genetic material to the next generation. Accordingly, the female becomes a key drive-wheel in the determination of which males (and which genetic mosaics) have the opportunity to have children who will, in turn, have grandchildren.

Human attachment/pair-bonding

Humans, across cultures, have two types of attachments which would not be predicted from the homologues of the great apes: chimpanzees, bonobos, gorillas. Humans — as a large, terrestrial primate — do illustrate (1) a reciprocal man-woman bond which can last years (this extended pair bond has the cultural overlay of marriage [2] and (2) a man(to)child bond which also can last years, i.e.,

the on-going social father. None of the great apes exhibits either of these two features. [3.]

The man-woman pair bond

Romantic love seems to be a human universal and is found across highly variegated social structures and ecologies (Jankowiak and Fischer 1992; Jankowiak 1995). For example, Jankowiak's survey of 168 cultures found "romantic love/passion" in 148 (89%) of the cultures. Such an emotion seems a key component in the forging of an extended human pair-bond. Fisher (1983) suggests that archaic *Homo* had begun developing a reproductive strategy wherein females exchanged (relative) sexual exclusivity for (relatively) unique provisioning on the part of a male. This strategy would form the basis to the nascent pair-bond which has proved so successful in human bio-cultural evolution. [4.] Such a shift in strategy would be aberrant for terrestrial primates in particular and mammals in general (Boesch 1994, Boesch and Boesch 1989, de Waal 1997, 1998, de Waal and Lanting 1997, Galdikas 1985, Goodall 1986, Mackinnon 1974, McGinnis 1979 Nishida and Hosaka 1996, Parish 1996, Smuts and Gubernick 1992, Stanford 1996, Taub 1984, Teleki 1973; see Kleiman [1977] for discussion on mammalian and avian monogamy). Typically, these adult males compete amongst themselves to achieve greater dominance within a male hierarchy; then females mate preferentially with the more successful males. The translation of increased physical dominance to increased reproductive success can range from slight to stark, see Ellis (1995) and Dewsbury (1982) for examples.

With the putative shift, females had to evaluate, not just the physical dominance and assertiveness of the competing males (who won), but also the psychological profile of the competing males: i.e., trustworthiness in reciprocity over time. Framed a little differently, sperm is essentially infinite. Female-female competition over mating protocols has little pay-off for the victor. The winner would accrue no advantage. However, food is finite and is valuable. Incremental food (via the male) gained from any successful female-female competition, would have survival value for the winning female. Whereas access to sperm may be a constant, access to food is a variable.

Thus, male-male competition for mating partners incorporated an additional psychological parameter (enhanced reliability or trustworthiness), and female-female competition for mating partners (who would reliably share food) arose to become important. [5.]

As ethnographies on both historical and contemporary cultures illustrate, males — who had been selected over millennia by females — return to the domicile and willingly and systematically share resources with the woman in the pair bond, i.e. his wife (Hewlett 1992, Human Relations Area Files 1949, Lamb 1987, Mackey 1985, Murdock 1957, 1967). The man-to-woman sharing is found across

subsistence and ecological parameters viz. Amazonia (Chagnon 1977, Stearman 1989), China (Chance, 1984), Tibet (Ekvall, 1968), the Dani of New Guinea (Heider 1979), Eskimos (Chance 1966), Japan (Norbeck 1976), Australian aborigines (Hart and Pilling 1960, Tonkinson 1978), the Dobe !Kung of the Kalahari desert (Lee 1984). This sharing of resources from man-to-woman is a universal; see Brown (1991) for additional human universals.

The provisioning is not totally exclusive. Systematic food sharing has been ritualized in many, if not all, societies. Rarely can a hunter claim a large kill for only his own family (Coon 1971, Lee 1982, Tonkinson 1978, Chance 1966). But, within these contexts, a man provides singular attention in terms of provisioning and protecting the legitimate children that he has fathered and his wife or wives (see HRAF, #22 - 26 [1949] for examples, and see Malinowski [1927] and Hendrix [1996] for theoretical discussions).

When resources are not forthcoming from a prospective groom, brides are difficult to acquire (Cashdan 1993) and wives are difficult to keep (Betzig 1989). For example, in a sample of 50 cultures which had economic deprivation as a sanctioned reason to divorce, the wife could divorce the husband in 49 of the cultures. In one, either of the spouses could initiate the divorce. In no culture could only the husband divorce the wife on the basis of her economic deficiencies (Betzig 1989). When the pattern of male provisioning does break down across the overall society, e.g. the Ik (Turnbull 1972), the breakdown signals an overall societal disintegration and is a focused topic of the ethnographer's analysis.

The systematic sharing of resources, which had been procured from beyond the perimeter of the domicile and then returned to the domicile, would not be predicted from any primate homologue. Accordingly, none of the great apes illustrates this pattern (Boesch 1994, Boesch and Boesch 1989, de Waal 1997, 1998, de Waal and Lanting 1997, Goodall 1986, Hrdy 1999, Kano 1983, Nishida and Hosaka 1996, Parish 1996, Smuts and Gubernick,1992, Stanford 1996, Susman 1984, Teleki 1973). However, the canid analogue (wolf [Mech 1970, 1992, Mowat 1963, Murie 1944], coyote [Dobie 1949, McMahan 1976, Meinzer 1995, Ryden, 1974, Young and Jackson 1951], fox [Alderton 1994], jackal [Lawick and Lawick-Goodall 1971, Moehlman 1980], and the hunting dog [Kuhme 1965]) would be predictive of the adult male returning from outside the perimeter of the domicile and sharing food with the mate (and, by extension, her/his young). Nishikawa (2002) provides a useful over-view of convergent evolution.

The monogamous, arboreal primates

The monogamous (pair-bonding), arboreal primates — e.g. the marmosets of the New World and the gibbons of Southeast Asia — also illustrate relatively high levels of paternalistic behaviors. For example, between suckling episodes, the

marmoset's male partner (presumptively the biological sire) will carry the infant (Jolly 1985). If two offspring are still with their parents, the male gibbon will tend to the juvenile; while the female gibbon will tend to the infant (Carpenter 1940, Chiver 1977, Leighton 1986). In terms of this article, the difference between these primates and the canid and human fathers is that the canid fathers and human fathers do leave the mother and young and travel widely to procure food. Once the food is procured, these males return to the mother-young dyad to relinquish the food for the consumption of the mother and the young. None of the arboreal primates has been reported to engage in such traveling alone and then returning to actively relinquish and share food. Given the phylogenetic distance between humans and the gibbons from each other and both from the New World primates, the behavioral profiles which are similar probably reflect behavioral convergences which, in turn, reflect ecological constrictions (analogues) rather than genetic continuity (homologues).

Of additional interest is the relationship between sexual dimorphism and the four categories of humans, canids, arboreal, pair-bonding primates, and the terrestrial great apes.

Lessened sexual dimorphism in *Homo*

As data in the next section suggest, sexual dimorphism is lower in *Homo sapiens* than would be expected given our generally agreed upon ecological heritage as (i) a large, (ii) terrestrial primate which is (iii) non-obligate monogamous. Dominance displays by men which are based on their own physical/biological attributes also seem to be substantially restricted. This section seeks to address one facet by which expected dominance displays by men would have lost positive selectivity and thereby reduced in degree, if not in kind.

Although dominance, as a construct, has a rich history with variegated definitions, this section has a narrow focus. A dominance display is defined here as a behavior or a physical characteristic on the part of one adult male which is directed at other adult males to allow differential access to breeding females. Successful dominance displays by an adult male would enhance that adult male's access to breeding females. Unsuccessful dominance displays or lack of dominance displays would decrease the male's access to breeding females (see Ellis [1995] and Dewsbury [1982) for examples of the relationship — sometimes stark and sometimes slight — between increased male dominance and increased reproductive success).

Parameters of sexual dimorphism in primates

Although there are exceptions, sexual dimorphism (e.g. by weight [from Hall 1985]) tends to be greater in (semi)terrestrial primates than in arboreal primates

(e.g. baboon [*Papio* 185] vs. spider monkey [e.g. *Ateles* 94], gorilla [e.g. *Pan gorilla* 219] vs. langurs [*Presbytis* 107]) [By convention, the sexual dimorphism ratio is computed by setting the female value at 100 and setting the male value in relation to the female value]. Again with exceptions, larger primates tend to have more sexual dimorphism than smaller primates (orangutan [e.g. *Pongo pygmaeus* 199] vs. night monkey [*Aotus trivirgatus* 102]). Sexual dimorphism also tends to be lesser or nonexistent in primates which tend to be monogamous (e.g. gibbon [*Hylobates* 104] vs. chimpanzee [*Pan troglodytes* 121]; marmoset [*Callithrix jacchus* 95] vs. macaque [*Macaca* 149]). The argument is that, when the males exchanged the harder to scan world of the trees for the easier to scan world of the ground, they were better able to assert dominance and have multiple sexual partners. Indeed, terrestrial primates are more prone to be polygynous than are arboreal primates (Jolly 1985, Hrdy 1999). Accordingly, after it was freed from problems of fissile tree limbs and incessant gravity, additional male size would be advantageous in creating dominance for the larger male and in creating submission in the smaller male (see Fleagle [1988]; Martin, Willner and Dettling [1994]; McHenry [1991]; Richard [1985] for examples and discussion). Hence, a more effective male-to-male dominance displays/aggression could then be translated to multiple partners which would lead to a greater number of descendants who, in turn, would pass on the genetic material underpinning the physical attributes of the "successful" display. The same argument would apply to increased canine size and enhanced piloerection or other display items (e.g. manes) which could be used to gain dominance and, thereby, to gain access to more sexual partners, and, hence, to sire more descendants.

There are three givens that apply here: (a) *Homo's* predecessor *Australopithecus* did exhibit a large degree of sexual dimorphism by size (Hall 1985; Plavcan and van Schaik 1997), (b) *Homo*, compared to *Australopithecus*, gradually increased in size (Hall 1985; Aiello 1994) and (c) *Homo* became exclusively terrestrial. From these three givens a, not unreasonable, inferred assumption would be that *Homo* would follow the basic trend of maintaining or increasing sexual dimorphism. However, sexual dimorphism decreased (Arsuaga et al. 1997; *Economist* 1994; Lewin 1987; Lockwood et al. 1996; McHenry 1991).

In terms of height, the sexual dimorphism of contemporary humans is 107 (s.d. 1.5; n = 93 [societies], i.e. women are 94% the height of men) (Alexander et al., 1979). The human canine is virtually (sexually) isomorphic, and piloerection is not a functional human trait. In terms of weight, the sexual dimorphism of (U.S.) humans is 130.0. Since the linear correlation between the weight of primate males and the sexual dimorphism of their species is significant (r_p = .569; p < .01; two-tailed; n = 47) (Hall 1985), then the sexual dimorphism of human males could be predicted from their weight. When the "sexual dimorphism ratio" is predicted from the average man's weight, the predicted value is a sex ratio for male-to-female of 187.4. This predicted value over-estimates the actual value of

130.0 by 1.55 standard deviations. (Using a similar method for data from Plavcan and van Schaik [1997], a similar result occurred. The correlation [r_p] of .389 was significant [$p < .01$; 2-tailed; n = 86]. The predicted sexual dimorphism ratio was 155 or 1.15 standard deviations larger than the actual male-to-female ratio.)

In other words, humans are far more sexually isomorphic than would be expected by the ecological circumstance of their phylogeny. It is argued here that there were lessened selective pressures for dominance displays in early *Homo*, and that an excellent candidate for one such agent which generated the negative selection is a shift in female preference toward provisioning in the definition of an appropriate mating partner. It is useful to reiterate that the canids mentioned above also tend toward minimal sexual dimorphism and facultative monogamy (Kleiman 1977). Complementary candidates to explain the reduced sexual dimorphism include the notions (from Hrdy 1999) that larger mothers — once terrestrial — were positively selected because of the sheer advantage that size has in manipulating the environment for herself and her children; (from Wrangham et al. 1999) that a derivative of a dietary shift to cooked foods and a man-woman negotiation wherein men helped protect the food source, and (from Immerman and Mackey 1999) that an infestation of sexually transmitted diseases within a troop would tend to favor monogamy and penalize promiscuity as practiced by more dominant males viz. due to increased sterility, and higher morbidity and mortality for mates and any subsequent progeny.

In gist, a shared ecological and phylogenetic heritage with the great apes would predict a large sexual dimorphic index. That is, a large, terrestrial primate is aligned with increased sexual dimorphism. An enhanced fathering index is aligned with reduced sexual dimorphism. The large, terrestrial primate — *Homo sapiens* — is aligned with an unexpectedly small sexual dimorphism.

The man(to)child affiliative bond

There is a cross-cultural tendency of men to associate with (their) children in public places — away from the domicile — during times when men are not precluded by work schedules or ritual (Mackey 1985, 2001). In a cross-cultural study of 23 cultures and of over 55,000 adult-child dyads, nearly a fifth of the surveyed children who were with adults were with men — no women present (Mackey 2001). This 20+% (sd = 5.9%) is difficult to conceptualize as mere error variance. [6.] Another third (sd = 14.5%) of the children with adults were with men, and women were also present. The remaining children with adults were with women, but no man was present. See Table 1. Compared to those times when men tended to be precluded by cultural norms from being with children, the percentages of children with men — both in men-only and in men and women adult groups — increased for each of the surveyed cultures (n = 17), plus increased in the aggregate, when those restrictive norms were absent. See Table

1. There is no theory which would suggest that the men who are proximate to these children would be other than consanguine kin.

Table 1

Mean percentage distribution of children in 23 cultures by adult group during times of availability of men to children at described loci (40,233 children) and during those times when cultural norms precluded availability of men to children (17 cultures, 18,637 children) (each culture is weighted equally) (adapted from Mackey [2001]).

Expected Availability of Men	Adult Group			
	Men only	Men and Women	Women only	Total
PRESENT				
Percentage	21.0%	34.7%	34.7%	100.0%
sd	5.9%	14.5%	12.0%	
ABSENT				
Percentage	13.0%	16.6%	70.4%	100.0%
sd	5.1%	7.1%	8.5%	
z-score (Present-Absent)	8.8*	22.0*		

* $p < .001$

Given the greater physical size and power of the man versus the child (and versus the wife/mother), it is suggested that the men were associating with the children because they — the men — chose to do so. The ethnographic literature is replete with examples of fathers being fond of their own children (Hewlett 1992, Lamb 1987, Mackey 1985). Framed differently, the data suggest an independent man(to)child affiliative bond which is part of *Homo's* bio-cultural heritage.

Again, these (man[to]child) behaviors would not be predicted from the primate homologues, but would be predicted by a canid analogue. The canid adult males do return from hunting/scavenging and share food with their young. Note that the canid adult males also systematically "play" with their pups, whereas the adult males of other social carnivores — lions (Guggisberg 1963, Rasa 1986, Rudnai 1973, Schaller 1972) and hyenas (Lawick and Lawick-Goodall 1971, Kruuk 1972) — neither provision nor "play" with their young, and are often a physical threat to the young of the social group. (For the context of social structure and ecology, see King (1980), Lovejoy (1981), Mackey (1976, 1985, 1986), Schaller and Lowther (1969), and Thompson (1978).

Thus, it is suggested that, as our distaff ancestors were selecting for mates (1)

with whom they could establish an extended affiliative bond (attachment) and (2) from whom reliable provisioning was predictable, they were simultaneously selecting for traits which would forge a social father: a man who would form attachments — bond — with his young and who would be psychologically willing to share resources with those young. See Tiger (1968) for discussion on the man-man bond.

Accordingly, a number of hypotheses would be forthcoming. The neuro-hormonal basis of the mother-child attachment would be expected to be similar (homologues) to the templates of the female great apes. However, the neuro-hormonal basis to man(to)woman attachment would be expected to differ from any affiliation template between the genders in the great apes. Given the similar behaviors of canid pair-bonding to man-woman attachment, an analogous profile with those canids would be expected.

Furthermore, the neuro-hormonal basis to man(to)child attachment would be expected to be different from any adult-male(to)young affiliation template in the great apes. Given the similar behaviors of man(to)child attachment to canid adult male(to)pup behaviors, an analogous profile with those canids would be expected.

Of course, the triangulation of the terrestrial great apes and the canids with the arboreal, monogamous primates (marmosets, tamarins, gibbons, siamangs) wherein aspects of paternal behaviors are also typical would be interesting.

Conclusion

Across cultures, men develop extended pair-bonds with women (they marry women) and provision these women. The men also nurture their own children. Within the context of these two universals, the argument is presented that the affiliation which mediates these behaviors is, in part, neuro-hormonal in character and thus part of the phylogenetic heritage of our species. The drive-wheel for these behaviors, which would not be predicted by knowledge of terrestrial primates, is argued to be based on a successful reproductive strategy of our female ancestors, a strategy analogous to that of female canids — convergent evolution — that enables them to exploit a novel resource for predictable sustenance for themselves and their offspring: men.

Notes

[1.] Elevated levels of the hormone prolactin have been aligned with male parenting behaviors in many birds, and rodents and the callitrichid monkeys: *Callithrix jacchus* and *Saguinus oedipus*. In birds, prolactin may be elevated in both male and female breeders during various stages of nest building, egg laying, incubating and feeding of young. (Ziegler 2000). Accordingly, prolactin is probably involved at some stage in initiating or maintaining men's paternalistic behaviors.

See Storey, Walsh, Quinton, and Wynne-Edwards (2000) for clinical supporting evidence. However, prolactin is a very old hormone and is found in fish and birds as well as across the mammalian domain (Hrdy 1999). Given that prolactin is available to great apes and to humans, but the paternalistic behaviors among the two groups are different, then the surveyed behavioral differences is unlikely to be explained by the presence of prolactin *per se*.

[2.] In humans, the mating preferences — marriage partners — are subject to a wide range of social pressures spanning the spectrum from nosy neighbors to attentive kin to the mandated cultural tradition of arranged marriages (Stephens 1963, Van den Berghe 1979, see Murdock's [1967] "Ethnographic Atlas" Column #12 [Modes of Marriage] for types and frequencies of wife procurement).

[3.] The arboreal primates, e.g. lesser apes and marmosets, are often monogamous and provide an additional source of context for human pair-bonding. However, this exercise will focus on the context of large, terrestrial primates.

[4.] This exercise is not intended to re-visit the nature-nurture debate. Let it suffice that the underlying assumption to this argument is that both socialization traditions and genetic information (and their interactions) affect the trajectory and manifestation of the development of human behavior. For theoretical discussions, see Barkow (1980, 1989, p. 343), Boyd and Richerson (1976, 1978, 1982, 1983, 1985), Dunbar, Knight, and Power (1999), Durham (1982, 1991), Lumsden and Wilson (1985), Lumsden and Wilson (1982), and Ridley (2003).

[5.] Although most (approx. 85%) of known societies have allowed polygyny, most men in these societies have only one wife at any one time. With the exception of the rare polyandrous societies, virtually all women are in monogamous marriages.

[6.] Both age and gender of the child, plus gender of the adult, influenced the proportions of adult-child dyads, see Mackey (2001) for a more finely grained analysis.

References

Alderton, D. (1994). *Foxes, Wolves, and Wild Dogs of the World*. New York, NY: Facts on File.

Aiello, L. C. (1994). Variable but singular. *Nature,* 368: 399-400.

Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., and Sherman, P. W. (1979) Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In Chagnon, N. A. and Irons, W. (Eds.). *Evolutionary Biology and Human Social Behavior: An anthropological perspective* (pp. 402-435). North Scituate, Mass.: Duxbury Press.

Arsuaga, J. L., Carretero, J. M., Lorenzo, C., Gracia, A., Martinez, I., Bermudez

de Castro, J. M. and Carbonell, E. (1997). Size variation in Middle Pleistocene humans. *Science,* 277: 1086-1089.

Barkow, J. H. (1980). Biological evolution of culturally patterned behavior. In Lockard, J. (Ed.). *The Evolution of Human Social Behavior* (pp. 277-290). NY: Elsevier.

Barkow, J. H. (1989). *Darwin, Sex and Status.* Toronto: University of Toronto Press.

Berg, S. J. and Wynne-Edwards, K. E. (2001). Changes in testosterone, cortisol, and estradiol levels in men becoming fathers. *Mayo Clinic Proceedings,* 76: 582-592.

Berridge, K. C. (2003). Pleasures of the brain. *Brain and Cognition,* 52: 106-28.

Betzig, L. L. (1989). Causes of conjugal dissolution. *Current Anthropology,* 30: 654-676.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour,* 48: 653-667.

Boesch, C. and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology,* 78: 547-573.

Boyd, R. and Richerson, P. J. (1976). A simple dual inheritance model of the conflict between social and biological evolution. *Zygon,* 11: 254.

Boyd, R. and Richerson, P. J (1978). A dual inheritance model of the human evolutionary process. *Journal of Social and Biological Structures,* 1: 127.

Boyd, R. and Richerson, P. J. (1982). Cultural transmission and the evolution of cooperative Behavior. *Human Ecology,* 10: 325.

Boyd, R. and Richerson, P. J. (1983). Why is culture adaptive? *Quarterly Review of Biology,* 58: 209-214.

Boyd, R. and Richardson, P. J. (1985). *Cultural Transmission and the Evolutionary Process.* Chicago: University of Chicago Press.

Brown, D. (1991). *Human Universals.* NY: McGraw-Hill.

Buss, D (1989). Sex differences in human mate preferences. *Behavioral and Brain Sciences,* 12: 1-49.

Buss, D. (1994). *The Evolution of Desire.* NY: Basic Books.

Buss, D. M. and Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review,* 100: 204-232.

Carpenter, C. R. (1940). A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comparative Psychology Monographs,* 6: 1-212.

Carter, C. S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology,* 23: 779-818.

Cashdan, E. (1993). Attracting mates. *Ethology and Sociobiology,* 14: 1-24.

Chagnon, N. (1977). *Yanomamo.* New York, NY: Holt, Rinehart and Winston.

Chance, N. (1984). *China's Urban Villages.* New York, NY: Holt, Rinehart and Winston.

Chance, R. A. (1966). *The Eskimo of North Alaska.* NY: Holt, Rinehart and

Winston.

Chiver, D. J. (1977). The lesser apes. In H. R. H. Prince Rainier III and Bourne, G. H. (Eds.). *Primate Conservation*. New York, NY: Academic Press.

Coon, C. S. (1971). *The Hunting Peoples*. Harmondsworth, UK: Penguin.

de Waal, F. M. B. (1997). The chimpanzee's service economy. *Evolution and Human Behavior,* 18: 375-396.

de Waal, F. M. B. (1998). *Chimpanzee Politics* (revised ed.) Baltimore: Johns Hopkins University Press.

de Waal, F. M. B. and Lanting, F. (1997). *Bonobo*. Berkeley, CA: U. of California Press.

Dewsbury, D. A. (1982). Dominance rank, copulatory behavior, and differential reproduction. *The Quarterly Review of Biology,* 57: 135-154.

Dobie, J. F. (1949). *The Voice of the Coyote*. Boston: Little, Brown and Co.

Dunbar, R. I. M., Knight, C. and Power, C. (1999). *The Evolution of Culture*. New Brunswick, NJ: University of Rutgers Press.

Durham, W. H. (1982). Interactions of genetic and cultural evolution: Models and examples. *Human Ecology*, 10: 289.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.

Economist, The. (1984). Big hairy ape-men. *The Economist*. 331: 85-86.

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals. *Ethology and Sociobiology,* 16: 257-333.

Ekvall, R. B. (1968). *Fields on the Hoof*. NY: Holt, Rinehart, and Winston.

Fisher, H. E. (1983). *The Sex Contract: The evolution of human behavior*. NY: Quill.

Fisher H. E., Aron, A., Mashek, D., Haifang, L. and Brown, L. L. (2002). Defining the brain systems of lust, romantic attraction, and attachment. *Archives of Sexual Behavior,* 31: 413-419.

Fleagle, J. G. (1988). *Primate Adaptation and Evolution*. NY: Academic Press.

Galdikas, B. M. F. (1985). Adult male sociality and reproductive tactics among orangutans at Tanjung Puting *Folia Primatologica*, 45: 9-24.

Gerald, M. S., Higley, S., Lussier, I. D. and Westergaard, G. C. (2002). Variation in Reproductive Outcomes for Captive Male Rhesus Macaques (*Macaca mulatta*) Differing in CSF 5-Hydroxyindoleacetic Acid Concentrations *Brain, Behavior and Evolution*, 60:117-124.

Goodall. J. (1986) *The Chimpanzees at Gombe*. Cambridge, MA: Belknap.

Guggisberg, C. A. W. (1963). *Simba*. Philadelphia: Chilton Books.

Hall, R. (Ed.) (1985) *Sexual Dimorphism in Homo Sapiens*. New York, NY: Praeger.

Hart C. W. M. and Pilling, A. R. (1960). *The Tiwi of North Australia*. New York, NY: Holt, Rinehart and Winston.

Heider, K. (1979). *Grand Valley Dani.* NY: Holt, Rinehart and Winston.

Hendrix, L. (1996). *Illegitimacy and Social Structures* Westport, CT: Bergin and Garvey.

Hewlett, B. S. (Ed.). (1992). *Father-child Relations*. New York, NY: Aldine de Gruyter.

HRAF (1949). *Human Relations Area Files*. New Haven, CT.: HRAF Press.

Hrdy, S. (1999). *Mother Nature*. New York, NY: Ballantine.

Insel, T. R. (1997). A neurobiological basis of social attachment. *American Journal of Psychiatry*, 154: 726-735.

Insel, T. R., Gingrich B. S. and Young L. J. (2001). Oxytocin: who needs it? *Progress in Brain Research*, 133: 59-66.

Insel, T. R. and Winslow J. T. (1998). Serotonin and neuropeptides in affiliative behaviors. *Biological Psychiatry*, 44: 207-219.

Insel, T. R. and Young, L. J. (2000). Neuropeptides and the evolution of social behavior. *Current Opinion in Neurobiology*, 10: 784-789.

Insel, T. R, and Young L. J. (2001). The neurobiology of attachment. *Nature Reviews Neuroscience*, 2: 129-136.

Jankowiak, W. (Ed.) (1995). *Romantic Passion.* New York, NY: Columbia University Press.

Jankowiak, W. and Fisher, E. (1992). A cross-cultural perspective on romantic love *Ethnology*, 31: 149-155.

Jolly, A. (1985). *The Evolution of Primate Behavior.* (2nd ed.) New York, NY: Macmillan.

Kano, T. (1983). An ecological study of the pygmy chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology*, 4: 1-31.

Kendrick, K. M. (2000). Oxytocin, motherhood and bonding. *Experimental Physiology,* 85 Spec No: 111S-124S.

King, G. E. (1980). Alternative uses of primates and carnivores in the reconstruction of early hominid behavior. *Ethology and Sociobiology,* 1: 99-110.

Kirkpatrick, B., Kim J. W. and Insel, T. R.(1994). Limbic system fos expression associated with paternal behavior. *Brain Research,* 658: 112-118.

Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, 52: 39-69.

Kruuk, H. (1972). *The Spotted Hyena: A study of predation and social behavior*. Chicago: University of Chicago Press.

Kuhme, W. (1965). Communal food distribution of and division of labour in African hunting dogs. *Nature*, 205: 443-444.

Lamb, M. E. (Ed.) (1987). *The Father's Role: Cross-cultural perspectives*. Hillsdale, NJ: Erlbaum.

Lawick, H. van, and Lawick-Goodall, J. van. (1971). *Innocent Killers*. Boston, MA: Houghton Mifflin.

Lee, R. B. (1982). Eating Christmas in the Kalahari. In Spradley, J. P. and

McCurdy, D. W. (Eds.). *Conformity and Conflict* (pp 14-21). Boston, MA: Little Brown, and Co.

Leighton, D. R. (1986). Gibbons: Territoriality and monogamy. In Smuts, B. B.; Cheney, D. L.; Seyfarth, R. M.; Wrangham, R. W. and Struhsaker, T . T. (Eds.), *Primate Societies* (pp. 135-145). Chicago: The University of Chicago Press.

Lewin, R. (1987). The earliest "humans" were more like apes. *Science*, 236: 1061-1063.

Lockwood, C. A., Richmond, B. G., Jungers, W. L., Kimbel, W. H. (1996). Randomization procedures and sexual dimorphism in Australopithecus. *Journal of Human Evolution,* 31: 537-548.

Lovejoy, C. O. (1981) The origin of man. *Science,* 211: 341-359.

Lumsden, C. J. and Wilson, E. O. (1985). The relation between biological and cultural evolution. *Journal of Social and Biological Structures,* 8: 343-359.

Lumsden, C. J. and Wilson, E. O. (1982). Précis of *Genes, Mind and Culture* and open peer commentary. *Behavioral and Brain Sciences*, 5: 1-37.

Mackey W. C. (1976). The adult male-child bond: An example of convergent evolution. *Journal of Anthropological Research,* 32: 58-73.

Mackey W. C. (1985). *Fathering behaviors: The dynamics of the man-child bond.* NY: Plenum.

Mackey, W. C. (1986). A facet of the man-child bond: The teeter-totter effect. *Ethology and Sociobiology*, 7: 117-135.

Mackey, W. C. (1996). *The American Father*. New York, NY: Plenum.

Mackey, W. C. (2001). Support for the existence of an independent man-(to)-child affiliative bond: Fatherhood as a bio-cultural invention. *Psychology of Men and Masculinity,* 2: 51-66.

Mackinnon, J. (1974). *In Search of the Red Ape*. New York, NY: Holt, Rinehart and Winston.

Malinowski, B. (1927). *The Father in Primitive Society*. New York, NY: Norton.

Martin, R. D., Willner, L. A. and Dettling, A. (1994). The evolution of sexual size dimorphism in primates. In Short, R. V. and Balaban, E. *The Differences Between the Sexes* (pp. 159-197). Cambridge: Cambridge University Press.

McCarthy, M. M. and Altemus, M. (1997). Central nervous system actions of oxytocin and modulation of behavior in humans**.** *Molecular Medicine Today*, 3: 269-275.

McGinnis, P. R. (1979). Sexual behavior in free-living Chimpanzees: consort relationships. In Hamburg, D. A. and McCown, E. R. (Eds.). *The Great Apes* (pp. 429-438). Menlo Park: Benjamin.

McHenry, H, M. (1991). Femoral lengths and stature in Plio-Pleistocene hominids. *American Journal of Physical Anthropology,* 85: 149-158.

McMahan, P. (1976). The victorious coyote *Natural History,* 84: 42-51.

Mech, L. D. (1970). *The Wolf.* Garden City, NY: Natural History Press.

Mech, L. D. (1992). *The Arctic Wolf: Living with the pack*. Stillwater, Minnesota: Voyageur Press.

Meinzer, W. (1995). *Coyote.* Lubbock, Texas: Texas Tech University Press.

Moehlman, P. D. (1980). Jackals of the Serengeti. *National Geographic*, 153: 840-843.

Mowat, F. (1963). *Never Cry Wolf*. Boston: Little, Brown and Co.

Murdock, G. P. (1957). World Ethnographic Sample. *American Anthropologist*, 59: 664-687.

Murdock, G. P. (1967). Ethnographic Atlas. *Ethnology*, 6: 109-236.

Murie, A. (1944) *The Wolves of Mount McKinley*. Washington, D. C.: U.S. Government Printing Office.

Nelson E. E. and Panksepp J. (1998). Brain substrates of infant-mother attachment: contributions of opioids, oxytocin, and norepinephrine. *Neuroscience Biobehavioral Review*, 22: 437-452.

Nishida, T. and Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In McGrew, W. C., Marchant, L. F. and Nishida, T. (Eds.). *Great Ape Societies* (pp. 114-134). Cambridge: Cambridge University Press.

Nishikawa, K. C. (2002). Evolutionary convergence in nervous systems: Insights from comparative phylogenetic studies *Brain, Behavior and Evolution,* 59: 240-249.

Norbeck, E. (1976). *Changing Japan* (2nd ed.). New York, NY: Holt, Rinehart, and Winston.

Parish, A. R. (1996). Female relationships in bonobo (*Pan paniscus*). *Human Nature, 7*: 61-96.

Pitkow, L. J., Sharer, C. A., Ren, X., Insel, T. R., Terwilliger, E. F. and Young, L. J. (2001). Facilitation of affiliation and pair-bond formation by vasopressin receptor gene transfer into the ventral forebrain of a monogamous vole. *The Journal of Neuroscience*, 21: 7392-7396.

Plavcan, J. M., and Schaik, C. P. van (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of Human Evolution, 32*: 345-374.

Porges, S. W. (1988). Love: an emergent property of the mammalian autonomic nervous system. *Psychoneuroendocrinology, 23*: 837-861.

Rasa, O. A. E. (1986). Parental care in carnivores. In Sluckin, W. and Herbert, M. (Eds.). *Parental Behavior* (pp. 117-151). Oxford: Basil Blackwell Ltd.

Ridley, M. 2003. *Nature via Nurture: Genes, experiences and what makes us human*. New York, NY: Harpers.

Richard, A. F. (1985). *Primates in Nature*. New York, NY: W. H. Freeman.

Rosenblatt, J. S. (1994). Psychobiology of maternal behavior: contribution to the clinical understanding of maternal behavior among humans. *Acta Paediatrica,* Suppl 397: 3-8.

Rudnai, J. A. (1973). *The Social Life of the Lion.* Wallingford, PA: Washington

Square.

Ryden, H. (1974). The "lone" coyote likes family life. *National Geographic,* 146: 279-294.

Schaller, G. B. (1972). *The Serengeti Lion*. Chicago: University of Chicago Press.

Schaller, G. B. and Lowther, G. R. (1969). The relevance of carnivore behavior in the study of early hominids. *Southwestern Journal of Anthropology*, 25: 307-336.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. and Struhsaker, T. T. (Eds.). (1986). *Primate Societies.* Chicago: University of Chicago Press.

Smuts, B. B. and Gubernick, D. J. (1992). Male-infant relationships in nonhuman primates: Paternal investment or mating effort? In Hewlett, B. S. (Ed.). *Father-child Relations: Cultural and biosocial contexts* (pp. 1- 30). New York, NY: Aldine de Gruyter.

Stanford, C. B. (1996). The hunting ecology of wild chimpanzees. *American Anthropologist*, 98: 96-113.

Stearman, A. M. (1989). *Yuqui: Forest nomads in a changing world*. New York, NY: Holt, Rinehart and Winston.

Stephens, W. (1963). *The family in cross-cultural perspective*. New York, NY: Holt. Rinehart and Winston.

Storey, A. E., Walsh, C. J., Quinton, R. L. and Wynne-Edwards, K. E. (2000). Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior,* 21:79-95.

Susman, R. L. (1984). *The Pygmy Chimpanzee: Evolutionary biology and behavior.* New York, NY: Plenum Press.

Symons, D. (1979). *The Evolution of Human Sexuality*. NY: Oxford University Press.

Taub, D. M. (1984). *Primate Paternalism*. New York, NY: Nostrand Reinhold.

Teleki, G. (1973). The omnivorous chimpanzee. *Scientific American*, 228: 33-42.

Tennov, D. (1979). *Love and Limerence.* New York, NY: Stein and Day.

Thompson, P. R. (1978). The evolution of territoriality and society of top carnivores. *Social Science Information,* 17: 949-992.

Tiger, L. (1968). *Men in Groups*. New York, NY: Random House.

Tonkinson, R. (1978). *The Mardudjdara Aborigines.* New York, NY: Holt, Rinehart, and Winston.

Turnbull, C. (1972). *The Mountain People*. New York, NY: Simon and Schuster.

Uvnas-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology,* 23: 819-835.

Van den Berghe, P. L. (1979). *Human Family Systems*. New York, NY: Elsevier.

Wang, Z., Moody, K., Newman J. D., and Insel T. R. (1997). Vasopressin and oxytocin immunoreactive neurons and fibers in the forebrain of male and female common marmosets (Callithrix jacchus).. *Synapse,* 27: 14-25.

Wrangham, R. W., Jones, J. H., Laden, G. D. Pilbeam, D. and Conklin-Brittain,

N. L. (1999). The raw and the stolen: cooking and the ecology of human origins. *Current Anthropology,* 40: 567-594.

Wynne-Edwards, K. E. (2001). Hormonal changes in mammalian fathers**.** *Hormones and Behavior,* 40: 139-145.

Wynne-Edwards, K. E. and Reburn C. J. (2000). Behavioral endocrinology of mammalian fatherhood**.** *Trends in Ecology and Evolution,* 15 :464-468.

Young, S. P. and Jackson, H. T. (1951). *The Clever Coyote*. Washington, D. C.: Wildlife Management Institute.

Young, L. J., Lim, M. M., Gingrich, B. and Insel, T. R. (2001). Cellular mechanisms of social attachment. *Hormones and Behavior,* 40: 133-138.

Ziegler, T. E. (2000). Hormones associated with non-maternal infant care: a review of mammalian and avian studies. *Folia Primatologica*, 71: 6-21.