

1 Behavioral and Neuroendocrine Interactions in Affiliation

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9 Affiliations take many forms in the social relationships of both human and nonhuman  
10 primates. Which relationships are most important will vary as a function of the social structure  
11 and breeding system that is typical of a species and will also vary with life history stages within a  
12 species. For example in species where males disperse and females remain, it is likely that the  
13 primary relationships (due to both genetic relatedness and social experience) will be between  
14 female kin with both mother-offspring and sister-sister relationships having a high priority. In  
15 species where females disperse and males remain there will be strong affiliation between  
16 brothers as well as between mothers and offspring. In pair bonded biparental and cooperatively  
17 breeding species, there is a strong affiliation or attachment between pair mates and between  
18 infants and their primary caregiver. For example, in experimental studies with biparental titi  
19 monkeys (*Callicebus moloch*) Mendoza and Mason (1986) have shown that when given a choice  
20 between mate and infant the parents will choose each other and when given a choice between  
21 parents, infants will choose their fathers which have been the primary caregivers. In  
22 cooperatively breeding species such as the cotton-top tamarin (*Saguinus oedipus*) where father  
23 and older siblings provide substantial infant care through carrying and food transfers, infants  
24 who have become independent will, when frightened, preferentially seek the individual (father or  
25 older sibling) that had been most active in carrying and food transfers (Kostan and Snowdon,  
26 2002).

27           Affiliative relationships may vary with life history stages. An infant's primary  
28 relationship will often be with its mother (though in species with biparental or cooperative care,  
29 it may be a father or sibling. As infants become independent of adult caregivers, primary  
30 affiliative relationships are likely to be established with other same-aged peers in species where  
31 multiple breeding females are present within the same group, or with older siblings in species  
32 with only one breeding pair. Following puberty, individuals in multi-male, multi-female groups  
33 are likely to form affiliative relationships with same sex individuals with the intensity of the  
34 relationships being greater in the non-dispersing sex. In species that form pair bonds, a strong  
35 heterosexual relationship is likely with affiliation being greatest in the initial stages of  
36 relationship formation and decreasing as the pair moves from courtship to parenthood where  
37 affiliation with infants will become important. These many social relationships, which change  
38 with life history, are sustained through a variety of proximate mechanisms both behavioral and  
39 neuroendocrine. This paper reviews several of these mechanisms: (1) social grooming, (2)  
40 nonconceptive sex, (3) social support and tolerance (4) parenting with specific mechanisms that  
41 begin for males in some species even during their mates' pregnancies, (5) Cooperation, prosocial  
42 behavior and teaching.

### 43           **Social Grooming**

44           Social grooming plays an important role in maintaining social relationships with the most  
45 common finding that subordinate animals are more likely to groom more dominant animals than  
46 the reverse, presumably as an indicator of status since grooming is rewarding to the recipient (see  
47 below). Furthermore, Dunbar (1991) has argued that there is a direct relationship between group  
48 size, number of social interactions, brain size and amount of grooming behavior.

49           Whereas these patterns of grooming are common in many terrestrial Old World primates,  
50 New World primates provide some interesting exceptions. First, there is a negative correlation  
51 between body size, group size and amount of grooming (Snowdon & Cronin 2009) with the  
52 smallest species living in the smallest groups (marmosets and tamarins grooming up to 21% of  
53 the day (Lazaro-Perea et al, 2004) and the largest species living in the largest groups not  
54 grooming at all (*Brachyteles arachnoides* muriquis, Strier, 1992). Furthermore there is evidence  
55 of grooming down the hierarchy in both capuchin monkeys (*Cebus apella*, Parr, et. al, 1997),  
56 common marmosets (*Callithrix jacchus*, Lazaro Perea et al, 2004) and cotton top tamarins  
57 (*Saguinus oedipus*, Ginther & Snowdon, 2009). In the cooperatively breeding marmosets and  
58 tamarins breeding adults groom alloparents more than the reverse and in cotton-top tamarins, the  
59 amount of grooming by a parent is directly related to the amount of infant care the recipient  
60 provided in the previous litter. Mothers groom most the alloparents that had carried most on the  
61 previous birth and fathers groom most those who had carried the least on the previous birth  
62 (Ginther & Snowdon, 2009). One explanation for these different responses by fathers versus  
63 mothers is that the carrying of mothers is reduced significantly with a single additional helper  
64 whereas the workload of fathers (and paternal weight loss, Achenbach & Snowdon, 2002) is  
65 reduced linearly with each additional helper (Zahed, Kurian & Snowdon, 2010). Thus mothers  
66 may be rewarding those who provided the most help in a previous birth while fathers are  
67 grooming to recruit additional helpers with the next birth.

68           In both wild common marmosets (Lazaro Perea et al. 2004) and in captive cotton-top  
69 tamarins (Ziegler et al. 2004) breeding males groom their mates significantly more than they are  
70 groomed by their mates. However, Lotker et al. (2007) found the opposite asymmetry in  
71 moustached tamarins (*Saguinus mystax*), with pregnant females grooming males more

72 frequently. If grooming provides some sort of reward to the recipient, then a sexual asymmetry  
73 among pair-bonded species may reflect greater male investment in maintaining the relationship  
74 due to paternal uncertainty or of greater female investment to retain males for infant care.

75         The assumption is that being groomed provides some sort of reward. Grooming has been  
76 shown to release endogenous opioids in the brains of monkeys that have been groomed, and  
77 work on the role of touch and massage in both rats and humans shows that these behaviors  
78 release the hormone oxytocin (Uvnäs-Moberg, 1998). Thus, there is a neuroendocrine basis for  
79 suggesting grooming is rewarding to recipients. The heart rate of recipients of grooming is also  
80 lowered in both pigtail macaques (*Macaca nemestrina*, Boccia et al 1989) and rhesus macaques  
81 (*Macaca mulatta*, Aureli, 1999).

82         A recent study by Shutt et al. (2007) measured fecal hormonal samples from Barbary  
83 macaques (*Macaca sylvanus*) in relationship to grooming and found a converse effect, namely  
84 that glucocorticoid levels were lower in the animal doing the grooming than in the recipient.  
85 These results taken together suggest positive neuroendocrine effects for both the groomer and the  
86 recipient of grooming, supporting the hypotheses that grooming has a rewarding and calming  
87 function.

### 88         **Nonconceptive sex**

89         Many primates engage in sexual behavior at times when conception is not possible. Why  
90 should animals mate when conception cannot occur? In captive macaques one explanation relates  
91 to enclosure size. When females can move away from or escape a male, sexual behavior is  
92 frequently concentrated at the time of ovulation (Wallen, 1982). Female solicitation of sex and  
93 receptivity is controlled by ovarian hormones which may play a critical role in male-female  
94 affiliation in macaques. In one noteworthy study several ovariectomized females lived in a large

95 indoor-outdoor enclosure with several males. Over several years of observation, there were no  
96 observed social interactions between males and females. They behaved as separate species. Then  
97 one Friday the females were injected with ovarian hormones and by Monday morning when the  
98 researchers returned, the males and females were close together, engaging in mounts and  
99 grooming (Tannenbaum & Wallen 1998). In this case affiliative behavior between sexes was  
100 initiated by female gonadal hormones.

101         However, there are many other examples in field and captive studies of primates where  
102 sexual activity extends well beyond a period of fertility. Thus female chimpanzees and baboons  
103 have a conspicuous sexual swelling around the anogenital region that signals ovulation, but is  
104 present for up to two weeks prior to ovulation. In a series of ingenious studies Bielert (1982)  
105 showed that swellings are estrogen dependent and that males are sexually aroused by the  
106 swellings, increasing masturbation rates as swelling increase in size but not showing any sexual  
107 response if housed in the same room as the female but unable to see her swelling. Females solicit  
108 mating from many different males throughout this period. The adaptive significance of this  
109 behavior for females living in multi-male, multi-female groups is that mating with many males  
110 confuses paternity, reduces threat of infanticide, and increases the likelihood that several males  
111 will support the female and her offspring. However, recent work using paternity testing has  
112 shown that male baboons preferentially display positive behaviors toward infants that they have  
113 sired (Alberts, 1999, Buchan et al. 2003) suggesting that the extended non-conceptive sex does  
114 not really confuse paternity.

115         In socially monogamous species where a strong relationship is formed between mates,  
116 non-conceptive sex is thought to also confuse male paternity. In this case ovulation is concealed  
117 (it seems) and it was thought that by concealing ovulation, a specific male would have to stay

118 with its mate for long periods of time and thus be available to the mate to help care for infants  
119 (Burley, 1979). However, a male could still benefit from mating with other females if he deserted  
120 his mate as soon as he could detect any signs of pregnancy, so the concealed ovulation of pair  
121 bonded species must have some other function. If infant survival is dependent on male parental  
122 care, then the male should stay with the female regardless of whether the female conceals  
123 ovulation or not. Is ovulation truly concealed in socially monogamous primates?

124         We found that our captive cotton-top tamarins had a conception rate of 85% in the post-  
125 partum estrous, but we could find no visual or behavioral evidence of ovulation. Females do not  
126 menstruate so there could be no way for a male to calculate when ovulation might occur. There  
127 was no change in the rate of scent marking or in the rate of male investigation of scent marks  
128 over the ovarian cycle. My long-time colleague and collaborator, Toni Ziegler, and I had a  
129 friendly argument. She thought that there had to be some cues to when ovulation occurred in  
130 order to explain the high rate of conception. I countered that all one needed to do was have sex at  
131 least once a day in order to ensure a high rate of conception. Ziegler devised a very clever  
132 experiment where scent marks were collected each day from an ovulating female who was  
133 unfamiliar to all of the test subjects. Each day the scent marks were introduced to pairs of  
134 animals where females were pregnant and, thus, not ovulating, and the behavior of the pair was  
135 observed. During the periovulatory period of the scent donor (the day before, the day of and the  
136 day after ovulation determined by hormonal measures) the recipient pairs showed increased rates  
137 of male erection and increased mounting of each other. In contrast there was no change in the  
138 rate of investigation of marks as a function of the ovulatory cycle (Ziegler et al. 1993). Thus  
139 although ovulation was concealed to us as human observers, it was not at all concealed to the  
140 monkeys. A subsequent study on pygmy marmosets (*Cebuella pygmaea*) also found behavioral

141 evidence that males could identify ovulation in their mates (Converse et al, 1995). Both  
142 marmoset and tamarin males can detect when ovulation occurred and the signal appeared to be  
143 through qualitative changes in scents in tamarins. But I was also correct. Paired tamarins mate an  
144 average of at least once a day throughout the ovulatory cycle and during pregnancy. So why is  
145 there so much non-conceptive sex in both pair bonded primates and in baboons, chimpanzees  
146 and some other species?

147         In order to answer this question I need to digress to consider some other species. One of  
148 the greatest stories in neuroendocrinology over the past two decades concerns the role of the  
149 neuropeptides, oxytocin and arginine vasopressin in pair bonding behavior. These classic studies  
150 looked at monogamous and polygamous species of a small rodent, the vole. Prairie voles are  
151 monogamous and form close pair bonds and males not only defend a territory, they also are  
152 active in caring for infants. Montane voles are polygamous and males neither defend territories  
153 nor do much with respect to infant care. Carter and colleagues (reviewed by Carter 1998) showed  
154 that brain oxytocin receptors were activated in pairbonded female prairie voles and brain  
155 vasopressin receptors were activated in pairbonded males. Injections of oxytocin to the brain of  
156 females would lead to formation of a paired relationship as much as natural courtship behavior  
157 and injections of an oxytocin antagonist would prevent a bond from occurring. Similar results  
158 were seen with vasopressin injections and vasopressin antagonists in male prairie voles.

159         What is the natural way in which a pair relationship develops in prairie voles? Voles  
160 spend a great deal of time mating when they first encounter one other. Copulations occur as often  
161 as every ten or fifteen minutes throughout the first two days of cohabitation and it appears to be  
162 after this period that brain oxytocin receptors are activated in females and brain vasopressin  
163 receptors are activated in males. But why so much sex? This extended period of sexual activity

164 goes well beyond what would be needed for fertilization. Both hormones are known to be  
165 involved in social learning and memory. Voles maintain a preference for the partner with which  
166 they have copulated and/or experienced changes in brain neuropeptides suggesting that voles  
167 become conditioned to aspects of their mates (odors, vocalizations, visual cues) during sexual  
168 activity. This conditioning process may be important in identifying and staying with one's mate.

169         Similar processes may occur in humans. In some remarkable studies in Germany, Krüger  
170 and colleagues (e.g. Krüger et al. 2003) collected serum samples from men and women during  
171 both masturbation and coital sex and found a surge of oxytocin and another neuropeptide,  
172 prolactin, at the moment of orgasm. If orgasms lead to an increase in these peptides in humans  
173 and can also be conditioned to stimuli from one's mate, then humans may be experiencing a  
174 process that is not much different from prairie voles.

175         In cotton-top tamarins we also see a high rate of sexual and other affiliative behavior  
176 when pairs are first formed (Savage et al. 1988) and using a recently developed urinary oxytocin  
177 assay, we have found a great increase in oxytocin levels from pre-pairing baselines, when  
178 animals are paired (Snowdon et al. 2010). In collecting informal anecdotes from humans, it  
179 appears that sexual activity is similarly high at the start of a relationship, decreasing thereafter.

180         These results may also suggest an alternative interpretation of the extended mating  
181 periods seen in baboons and chimpanzees. If males in these species are able to identify their  
182 progeny, then females mating with multiple males may have little to do with paternity confusion  
183 to avoid infanticide. Rather, at the proximate level mating with multiple males may help females  
184 induce positive relationships with other group members. If a coherent group structure has  
185 benefits to members in terms of more efficient foraging, or better predator defense, then non-



186 conceptive sex may function to reward other group members much as grooming was  
187 hypothesized to reward alloparents in cooperatively breeding species.

188         Non-conceptive sex may also function to restore a relationship that has been perturbed in  
189 some way. In several studies done for other purposes, we have noted an increase in non-  
190 conceptive sex following perturbations of the relationship. As noted above when we transferred  
191 odors of a novel, ovulating female to a pair, we observed a significant increase in mounting  
192 relative to the rate seen to the odor of the same donor female when she was not ovulating  
193 (Ziegler et al. 1993). But the rate of mounting to the odors of a non-ovulating female was also  
194 significantly greater than baseline levels of mounting one's own mate. In another study involving  
195 odor transfers from reproductive, cycling females versus reproductively inhibited non-cycling  
196 females, there was again an increase in mounting as well as an 8-fold increase in female  
197 solicitation behavior (Washabaugh & Snowdon 1998). In another study we separated pairs for 30  
198 min and found increased rates of vocalizations and in agitation behavior during separation. On  
199 reunion, we observed an increase in mounting (Porter, 1994). Common to all of these examples  
200 is a social manipulation that might be viewed as threatening an established relationship. The  
201 increased sexual arousal (erections by males, solicitations by females) and increased mounting  
202 suggest that non-conceptive sex functions in established pairs to restore a relationship after some  
203 disruption. The well-known sexual responses of bonobos (*Pan paniscus*) to inter-individual or  
204 group tensions suggest a similar function of non-conceptive sex in a quite different species.

205         One of the most exciting results to emerge from the work on voles was the comparison  
206 between monogamous and polygamous species. Presumably a strong pair bond is most important  
207 in a monogamous species where the female must depend on the male to assist with infant care,  
208 and the male before investing energy into infant care should be relatively confident about

209 paternity. In the polygamous species where males do little, if any, infant care and males would  
210 have little, if any, paternal certainty these mechanisms would have less value. So it is not  
211 surprising to find differences between monogamous and polygamous voles not only in levels of  
212 oxytocin and vasopressin, but also in the distribution of receptors in the brain (see Carter 1998  
213 for review).

214         Similar results have been found in a related pair of rodent species studied by Marler and  
215 colleagues (Marler et al. 2003 for review). California mice (*Peromyscus californicus*) are not  
216 merely socially monogamous but genetically monogamous (Ribble, 2000). The white footed  
217 mouse (*Peromyscus leucopus*) is polygamous. Male California mice actively defend territories  
218 and care for infants and they have much higher brain levels of arginine vasopressin than do white  
219 foot mice with a different distribution of vasopressin activity in the brain. Cross-fostering studies  
220 between species show that male white-footed mice will acquire some of the aggressive and  
221 paternal behavior of California mice as well as a more similar brain distribution of vasopressin.

222         Between species variation in levels of neuropeptides is exciting, but these demonstrations  
223 do not address an even more interesting question: Is there individual variation within a species?  
224 Can similar mechanisms be shown to be involved in regulating individual differences? Recent  
225 work on male prairie voles has found within species polymorphisms in the promoter region of  
226 the arginine vasopressin 1-alpha receptor (*AVPR1a*) gene. A greater number of repeats in the  
227 promoter region are associated with greater affiliation, and mate fidelity (Hammond & Young,  
228 2005). Recently, a similar result has been reported for men (Walum et al., 2008). Three types of  
229 repeat polymorphisms on the *AVPR1A* gene were observed with one type, RS3, being negatively  
230 related to several measures of pair bonding. Males with one or more alleles carrying RS3 were  
231 rated as less bonded to their partners, more likely to have experience a marital crisis or threat of

232 divorce and more likely to be cohabiting than married. Partners of these men reported lower  
233 levels of affectionate expression.

234         In observations of pairs of cotton-top tamarins we observed great variation in the amount  
235 of affiliative behavior. Some pairs had a high degree of affiliative behavior (contact, grooming,  
236 and nonconceptive sex) whereas other pairs had very low levels. We hypothesized that this  
237 variation in affiliation may be reflected in levels of prolactin and oxytocin as well. In an initial  
238 study we measured levels of affiliation and urinary prolactin levels in female tamarins and found  
239 a close positive correlation between sexual and affiliative behavior and their prolactin levels. In a  
240 replication we studied both males and females and found a similar correlation for each sex as  
241 well as between the mean values for a pair and affiliative and sexual behavior (Snowdon &  
242 Ziegler in preparation).

243         We have developed and validated a urinary oxytocin assay and studied pairs of tamarins  
244 with no offspring. We collected samples from males and females over a three week period to  
245 encompass the complete ovulatory cycle and we simultaneously observed a variety of social  
246 behaviors. Both oxytocin levels and affiliative behavior showed a ten-fold range of variation. We  
247 found significant positive correlations between oxytocin levels and affiliative behavior for males  
248 and females separately and when analyzed as pairs (Snowdon, et al, 2010). We found no  
249 difference in mean oxytocin levels between male and female tamarins. In the related common  
250 marmoset Wang et al. (1997) found no sex difference in the distribution of oxytocin  
251 immunoreactive cells in the brain, so it may be likely that in cooperatively breeding primates  
252 both sexes are equally responsive to oxytocin.

253         A multiple regression analysis of the components of affiliative behavior on oxytocin  
254 levels showed that amount of contact and grooming behavior explained a significant amount of

255 variance in female oxytocin levels, whereas sexual activity explained a significant amount of  
256 variance in male oxytocin levels (Snowdon et al. 2010). Furthermore, in pairs with high oxytocin  
257 levels females solicited sex more than in other pairs and males initiated bouts of huddling and  
258 grooming more than in other pairs. It is as though each mate is providing the behavior most  
259 needed by the other to maintain high oxytocin levels. There appear to be two different  
260 mechanisms that explain variation in oxytocin levels that differ by sex, but to the extent that  
261 oxytocin can serve as a proxy for relationship quality, the combination of grooming behavior and  
262 non-conceptive sex may be the proximate mechanisms jointly needed for maintaining positive  
263 relationships.

264         The amount of affiliative behavior may also directly affect reproductive success. Silva  
265 and Sousa (1997) studied sexually naïve common marmosets in newly formed relationships and  
266 the pairs where a female conceived within ten weeks after pairing exhibited significantly more  
267 affiliative behavior and behavioral coordination than the pairs that failed to conceive within ten  
268 weeks.

269         Studies on humans also suggest a role for oxytocin in relationships. Women asked to  
270 recall a negative experience of loss or abandonment showed decreases in oxytocin levels that  
271 were proportional to the amount of negative emotions expressed (Turner et al, 1999). When  
272 engaging in affiliative cues, but not sexual cues, with their partners women had correlated  
273 increases in oxytocin levels (Gonzaga et al. 2006). These results are parallel to the findings on  
274 tamarins that affiliative cues are more important than sexual cues in female oxytocin levels.  
275 Parallel studies on men are needed. Grewen et al. (2005) did look at both sexes and reported  
276 higher oxytocin levels in relationships with strong partner support.

277

278           **Social support and tolerance**

279           An alternative to direct affiliation through grooming or sexual behavior in pair bonded  
280 species is social support and social tolerance in relationships not characterized by pairbonds.  
281 Abbott et al. (2003) examined data on social support, rank differences and cortisol levels in a  
282 variety of species ranging from cooperatively breeding marmosets and tamarins to rhesus  
283 macaques and baboons. In cooperatively breeding species, only one female is typically able to  
284 ovulate and breed within a group, creating a clear reproductive dominance, yet the  
285 reproductively suppressed females showed low levels of cortisol that were no different from  
286 those of the breeding adults. The highest levels of cortisol are seen in newly paired marmosets  
287 and tamarins when they begin to breed. In contrast in baboons and macaques there is clear  
288 evidence that subordinate animals have much higher cortisol levels. Abbott et al. (2003) argue  
289 that social support coupled with infrequent dominance displays lead to the low levels of cortisol  
290 seen in subordinate marmosets and tamarins.

291           As noted earlier we have observed that breeding adults of both wild common marmosets  
292 and captive cotton-top tamarins groom subordinate group members more often than they are  
293 groomed in return (Lazaro-Perea et al. 2004; Ginther & Snowdon, 2009 ). Furthermore, we have  
294 observed a high degree of tolerance of subordinate male sexual behavior in tamarins. Unlike  
295 adult daughters, adult sons show no signs of reproductive suppression (Ginther et al. 2001) and  
296 adult sons exhibit levels of sexual activity as great as reproductive males, but they direct sexual  
297 behavior to brothers, to sisters and even mothers. Yet even in the extreme case of sexual  
298 behavior toward the breeding female we see no evidence of aggression from breeding males or  
299 females. A son who has just attempted a mount with his mother is 95 times more likely to be  
300 groomed by a parent than to receive aggression. This extraordinary tolerance of sexual activity

301 by adult sons may be an expression of tolerance that functions to retain the infant carrying  
302 services of subordinate animals (Ginther & Snowdon, in preparation). Supporting this idea of  
303 tolerance between fathers and sons, an analysis by Price and McGrew (1991) of which types of  
304 departures from monogamy were stable in groups of captive cotton-top tamarins showed that  
305 only father-son polyandry led to stable groups with successful reproduction. Baker et al. (1999)  
306 found that father and son pairs of common marmosets lived together and shared copulation with  
307 an unrelated female without any aggression.

308         At the opposite extreme of the primate world is the mountain gorilla (*Gorilla berengei*  
309 *berengei*). Long thought to live in harems dominated by a single silverback male, many groups  
310 have two or more silverback males. Hormonal sampling revealed clear differences in  
311 testosterone levels between the dominant and subordinate silverback male but no differences in  
312 cortisol (which was low in both dominant and subordinate males, Robbins & Czekala, 1997).  
313 Behavioral relationships between adult males are characterized by extremely low levels of  
314 aggression and high levels of social tolerance, even to the extent of both males copulating with  
315 the same female within a short time of each other (Robbins, 1999). Paternity analyses of 48  
316 gorillas indicated that the dominant male sired 85% of the individuals whereas the subordinate  
317 male sired 15% (Bradley et al. 2005). That both males are able to sire offspring in the same  
318 group while showing tolerance, but not aggression, provides another example of tolerance.

319         Analyses of long-term records of mountain gorillas at the Karisoke Research Station in  
320 Rwanda, indicate that a subordinate male has greater potential reproductive success by remaining  
321 in the group compared with seeking reproductive opportunities elsewhere and that the sons of  
322 dominant males are more likely to mate successfully if they grow up in a group with multiple  
323 silverback males (Robbins, 1995). Furthermore, although infanticide has been observed in

324 mountain gorilla groups with a single male when the male dies, infanticide has never been  
325 observed in groups with multiple adult males. Thus, by exhibiting tolerant rather than aggressive  
326 relationships, silverback male mountain gorillas benefit proximally from low levels of stress and  
327 ultimately from attaining greater reproductive success.

### 328 **Parenting**

329 Parenting can be considered as a special case of affiliation and although all mammalian  
330 mothers must exhibit some form of affiliative relationship with their infants, the involvement and  
331 even attachment of other family members with infants is of special interest. We rarely think of  
332 mammalian males as having relationships with infants, so, when they do, their behavior and the  
333 mechanisms leading to that behavior are of considerable interest.

334 For a long time it was difficult to find specific mechanisms for maternal care since birth  
335 is characterized by a drop in maternal estrogen and progesterone levels. Prolactin which is  
336 involved in preparing the mammary glands for milk production, has been shown to be a critical  
337 hormone for the behavioral control of infant care as well (reviewed by Rosenblatt, 1990). The  
338 production of prolactin is stimulated by the high levels of estrogen that are present during  
339 pregnancy. In addition the hormone oxytocin which is involved in uterine contractions and the  
340 milk let-down reflex in nursing is also stimulated by estrogen (Sprangers et al. 1989; Ochedalski  
341 et al. 2007).

342 Estrogen also stimulates the growth of neurons in the hippocampus an area important to  
343 spatial learning and memory as well as stress regulation (Woolley & McEwen, 1992, 1993).  
344 Following on these results, Kinsley, Lambert and colleagues found that primiparous and  
345 multiparous mother rats had better performance on a spatial maze task than females with no  
346 maternal experience (Kinsley et al. 1999) and that motherhood reversed the cognitive decline

347 seen with aging compared with age-matched virgin controls (Gatewood et al. 2005). The brains  
348 of multiparous females had significantly less amyloid precursor protein known to be involved in  
349 Alzheimer's disease in humans. Multiparous mothers were more able to multi-task and showed  
350 more exploratory behavior and less fear of novelty than did virgin controls (Love et al, 2005).  
351 Oxytocin has been proposed as a mediator of the increased spatial learning seen in mothers  
352 (Tomizawa et al. 2003).

353       Much less is known about the paternal brain than the maternal brain, but several  
354 interesting parallels emerge in recent work. The California mouse (*Peromyscus californicus*) is  
355 one of the few mammals known to have genetic as well as social monogamy. Male California  
356 mice also show increased prolactin levels after infant birth (Gubernick & Nelson, 1989) and  
357 experienced male California mice, but not pup-exposed males of a polygamous species show  
358 increased neuronal growth in the hippocampus (Franssen et al. 2009) and male California mice  
359 show greater oxytocin immunoreactivity in brain areas related to paternal care than polygamous  
360 mice (Everette et al. 2006, 2007).

361       Testosterone has been thought to be involved in aggressive behavior leading to the  
362 Demonic Male hypothesis of Wrangham and Peterson (1996). In monogamous males that exhibit  
363 a high degree of paternal care, it would be logical to expect low levels of testosterone and one  
364 could hypothesize that removing testosterone might make a male even more nurturing of infants.  
365 However when Trainor & Marler (2001) castrated male California mice, they found a reduction  
366 of paternal care. Castrated males were poorer at parenting than intact males. How could this be?  
367 Trainor and Marler reasoned that testosterone might be converted to estrogen in paternal males  
368 and when they blocked the enzyme that converts testosterone to estrogen in gonadally intact  
369 males, they observed a disruption of paternal behavior. When estrogen was given to castrated



370 males they showed high quality paternal care (Trainor and Marler, 2002). Thus, testosterone  
371 appears to be an important hormone in male paternal care and does not necessarily lead to  
372 demonic males.

373         Many parallels have been observed in cooperatively breeding marmosets and tamarins.  
374 Kozorovitskiy et al. (2006) reported dendritic changes and increases in arginine vasopressin  
375 receptors in the prefrontal cortex of male marmosets with extensive paternal experience. The  
376 prefrontal cortex in humans is activated by stimuli from one's own infant and is the location for  
377 receptors of many of the affiliative hormones such as vasopressin, prolactin and oxytocin. Male  
378 marmosets also have elevated prolactin levels especially when they have been recently carrying  
379 infants. Dixson and George (1982) first reported this increased prolactin and Mota et al. (2006)  
380 subsequently replicated the study with both fathers and alloparents, reporting increased prolactin  
381 levels in both types of males immediately after carrying infants. Mota et al. (2006) also reported  
382 no differences in basal prolactin levels prior to birth compared with levels obtained when males  
383 were not carrying infants after birth suggesting that elevated prolactin is a direct response to  
384 infant carrying. Roberts et al. (2001b) also found increased prolactin levels in subadult  
385 marmosets after they carried infants. Roberts et al. (2001a) manipulated prolactin levels by  
386 injecting bromocriptine to subadult animals and found some disruption of infant care. However,  
387 Almond et al. (2006) gave a different prolactin blocker (cabergoline) to paternally experienced  
388 male marmosets and found no effect on male infant care. Their only finding was that males  
389 showed greater interest in infants when injected with the prolactin blocker.

390         There are several differences between the studies- experienced fathers versus subadults,  
391 two different blocking agents, and an experimental test with unrelated infants versus  
392 observations of fathers in natural situations. But one intriguing possible explanation is that for

393 males without infant care experience, prolactin may be a necessary stimulus for infant care  
394 whereas for experienced fathers, prolactin is no longer needed to initiate infant care, but serves to  
395 reward fathers for care. In this case the fathers in the Almond et al. (2006) study may be seeking  
396 additional infant contact to make up for the missing prolactin reward. (Remember that prolactin  
397 levels increase in humans at orgasm suggesting a potential reward function.)

398         Fathers experience other neuroendocrine and behavioral changes. When common  
399 marmoset males were presented with the odor of a novel ovulating female, many males showed  
400 increased erections and increased sniffing and licking at the scent compared to a vehicle control  
401 odor. Blood samples were collected 30 min after the stimulus presentation and in many males  
402 there was a significant increase in testosterone. There was considerable individual variation, but  
403 when males were categorized by whether they were fathers or not, none the fathers showed any  
404 interest in the odor and none showed increases in testosterone levels. The entire effect was due to  
405 the response of non-fathers (Ziegler et al. 2005). Experienced fathers and non fathers were  
406 tested with odors of infants versus vehicle control with a blood sample taken just 20 minutes  
407 after stimulus presentation. Testosterone levels in fathers decreased significantly after  
408 encountering an infant's odor whereas there was no change in hormonal levels in control males  
409 (Prudom et al. 2008). Thus something about the experience of fatherhood changes the father's  
410 neuroendocrine responses to odor cues from novel, ovulating females and to odors from infants.

411         Marmoset fathers also show great interest in infants whether their own or someone else's.  
412 It is difficult to examine directly the behavior of fathers in the context of a family group since  
413 other group members often compete to carry infants and fathers generally reduce infant care with  
414 increased number of alloparents. To study paternal interest in infants more directly, Zahed et al.  
415 (2008) created a test chamber where males could be tested with infant stimuli separately from the

416 rest of the family. Fathers were tested with their own infant or an unrelated infant present and  
417 were also tested with vocalizations of their own and an unrelated infant. Strikingly, father  
418 responded equally to their own infants and to novel infants, but the novel infant rejected all  
419 attempts by the male to pick it up. Fathers also did not distinguish between the calls of their own  
420 versus strange infants. In contrast, when parentally inexperienced males were tested with a  
421 strange infant or a vocalization they showed relatively little interest compared with fathers  
422 (Zahed et al. 2008). Thus fatherhood also affects the responsiveness of a male to infant cues.

423         Both common marmoset males and cotton-top tamarin males show weight gain during  
424 their mate's pregnancy that is out of phase with maternal weight gain meaning that males are not  
425 just eating when their mates are eating (Ziegler et al. 2006). This raises the question of how  
426 males "know" that their mates are pregnant. As noted above, female hormones change  
427 throughout pregnancy leading to the production of hormones critical for nursing and other infant  
428 care, but are their changes in male hormones during pregnancy and, if so what triggers these  
429 hormonal changes? Many of the effects of fatherhood described above have compared males  
430 with no paternal experience with males that have been fathers multiple times. Are there  
431 differences between first time and experienced fathers?

432         We monitored hormones in cotton-top tamarin males through urine samples and therefore  
433 could not get fine detail on whether prolactin levels were elevated transiently as a result of  
434 carrying infants. However, like Mota et al (2006) we found that pre-partum prolactin levels in  
435 males did not differ from post-partum levels but we also found a positive correlation between  
436 prolactin concentration and the number of births a male had been involved with (Ziegler et al.  
437 1996). Furthermore male prolactin levels prior to birth were as high as those of nursing mothers

438 when nursing. Taken together the results suggest that male hormone levels may be changing  
439 prior to birth and that there may be differences between experienced and first time fathers.

440 We followed ten pairs of tamarins throughout their mate's pregnancy; half with multiple  
441 previous pregnancies and half which were first time parents. There were clear differences  
442 between the two groups with hormonal patterns of experienced fathers beginning to change in  
443 mid-pregnancy whereas hormones in first time fathers did not change until the last month before  
444 birth (Ziegler et al., 2004). Experienced fathers had higher levels of testosterone, estrone and  
445 cortisol in the last month of pregnancy than first time fathers, and experienced fathers had higher  
446 levels of prolactin in all months except the month prior to birth when both experienced and first  
447 time fathers had high levels. We also made behavioral observations on the pairs over the  
448 pregnancy and saw little affiliative behavior in the experienced pair. However, in the month prior  
449 to birth first time parents showed a significant increase in sexual and affiliative behavior,  
450 suggesting that these affiliative interactions may have been important in increasing the first time  
451 father's prolactin levels.

452 However, we still need to explain the changes in hormones in experienced fathers. We  
453 examined female hormone levels to see if we could identify a potential cue. Midway through  
454 pregnancy all mothers whether experienced or first time showed a significant peak in excretion  
455 of glucocorticoids, and in experienced fathers, but not first time fathers, there was an increase in  
456 glucocorticoids within a week of the female excretion. Thus, changes in female excretion of  
457 glucocorticoids may be the trigger for the hormonal changes that subsequently occur in  
458 experienced fathers (Ziegler et al. 2004).

459 Where do the maternal glucocorticoids come from? One intriguing possibility is that the  
460 fetal adrenal gland becomes active in mid-pregnancy and a mother would benefit from clearing

461 these excess glucocorticoids from her body. If this is the case, then it is the fetus working  
462 through the mother's body that is providing the signal to prepare the father's hormones for  
463 parental care.

464         However, in this study there were two possible confounds. The experience of mothers co-  
465 varied with that of fathers and many experienced parents had recent infants to care for during the  
466 pregnancy. To control for both of these confounds, we paired experienced fathers with first time  
467 mothers with no infants present and we replicated the original results with experienced fathers.  
468 First time mothers showed the mid-gestation peak in glucocorticoids and their experienced mates  
469 immediately responded with changes in their hormones (Almond et al. 2008).

470         To summarize, parental care is a critical form of affiliative care for mammalian females  
471 as well as for males in biparental and cooperatively breeding species. Similar hormonal and  
472 neural changes occur in both sexes with fathers appearing to anticipate infant births with  
473 endocrine changes occurring during pregnancy. In both California mice and tamarins  
474 testosterone appears to play an important role in paternal care likely through being converted to  
475 estrogens, which in turn stimulate the production of prolactin and oxytocin. In first time pairs of  
476 tamarins, the hormonal changes do not occur until the end of pregnancy at a time when sexual  
477 and affiliative behavior increases. But experienced fathers appear sensitive to changes in female  
478 urinary glucocorticoids, likely produced by the fetus. It is not clear whether prolactin is a  
479 necessary hormone for inducing paternal care or whether it serves to reward fathers for carrying  
480 infants, or both. Parental experience may play an important role in understanding the role of  
481 prolactin. Fatherhood changes male brains in similar ways to how motherhood changes female  
482 brains, and neuroendocrine responses to cues from novel females and from infants work

483 differently in fathers versus non-fathers serving as a potential proximate mechanism to maintain  
484 mate fidelity and responsiveness to infants.

485         So far I have considered parenting from the perspective of parents, but infants are also an  
486 important factor. We examined the care infants received and, across a wide variation in group  
487 size and in parental experience, the infants received an equal amount of care- both nurturing and  
488 rejecting. One consequence of multiple caregivers is the reduction of variation of what infants  
489 experience (Washabaugh et al. 2002). And infants develop attachments to the individuals who  
490 provided the most infant care. Kostan and Snowdon (2002) recorded which family members  
491 were most involved in carrying infants and in transferring food to them and then when these  
492 infants were independent juveniles, we presented a brief threatening stimulus (a standard test of  
493 attachment). In all cases, the infants ran to be close to the individual that had spent the most time  
494 with that infant. In no case was the mother involved. The primary affiliative relationship of  
495 juveniles was established with the one who provide them as infants with the greatest affiliation.

#### 496         **Cooperation, donation and teaching**

497         There have been several recent studies examining variation in cooperative behavior in  
498 nonhuman primates. Experimental studies of cooperation seek whether animals will jointly work  
499 to solve a problem that cannot be solved by one animal alone. Typically this involves the use of  
500 an apparatus to obtain food where two animals must work together simultaneously in order to  
501 obtain food. Early studies were on chimpanzees (*Pan troglodytes*) and orangutans and reported  
502 that cooperative problem solving occurred but typically with a dominant individual coercing a  
503 subordinate with the dominant individual receiving more than 90% of the rewards (Chalmeau et  
504 al. 1994, 1997a)

505           Research with capuchin monkeys led to ambiguous results, with one research group  
506 finding no evidence of cooperative behavior, suggesting that any solutions occurring were  
507 accidental due to the attraction of both individuals toward food (Chalmeau et al, 1997b;  
508 Visalberghi et al. 2000) whereas de Waal and colleagues found that capuchin monkeys would  
509 cooperate to obtain a food reward (Mendres and de Waal, 2000). In the latter study capuchin  
510 monkeys appeared to understand the role of the partner since they would not attempt to solve to  
511 the problem when the partner was not present and not visible. Coussi-Korbel and Fragaszy  
512 (1995) have argued that the social dynamics of a species or population will have an effect on  
513 social learning and cooperative activities. In species with high levels of competition and  
514 aggression, there will be low levels of social tolerance and, therefore, slower rates of social  
515 learning and reduced cooperative behavior. Conversely, the reverse would be true in species with  
516 high degrees of social tolerance and behavioral coordination. Indeed, research on chimpanzees  
517 illustrates that they perform better in social situations where competition is involved (Hare &  
518 Tomasello, 2004) whereas the more socially tolerant congeneric bonobo (*Pan paniscus*)  
519 performed more successfully in cooperative tasks than chimpanzees (Hare et al. 2007).

520           Cooperatively breeding species should be among the best performers in cooperative tests  
521 since they have a high degree of social tolerance as well as coordination of behavior in order to  
522 share duties of infant care, food locating and vigilance (Snowdon, 1996). Indeed cotton-top  
523 tamarins rapidly acquired cooperative behavior with an apparatus that required simultaneous  
524 pulling of trays to obtain food (Cronin et al. 2005). When one animal was separated, the other  
525 animal still showed interest in the apparatus but attempted to solve the task at a significantly  
526 lower rate indicating an understanding of the need of the partner to solve the task. In the original  
527 task both individuals received food rewards simultaneously. In subsequent studies the animals

528 still performed at a high rate even when only one food reward was available (Cronin and  
529 Snowdon, 2008). Successful performance decreased from 99% to 75% when only one animal at  
530 a time received all of the rewards on a single day in alternation with the other animal receiving  
531 all the rewards. Pairs sustained reciprocal behavior even with up to eleven days elapsing between  
532 test sessions. In a final study food was placed adjacent to one individual but rolled down a ramp  
533 to the other individual. Over ten sessions cooperative behavior was maintained by the animal  
534 receiving no food. The overall performance of 99% on two reward sessions and 75% on one-  
535 reward session contrasts with the non-cooperatively breeding capuchin monkey results of 75%  
536 on two reward trials and only 38% on one-reward trials. Even though some capuchin monkeys  
537 can solve the cooperative task, they do not perform as well as cooperatively-breeding tamarins.

538         Another way to examine prosocial behavior such as cooperation is to see if one animal  
539 will voluntarily donate food to another, both when there is no additional cost to the donor and  
540 when the donor receives no reward. Using the first paradigm Silk et al. (2005) and Jensen et al.  
541 (2006) found that chimpanzees would not preferentially provide food for a conspecific even  
542 when there was food for the actor as well. In a follow-up study using a more stringent paradigm  
543 where the potential donor receives nothing and only the partner is rewarded, Vonk et al. (2008)  
544 found no evidence of donation. In contrast Warneken and Tomasello (2006) did find evidence of  
545 altruistic behavior in chimpanzees comparable to that of young children when the tasks did not  
546 involve food. Perhaps chimpanzees are so distracted by food that they can express altruistic  
547 behavior only in situations that do not involve food.

548         Burkart et al. (2007) reasoned that cooperatively breeding species would be more likely  
549 to show prosocial or donation behavior than other species and they found that common  
550 marmosets would readily pull a tray that delivered food only to a partner with no reward for the



551 actor. At the same time we designed a virtually identical study with cotton-top tamarins using the  
552 same rationale. We tested both the paradigm where an animal could donate food to its mate  
553 while receiving food itself as well as the more stringent test of having only a single reward for  
554 the partner. Surprisingly, despite having a similar apparatus, similar training and similar testing  
555 techniques, we found that cotton-top tamarins would not preferentially donate food to their mates  
556 (Cronin et al. 2009). Further support for the lack of prosocial behavior comes from the finding  
557 that tamarins were even less likely to donate food when the partner gave food vocalizations or  
558 reached toward the food (Cronin et al. 2009).

559         It is difficult to account for the contradictory results between marmosets and tamarins,  
560 especially when the training and testing paradigms were so similar. There may be something  
561 different between the two species that is not captured by the variable of cooperative breeding or  
562 there may have been environmental differences. For example, the tamarins were tested in home  
563 cages where they could do many other activities whereas marmosets were tested in smaller, more  
564 confining test cages.

565         Temporal dynamics may also affect when and how donation behavior is observed. Cronin  
566 et al. (2010) developed a paradigm using the same tray pulling apparatus as Cronin et al., (2009)  
567 but with a single tray. One tamarin pulled the tray to provide food for itself as well as to its mate  
568 for 5 min. Roles were immediately reversed, and the recipient could now pull the tray but only  
569 the mate received food. A negative condition consisted of placing a block on the tray movement  
570 so that food was visible to both animals but neither could receive food, and then roles were  
571 reversed. A non-social control consisted of having both animals receive rewards, but then instead  
572 of reversing roles, the previous donor was moved elsewhere and the previous recipient had an  
573 empty cage. In the first 100 s after role reversal tamarins presented food to their mate

574 significantly more often after having received food than not having received food, but they also  
575 pulled just as often after a positive experience when there was no recipient in the adjacent cage.  
576 The tamarins did not show reciprocity but rather initially reacted positively independent of  
577 whether a recipient was present or not. However, by the last 100 s of the 5 min test, tamarins,  
578 regardless of whether they had a positive or negative experience with the mate, donated food  
579 equally often to the mate and significantly more than in the nonsocial condition. The dynamics of  
580 donation changed with time, but eventually tamarins demonstrated prosocial behavior without  
581 requiring reciprocity.

582         What mechanisms can sustain cooperation and donation behavior? Perhaps donation and  
583 exchange of cooperative behavior simply engender good feelings and do not require much  
584 cognitive ability (as in the first part of the Cronin et al. 2010) study. Studies of rats by Rutte and  
585 Taborsky (2007, 2008) find that rats will maintain what they call “generalized reciprocity”. If a  
586 rat has recently experienced an interaction with another rat in which it has received a reward, it  
587 will then act to provide a reward in to the individual rat that had provided a reward previously..  
588 Rutte and Taborsky argue that being the recipient of something good may engender good  
589 feelings that are simply transferred to the next interaction.

590         What is the biological source of feeling good? Recent studies in humans suggest that  
591 oxytocin is associated with generosity in humans (Zak et al. 2007) and that oxytocin also  
592 increases trust in humans as evidenced by performance on games involving cooperation and trust  
593 to maximize rewards (Kosfeld et al, 2005; Zak et al. 2005). Thus if being the recipient of a gift  
594 leads to increased oxytocin which in turn makes one more generous and trusting, we can  
595 imagined a scenario whereby altruistic behavior can be sustained without requiring the positing  
596 of any complex cognitive mechanisms. The role of oxytocin increasing trust compares with the

597 results reported earlier on how grooming and nonconceptive sex increase oxytocin levels  
598 suggesting that a variety of socially administered rewards serve to increase trust and well-being  
599 between individuals.

600 Teaching represents another example of altruistic or prosocial behavior. Caro and Hauser  
601 (1992) have provided an operational definition of teaching behavior that requires some specific  
602 behavior directed toward another that incurs a cost toward the animal performing the behavior  
603 that leads to long term change in the behavior of the observer. Teaching is more than simple  
604 social learning which can occur through observation alone, since teaching requires some directed  
605 action on the part of another.

606 King (1994) has observed that in most nonhuman primates mothers do not teach young  
607 about foraging skills or what foods to select. The infant observes the mother closely, but there is  
608 no direct action by the mother to improve the performance of the infant. King suggests that the  
609 only nonhuman primates to show teaching are the marmosets and tamarins. In these species it is  
610 commonly observed that an adult will offer food or tolerate scrounging from an infant (Brown, et  
611 al. 2004). In a longitudinal study of food transfers in cotton-top tamarins Joyce and Snowdon  
612 (2007) found that adults initially offered food to infants, but as the infants became older, the  
613 adults tolerated food transfers less. Adults made a specific vocalization that was observed only in  
614 the context of food transfers, and food transfers with infants were successful only when the  
615 adults vocalized. Adults began food transfers significantly sooner with twin infants than with  
616 singletons suggesting a greater cost to nursing twins. Furthermore, infants who received food  
617 transfers at an earlier age were feeding independently significantly sooner than infants with food  
618 transfers beginning at a later age (Joyce & Snowdon, 2007). Thus food transfers may be a form

619 of teaching since adults provide specific cues to infants; sharing food is costly for adults and  
620 infant behavior changes as a function of the age of onset and intensity of adult food transfers.

621 This is not an artifact of captivity. Rapaport (2006) studying golden lion tamarins  
622 (*Leontopithecus rosalia*) found that whereas juveniles could readily eat fruit on their own, they  
623 were much less successful foraging for insects. She documented a high level of food  
624 vocalizations and food transfers of insect food toward juveniles that decreased with the age of  
625 the juveniles. Furthermore, she documented (Rapaport & Ruiz Miranda, 2002, 2006) several  
626 cases of scaffolding behavior where an animal would give food vocalizations but not offer any  
627 food when the juvenile approached. The juvenile searched in the proximity and found an insect  
628 nearby. So adult tamarins do not simply provide food transfers to infants and juveniles, but  
629 appear to systematically provide less assistance to their young as they develop skills.

630 Cooperatively breeding meerkats also demonstrate teaching behavior by adults stunning  
631 potentially harmful prey before transferring them to the young (Thornton & McAuliffe, 2006).

632 We have found similar results in a captive experimental study of cotton-top tamarins  
633 (Humble & Snowdon, 2008). We developed an apparatus from which food could be obtained  
634 through one of two methods and trained one parent in each family group with one of the  
635 methods. Juvenile tamarins (ages 25-36 weeks) were then tested one twin with each parent. Most  
636 of the adult demonstrators gave the infant food transfer vocalizations during the tests, even  
637 though their young had been feeding independently for several months. Ironically the most  
638 successful juvenile learners were the ones who received transferred food least often. Once a  
639 juvenile successfully solved the problem, the adult demonstrators vocalized and engaged in food  
640 transfers significantly less often. The results parallel the field results of Rapaport. Adult tamarins  
641 reinstated food transfers with juveniles during a novel foraging task and they ceased food

642 transfers as soon as the juvenile was successful by itself. When we replicated the same task with  
643 adults, we found no evidence of food transfers but most adults learned the task more readily than  
644 the juveniles and with shorter amounts of direct observation (Dillis, Humle and Snowden, 2010).  
645 Taken together these results suggest that tamarins adjust food transfers and accompanying  
646 vocalizations according to the skill level of their companions, a rudimentary form of ‘theory of  
647 mind’.

648         These results on tamarins contrast sharply with a parallel study on ant-dipping behavior  
649 in chimpanzees at Bossou in Guinea. Even though driver ants can inflict considerable pain when  
650 they bite, mother chimpanzees gave no evidence of assisting their infants and juveniles as they  
651 learned to ant dip (Humle et al. 2009). In this case, chimpanzees must learn difficult foraging  
652 skills on their own with no assistance from a parent.

### 653         **Summary and conclusions**

654         This paper has examined the behavioral and neuroendocrine mechanisms involved in a  
655 variety of affiliative interactions. Grooming and other physical contact are obvious in a wide  
656 variety of social relationships and can induce neuroendocrine changes such as increased  
657 endogenous opioids and oxytocin levels, reduced levels of glucocorticoids and reduced heart  
658 rate. Together the physiological changes induced by grooming activate brain reward systems and  
659 induce calming behavior. Furthermore, the act of grooming may itself bring benefits to the  
660 groomer as well as the groomee.

661         Nonconceptive sex is seen in species with many different social systems. Although  
662 nonconceptive sex is often thought to function primarily to confuse paternity, the finding that  
663 males of socially monogamous species are able to detect ovulation and still engage in frequent  
664 nonconceptive sex suggests other functions must be involved. The findings that levels of the

665 neuropeptides prolactin and oxytocin are elevated at orgasm in men and women, suggests that  
666 nonconceptive sex may function to reward partners, and thus be critical in forming and  
667 maintaining relationships. Increased sexual behavior in response to social perturbations in  
668 tamarins suggests that nonconceptive sex may also play an important role in restoring  
669 relationship equilibrium between mates. Basal oxytocin and prolactin levels are directly related  
670 to the amount of affiliative behavior seen in tamarin pairs with variation in male oxytocin levels  
671 being explained best by sexual activity and variation in females being explained best by contact  
672 and grooming behavior.

673         Social tolerance is a less active form of affiliative behavior, but subordinate individuals in  
674 species with high social tolerance have significantly lower levels of stress hormones than  
675 subordinates in species with low levels of tolerance.

676         Parenting is a special form of affiliative behavior but because maternal care is obligatory  
677 to all mammals, there has been relatively little attention to maternal care as a specific form of  
678 affiliation. However, since care by fathers and alloparents is often not as obligatory as maternal  
679 care is, the mechanism leading to male infant care are of interest. Fatherhood significantly  
680 changes the brain and neuroendocrine system, with increased dendritic growth and vasopressin  
681 receptors in the prefrontal cortex, a lack of testosterone response to odors from novel females  
682 and a decreased testosterone response to scents of infants compared with non-fathers.  
683 Experienced fathers respond avidly to infant cues and do not appear to discriminate between  
684 their own infants and unrelated infants.

685         Fathers show hormonal changes prior to the birth of infants with experienced fathers  
686 showing the changes sooner than first time fathers. Experienced fathers appear to begin a  
687 cascade of hormonal changes within a week of the pregnant female excreting increased

688 glucocorticoids, likely from the activation of the fetal adrenal gland, making it likely that the  
689 fetus is changing the hormones of its father to prepare him for infant care. This appears to be a  
690 learned response since first time fathers do not respond to the increased glucocorticoid levels.  
691 However, first time parents showed a significant increase in grooming, contact and sexual  
692 behavior in the month before birth suggesting that an increase in affiliation might lead to  
693 hormonal changes in first time fathers.

694         Testosterone, often thought to be involved exclusively in aggressive behavior is also  
695 necessary for male parental care. Some of the testosterone is metabolized into estrogen which in  
696 turn is critical to stimulate prolactin and oxytocin. Thus, testosterone plays a critical role in the  
697 affiliative and nurturing behaviors of infant care.

698         Species differ greatly in their ability to display cooperative and altruistic behavior. Those  
699 species that are less aggressive, show more social tolerance and more coordination of social  
700 behavior appear more likely to exhibit cooperative behavior and to donate resources to others. It  
701 is possible that prosocial exchanges lead to changes in hormones like oxytocin, producing good  
702 feelings that can be conditioned to specific partners or can lead to an overall increase in  
703 generosity.

704         Teaching behavior is rare among most nonhuman primates even under conditions of risk  
705 to the infant, but it is clearly evident in cooperatively breeding species and in golden lion  
706 tamarins, cotton-top tamarins, and meerkats there is clear evidence of adults adjusting their  
707 teaching to the skill level of their offspring.

708         Affiliative and altruistic behaviors now pose many interesting questions and deserve to be  
709 studied as much as competition, dominance and aggression have been studied historically.  
710 Affiliative and altruistic behaviors play an important role in group cohesion and infant

711 development. We are just beginning to understand the sources of variation in affiliative and  
712 altruistic behavior as well as the neural and hormonal mechanisms involved. But understanding  
713 the behavioral and neuroendocrine mechanisms of affiliation is an important task for future  
714 research.

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