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Sex Differences in Behavioral and Hormonal Response to Social Threat: Commentary on Taylor et al. (2000)

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Taylor and colleagues proposed that women uniquely respond to stressors by tending to children and befriending other women rather than by fighting or fleeing (S. E. Taylor et al., 2000). In this article, the authors expand Taylor et al.'s evolutionary frame and incorporate several unique aspects of human social dynamics. First, humans are characterized by extensive paternal investment, and thus men's tending is predicted and observed in some stressful contexts. Second, the dynamics of women's befriending suggest an evolutionary elaboration of the mechanisms that support reciprocal altruism. Third, coalitional male–male competition indicates that men's befriending is a predicted component of their fight-or-flight response. Finally, men's tending should result in the evolution of female–female competition over this form of parental investment.

Taylor and colleagues provided an important and, in many respects, groundbreaking evolutionary analysis of women's neuroendocrine and social responses to threats and other stressors (Taylor et al., 2000). They proposed that women do not fit the traditional fight-or-flight stress response paradigm developed from research with men (Dabbs & Dabbs, 2000) but instead tend and befriend. *Tending*, the protection and care of offspring, and *befriending*, the formation and maintenance of a small network of interpersonal relationships with other women, are proposed as an integrated and evolved strategy of women defending themselves and their offspring with protective coalitions. Tending and befriending are posited to have evolved from the attachment and nurturance systems involved in maternal care, including oxytocin and endogenous opioids, whose effects are moderated by estrogens. The behavioral and neuroendocrine mechanisms involved in tending and befriending were contrasted with the mechanisms for fight and flight, which were characterized as being more commonly expressed in men than in women and "organized and activated by androgens" (Taylor et al., 2000, p. 417). Androgens may work as antagonists with respect to the neuroendocrine systems (e.g., expression of oxytocin) that dispose women toward tending and befriending.

In all, Taylor et al. (2000) have made a potentially seminal contribution to the understanding of women's social relationships and in understanding sex differences in patterns of social affiliation and neuroendocrine response to stressors. There are several areas, however, in which we disagree with Taylor et al. and other areas in which we suggest friendly elaboration of their model. We

focus on the following issues: (a) the importance of male parenting; (b) evolutionary interpretations of tending and befriending, with specific questions concerning whether befriending evolved from tending; (c) patterns of philopatry and male coalitions in hominid evolution; and (d) the nature and source of female–female competition. The first two issues are addressed in the section below and the third and fourth in separate sections. Where relevant, the types of stressors that elicit tending or befriending in women and men are discussed, as these were not fully elaborated by Taylor et al.

Tending and Befriending

Tending is a form of parental investment. The nature and extent of this investment by one or both sexes strongly influences the dynamics of intersexual and intrasexual relationships, termed *sexual selection* (Andersson, 1994; Darwin, 1871; Trivers, 1972; Williams, 1966). Species in which females provide the majority of parental effort, such as chimpanzees (*Pan troglodytes*) and lions (*Panthera leo*), are characterized by intense male–male competition for access to females or for control of the resources (e.g., breeding territory) females need to raise their offspring. In these species, female tending and male fighting are salient features of reproductive dynamics. The reverse situation occurs in species in which males provide the majority of parental effort, such as red-necked phalaropes (*Phalaropus lobatus*), where sexual selection involves female–female competition over resources provided by males.

Humans are one of few mammalian species in which both females and males parent (Geary, 2000; Geary & Flinn, 2001; Murdock, 1981). The first section below provides consideration of how human paternal investment is related to predictions regarding tending in men, and the second focuses on the relation between tending and befriending in women. The implications of men's tending for understanding competitive relationships among women are discussed in a later section.

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Men's Tending

Among primates, the expression of both paternal and maternal investment appear to be influenced by similar hormonal and contextual factors, although there are differences as well (French & Schaffner, 1999; Insel & Young, 2000; Nunes, Fite, & French, 2000; Pryce, 1993). For humans, it is likely that combinations of hormonal, experiential, and contextual factors contribute to maternal and paternal investment, some of which differ between the sexes and some of which do not. Corter and colleagues have found that high cortisol levels are correlated with attentive and sensitive parenting of newborns in both mothers and fathers (Corter & Fleming, 1995; see also Stallings, Fleming, Corter, Worthman, & Steiner, 2001), although there are also hormonal correlates that differ for mothers and fathers (e.g., Fleming, Ruble, Krieger, & Wong, 1997). Storey and colleagues assessed the relation between serum hormone levels and sensitivity to infant cues (e.g., crying) in couples who were expecting a child (Storey, Walsh, Quinton, & Wynne-Edwards, 2000). In response to infant distress cues, men who responded with concern and a desire to comfort the infant had higher prolactin levels and lower testosterone levels than did other men. "Men with more pregnancy symptoms (couvade) and men who were most affected by the infant reactivity test had higher prolactin levels and greater post-test reduction in testosterone" (Storey et al., 2000, p. 79). Added analyses suggested these hormonal patterns may have been moderated by the nature of the man's relationship with his wife.

For men, a combination of other hormonal and interpersonal factors appear to suppress testosterone levels, which, in turn, may result in the inhibition of the motivational and behavioral dispositions associated with fight or flight (Mazur & Booth, 1998). The inhibition of these dispositions may enable the expression of paternal tending in some contexts (Muller & Wrangham, 2001). Of course, it is likely that some of the hormonal and neuroendocrine systems that support tending differ in women and men, and thus these patterns may not be completely relevant to tending in women. The point is that men do not always react to stressors with a fight or flight response, and, in fact, in some contexts show many of the same tending behaviors that Taylor et al. (2000) described for women.

Women's Tending and Befriending

We propose that the evolution of befriending may have been more strongly related to the mechanisms that support reciprocal altruism than the tending mechanisms proposed by Taylor et al. (2000; see Geary, 1998, 2002). Befriending is defined by a shared ethos of equality and high levels of reciprocal intimacy, as well as the mutual sharing of time, resources, and social support (Taylor et al., 2000). The dynamics of these relationships mirror those that define friendships (Hartup & Stevens, 1997) and are the predicted pattern for an evolved system supporting reciprocal altruism—that is, the formation and maintenance of relationships among nonkin (Tooby & Cosmides, 1996; Trivers, 1971). Unlike women's befriending, mother–offspring relationships are not defined by reciprocity and, in fact, are characteristically nonsymmetrical in all species (Trivers, 1974). Moreover, it is not clear whether the evolved tending system involves emotional nurturance, as such behaviors are not a universal feature of mother–child relationships

(Goldberg, Grusec, & Jenkins, 1999; MacDonald, 1992), although the providing of emotional support is one of the defining features of women's befriending.

There are also developmental patterns that suggest different mechanisms in the evolution of tending and befriending. Although the function of a long development period in humans is sometimes debated, a plausible interpretation is that it enables the practice and refinement of the competencies that covaried with survival and reproductive outcomes in our ancestors (Geary & Bjorklund, 2000). If tending and befriending have a common evolutionary history, then there should be developmental similarities in the focus and form of these social behaviors. During childhood and adolescence, girls engage in both play parenting and actively form and maintain relationships with other same-age girls, but these social behaviors differ in both function and form. Play parenting is typically directed toward younger children, or child substitutes (e.g., dolls), and involves the rehearsal of parenting activities, such as the feeding and bathing of children. Social relationships, in contrast, are almost always with same-age peers and involve nonparental activities, such as discussion of boys or relational aggression (i.e., gossiping about and backbiting other girls; Crick, Casas, & Mosher, 1997).

The argument is not that there is no overlap in the behavioral and neuroendocrine systems that support tending and befriending. Clearly, there are overlaps, as aptly described by Taylor and colleagues (Taylor et al., 2000). It is, of course, possible that the befriending system evolved from a combination of mechanisms involved in tending and in reciprocal altruism. Nonetheless, at a social and behavioral level, befriending is more similar to reciprocal altruism than to tending.

Befriending in Men and Women

Men's social affiliations were mentioned by Taylor et al. (2000) but were not the focus of their theoretical argument. Taylor et al. did, however, contrast the social behavior of women and men under stressful conditions and argued that women are more likely to affiliate under these conditions than are men. Under laboratory and in some other well-studied contexts, such as following divorce, women do indeed show more social affiliation than do men (Belle, 1987). However, laboratory studies and studies of stressors in Western societies are not always representative of the stress-inducing contexts that were likely to have been of importance during human evolution. The goal here is to provide a theoretical elaboration of the Taylor et al. model by considering the social ecology within which humans most likely evolved, as related to men's and women's befriending.

Philopatry

An important frame for understanding the social ecology of human evolution is *philopatry*, that is, the tendency of members of one sex to stay in the birth group and members of the other sex to migrate to another group. Taylor et al. (2000) used female coalitional behavior in other primates to make inferences about the evolution of befriending in women. The reviewed studies were largely of female kin-based coalitions in several species of old-world monkey, species in which females are the philopatric sex (e.g., Wrangham, 1980). Female-biased philopatry results in a

social ecology that favors the evolution of kin-based coalitions among females, at least when coalitional behavior covaries with survival or reproductive outcomes (Hamilton, 1964, 1975; Sterck, Watts, & van Schaik, 1997). These coalitions typically compete over access to high quality food sources, such as fruit trees (Wrangham, 1980). Offspring borne in coalitions that gain control of these resources are healthier and survive in greater numbers than do offspring borne in other coalitions (Silk, 1987). These coalitions also provide support during periods of social conflict and otherwise function to control the dynamics of social living, as described by Taylor et al. In contrast, for “most monkeys with multimale groups, tolerant or cooperative relationships among males are rare or unknown” (Nishida & Hiraiwa-Hasegawa, 1987, p. 174). In these species, antagonistic relationships among males are well described by fight or flight and the social coalitions of females by tend and befriend.

However, female-bonded species may not provide the most appropriate analogy for making inferences about the evolution of befriending in humans. Male-biased philopatry in chimpanzees, bonobos (*Pan paniscus*), and humans (*Homo sapiens*) suggest that the modal social ecology during hominid evolution was male philopatry, not female philopatry (Foley & Lee, 1989; Ghiglieri, 1987; Goodall, 1986). There is, of course, variability in migration patterns across chimpanzee, bonobo, and human communities, but the modal pattern is for females to migrate and males to stay in the birth group (Pasternak, Ember, & Ember, 1997; Seielstad, Minch, & Cavalli-Sforza, 1998). A male kin-based social ecology creates the potential for the evolution of motivational and behavioral dispositions for males to form kin-based coalitions, and such dispositions are expressed in humans and chimpanzees (Wrangham, 1999).¹

Men's Befriending

Male befriending and the resulting formation of kin-based coalitions is a common feature of social life in chimpanzees and humans in preindustrial societies, although it is only intermittently observed in bonobos (Goodall, 1986; Hohmann, Gerloff, Tautz, & Fruth, 1999; Kano, 1992; Pasternak et al., 1997). For humans and chimpanzees, male befriending is sometimes seen among unrelated or distantly related males, suggesting strong benefits to coalitional behavior for the males of these species (Betzig, 1986; Mitani, Merriwether, & Zhang, 2000). Indeed, Taylor and her colleagues described social affiliation in men, noting that “men have been observed to form groups for purposes of defense, aggression, and war . . . [they] tend toward larger social groups than is true of women . . . and these groups are often organized around well-defined purposes or tasks” (Taylor et al., 2000, p. 419). The functional significance of this behavior was not the theoretical focus of their model but is nonetheless relevant to the broader issue of befriending.

For chimpanzees, humans, dolphins (*Tursiops truncatus*), and other species in which male coalitions form, coalitional behavior is related to male-male competition over access to females or for control of the resources females need to raise their offspring (Alexander, 1989; Betzig, 1986; Chagnon, 1988; Daly & Wilson, 1988; Geary, 1998; Goodall, 1986; Irons, 1983; Keeley, 1996; Pasternak et al., 1997; Tiger, 1969; Wrangham, 1999). In preindustrial societies, coalitional warfare is common and social poli-

ticking and alliance formation is a crucial element of the social life of men (e.g., Chagnon, 1977; Keeley, 1996; Pasternak et al., 1997). Within this social network, men's relationships reflect a balance of cooperative and competitive behaviors. Cooperation is needed to maintain the coalition, and competition emerges from attempts to increase individual status within the dominance hierarchy of the coalition. Once established, the dominance hierarchy facilitates the social cooperation needed for coalitional competition.

For chimpanzees, humans, and other species, larger coalitions typically have a competitive advantage over smaller coalitions (Packer, Gilbert, Pusey, & O'Brien, 1991; Wrangham, 1999). The advantage of group size in male coalitional competition, and in political negotiations, places constraints on the types of mechanisms that can support men's befriending. Although core relationships among individual men, as in chimpanzees, are expected, the mechanisms that support befriending in men cannot be as time intensive and emotionally intensive as those evident in women. This is because the high-intensity investment (e.g., time involved in maintaining the relationship) associated with women's befriending would per force limit the number of social alliances men could develop and thus limit coalition size. Stated differently, evolved motivational and emotional mechanisms that enable men to form large competition-related social groups based on low-intensity activities is a necessary correlate of coalitional competition. Proximity, shared activities, “horse play,” and so forth often appear to be sufficient for forming the affective and affiliative ties that define befriending in boys and men, as related to coalition formation (Savin-Williams, 1987).

Again, developmental patterns appear to reflect evolutionary function. The development and maintenance of boys' friendships is often achieved through shared activities and often in social contexts in which coalitional behavior is needed to achieve mutual goals (e.g., Lever, 1978; Savin-Williams, 1987; Sherif, Harvey, White, Hood, & Sherif, 1961). Many of these developmental activities, such as team sports, mirror and thus provide practice for primitive warfare (Geary, 1998). Moreover, boys and men, unlike girls and women, show increased cortisol and testosterone responses with the formation of same-sex coalitions during group-level competition—the expected endocrine reactions associated with an evolved fight response, when the fight occurs in the context of group-level competition (Dabbs & Dabbs, 2000; Wagner, Flinn, Gangestad, Thornhill, & England, 2001).

Low-intensity investment in boys' and men's befriending might be a consequence of male philopatry. In natural settings, most of the boys and men in the local group will be kin and thus the maintenance of these relationships will not require the same level of reciprocity as will relationships with nonkin (Chagnon, 1988; Hamilton, 1964). In any case, men's befriending and coalitional fighting are coevolving features of social life in preindustrial societies and almost certainly throughout much of recent human

¹ Coalitional behavior is evident in female bonobos, although it is less common in the wild than in captive populations (Hohmann et al., 1999). The point is not that coalitional behavior or befriending cannot occur among females when males are the philopatric sex. Rather, the point is that male-biased philopatry results in a social ecology that must be considered when providing an evolutionary interpretation of female befriending.

evolution (Alexander, 1979, 1989; Geary & Flinn, 2001; Wrangham, 1999). Finally, it must be noted that men's coalitions provide a protective social ecology within which women's tending and befriending, as described by Taylor et al. (2000), are expressed.

Women's Befriending

On the basis of male philopatry, girls and women are predicted to have an evolved motivational disposition to maintain same-sex relationships around an ethos of equality and reciprocity (Geary, 2002), as contrasted with the dominance hierarchies that form with groups of boys and men. In social contexts in which women migrate to the group of their husband, the most likely source of social support is other often unrelated or distantly related women (Pasternak et al., 1997). In this circumstance, selection will favor women who have the social competencies needed to develop relationships with unrelated women and through this maintain a supportive social network. As noted, these social competencies define friendship and reciprocal altruism—relationships with non-kin (Trivers, 1971)—which, in turn, well describe the dynamics of women's relationships.

On the basis of male philopatry and kinship, women's relationships are not only predicted to require more intense investment to maintain, they are also predicted—and appear—to be more readily disrupted by conflict than relationships among men (de Waal, 1993). Conflicts in men's relationships are a normal aspect of the formation of within-group dominance hierarchies. Kinship and the benefits of group size in coalitional conflict result in selective advantages for men who maintain the coalition, following within-group conflict. The mechanisms for maintaining women's social networks, in contrast, evolved under a different social ecology, one that was not defined by philopatry or the benefits of large coalitions.

Female–Female Competition

Taylor and colleagues (2000) note that male-on-male physical aggression is more common than female-on-female physical aggression in many species. Indeed, extreme and life-threatening levels of female-on-female aggression are likely to be selected against, because of the associated reproductive costs, which are not born by males (see Campbell, 1999). At the same time, it was acknowledged that relationships among women are not always nurturing and cooperative, but it was suggested that women's "aggressive behavior may be more moderated by social norms and learning and by cultural, situational, and individual differences" (Taylor et al., 2000, p. 414). The implication is that there is not a strong evolutionary foundation for female-on-female aggression in humans.

We disagree. As with other species of primate (Smuts, 1987), women are predicted to compete over social and material resources, including paternal investment. Men's tending creates a more uniquely human form of female–female competition; that is, competition for high-quality men who are able and are willing to invest their resources in the woman and her children (Buss, 1994; Gaulin & Boster, 1990). The associated competition is typically expressed in terms of relational aggression (Crick et al., 1997), as noted by Taylor et al. (2000). At the root, relational aggression functions to exclude sexual and other female competitors from the

social group and to disrupt the above described social networks that women work to develop (Geary, 2002). In most preindustrial societies, female-on-female aggression, relational and otherwise, is likely to involve competition among cowives, as high-status men in these societies are typically polygynously married (Daly & Wilson, 1983). Female–female competition over social and other resources may also occur between other women, such as between a wife and her husband's sister in matrilineal societies; in these societies, men are expected to invest in their sister's children (Flinn, 1981).

In the United States and other Western nations, polygyny is socially suppressed. Once married, women in these cultures do not usually experience the same level of female-on-female relational, and sometimes physical, aggression as might have been common during human evolution. In other words, the befriending aspect of Taylor et al. (2000) may belie the more competitive side of adult relationships among married women, because the social context—outlawing of polygynous marriages (see Flinn & Low, 1986)—removes an important source of such conflict, cowives. Moreover, many women in Western society are socially isolated in comparison with women in preindustrial societies and thus removed to some extent from the above noted broader female–female competition.

Conclusion

Taylor et al. (2000) presented a groundbreaking analysis of relationships among women. Their evolutionary model proposed new adaptive explanations and underlying neuroendocrine mechanisms that support these relationships and has implications for understanding sex differences in human stress response. We suggest an elaboration of their model based on a broader evolutionary perspective that emphasizes human paternal investment and the likelihood that males were the philopatric sex throughout much of human evolution.

Parental investment appears to be an evolved feature of the reproductive strategy of men (Geary, 2000) and is relevant to two issues related to tending and befriending. First, the Taylor et al. (2000) framework for understanding tending can be expanded to include men, although it is very likely that there are differences as well as similarities in the neuroendocrine mechanisms supporting tending in women and men (Corter & Fleming, 1995). An important evolutionary corollary is that men's tending is predicted to—and does—occur in some stressful contexts (Storey et al., 2000). Second, across-species patterns indicate that when males parent, females compete over this investment (Trivers, 1972). Taylor et al. (2000) do not deny that relationships among girls and women are sometimes competitive but do suggest that female-on-female aggression is more strongly related to learning and culture than is male-on-male aggression. Clearly, patterns of same-sex aggression differ for men and women (Daly & Wilson, 1988), but evolved forms of female-on-female aggression follow as an evolutionary consequence of male parenting. In studies of Western girls and women, this often takes the form of relational aggression (e.g., Crick et al., 1997), which may belie the intensity of female-on-female aggression, relational and otherwise, in other contexts and during human evolution.

Male philopatry provides an essential frame for understanding the social ecology in which befriending mechanisms evolved in

women and men. One result is the creation of a social ecology in which a motivational disposition for males to form kin-based coalitions can evolve, at least when coalitional behavior covaries with reproductive outcomes (Wrangham, 1999). Such a disposition exists in boys and men, although it is primarily expressed in social contexts that favor formation of male coalitions, such as group level male–male competition (Geary, 1998; Savin-Williams, 1987). One corollary is that to support coalitional competition, the fight in the fight or flight response must include an element of befriending for boys and men (Tiger, 1969). Evolved mechanisms that foster befriending in boys and men under conditions of social threat, however, cannot involve all of the same befriending mechanisms described by Taylor et al. (2000) for girls and women. The time-intensive befriending mechanisms found in girls and women would constrain the size of boys' and men's coalitions, hence resulting in a competitive disadvantage.

Male philopatry also leads to the prediction that the evolution of women's befriending will strongly involve the mechanisms that support reciprocal altruism (Geary, 1998, 2002). Residential groups were more likely to have included distant or unrelated females than males during human evolution. Female nonkin relationships would be based on reciprocal altruism; that is, an exchange of social and emotional support, information, resources, and so forth that are considered to be advantageous to both parties (Hartup & Stevens, 1997; Trivers, 1971). The befriending patterns described by Taylor et al. (2000) are congruent with the view that social relationships among girls and women are strongly influenced by reciprocal altruism, whether or not tending mechanisms are also involved.

Future studies that assess sex differences in endocrine responses in different social contexts and under different social conditions—as illustrated with the elevation of boys' and men's cortisol and testosterone levels with coalitional competition—are needed to test these elaborations of the Taylor et al. (2000) model (cf. Flinn, 1999; Flinn, Baerwald, Decker & England, 1998; Flinn, Quinlan, Decker, Turner, & England, 1996). We think it will be useful to expand the Taylor et al. model to capture additional complexities of the evolution of human social relationships and sex differences in these relationships. We suggest consideration of social dynamics in other hominoids, social patterns that are unique to humans, and social dynamics that occur in preindustrial contexts, especially those that are more similar than Western society to the social contexts in which human biobehavioral evolution occurred.

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