

Cooperation between the Sexes

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Despite a shared evolutionary history and many common characteristics—intelligence, tool use, slow life histories, and other traits discussed throughout this volume—patterns of mating and parental investment between humans and chimpanzees are remarkably dissimilar. These dissimilarities have a profound impact on the nature of social relationships between the sexes. In this chapter we synthesize recent research on free-ranging chimpanzees, human foragers, and forager-horticulturalists,¹ documenting these distinct patterns of interaction between females and males.

We begin by developing an evolutionary and ecological framework to understand the divergence in patterns of cooperation between the sexes in *Pan* and *Homo*. We review the state of evidence bearing on this topic from the study of wild chimpanzees and human foragers, respectively. We then address the implications of these patterns for the life history of family formation and reproduction in each species. We conclude by discussing prospects for future research.

Theory: Mating, Parental Investment, and Sex Roles

The evolutionary theories of parental investment and sexual selection provide a framework for understanding the divergent mating systems of chimpanzees and humans. This section describes a theory that integrates classic and recent models of parental investment and sexual selection (Trivers 1972; Emlen and Oring 1977; Maynard Smith 1977; Grafen and Sibly 1978; Clutton-Brock 1991; Kokko and Johnstone 2002; Kokko and Jennions 2008) applied to the case of these two species. This theory—synthesized in Hooper et al. (2014)—suggests that the evolution of sex roles in mating and parenting depend on (1) the returns to providing different forms of investment in offspring, (2) the shape of the trade-offs between these investments and mating effort, and (3) the dynamics of best response to the behavior of the opposite sex.

According to the theory, reproductive-age animals face a decision between investing in conceived offspring versus pursuing new opportunities for fertilization and conception. Investments in offspring come principally in the form of energy (i.e., metabolic resources, food) or care (protection from harm, direct attention to needs). Selection acts on the amount of energy and care delivered by parents, given that increased investment in care will tend to reduce investments in energy (and vice versa), and that both of these investments will tend to deplete resources available for seeking future reproductive opportunities.

When providing care trades off harshly with producing energy—when carrying infants while foraging, for example, increases risks of mortality or greatly reduces returns—or when there are increasing returns to specialization in the production of energy or care, a single parent cannot efficiently provide the mix of both energy and care necessary for offspring success. Under these conditions, two parents that specialize and combine their inputs may be able to achieve a level of offspring fitness more than double that of a single parent balancing both roles (Hooper et al. 2014). This multiplicative advantage of joint provisioning can provide an important motive for males to remain with mates and offspring, rather than deserting them in favor of the next mating opportunity (Maynard Smith 1977; Kokko and Johnstone 2002). It is likely that these advantages, combined with extraordinarily high need of offspring concomitant with the slow human life history, are fundamental

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factors motivating cooperative biparental investment in human foragers, as discussed below.

There are a number of conditions under which the fitness generated by two contributing parents is unlikely to be greater than twice that generated by one parent serving both roles. When optimal diets are more permissive of simultaneous infant care and foraging, when young can be safely hidden away during foraging, or when there are diminishing returns to specialization in energy or care, one sex (usually the male) is likely to face greater gains from a resumption of mating effort than continued parental investment. Generally, the greater the substitutability (rather than complementarity) of female and male inputs, the more likely is the outcome of desertion by one sex and uniparental care by the other (Kokko and Johnstone 2002; Hooper et al. 2014).

Among mammals, maternal commitments to lactation, typically low paternity certainty, and few gains from specialization make females most often responsible for the full cost of investment in offspring (Clutton-Brock 1989). Given that the vast majority (>95 percent) of the chimpanzee diet consists of foods that can be collected or extracted with a clinging infant or accompanying juvenile (Kaplan et al. 2000; Watts et al. 2012; Carmody, this volume), trade-offs between the efficiency of foraging and care are relatively weak. These conditions are likely to underlie the observed *Pan* equilibrium of female-only investment in offspring, and relatively undifferentiated patterns of foraging behavior between the sexes.

In contrast to other primates, hunted foods play a critical role in human diets, accounting for an average of about 60 percent of calories consumed (Kaplan et al. 2000). Hunting has two important characteristics that are critical for understanding human pair-bonds and male parental investment. First, it is largely incompatible with childcare (except under special circumstances; Gurven and Hill 2009). Second, it provides protein and lipids, and thus may provide more valuable calories than plant foods (Hill 1988). For both reasons, hunting increases the marginal value of male inputs to both women and children, which we propose is a prime driver in shifting the human mating system away from the standard mammalian pattern.

In this theory, the returns to renewed mating effort bind the equilibrium level and duration of parental investment for each sex. All else being equal, paternal investment will tend to decline as opportunities for further mating increase (Blurton Jones et al. 2000; Schacht and Bergerhoff Mulder 2015). In

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general, male parental investment tends to decrease when the costs of mate search are low (e.g., when females are spatially clustered), or when the ratio of females to males in the mating pool is high (Clutton-Brock 1991; Kokko and Jennions 2008). In the human case, where pair-bonds form and males invest, the extent of monogamy versus polygyny is affected by the degree of inequality in male resources, and the extent to which the value of male inputs diminishes with division between multiple wives and offspring (Borgerhoff Mulder 1992). Among foragers, both food sharing and the inability to accumulate durable resources tend to reduce inequality in resources among males, leading to more monogamous mating systems (Marlowe 2005; Kaplan et al. 2009; Kelly 2013; Hooper et al. 2014; Jaeggi et al. 2016).

Paternal investment is predicted to decrease as females place relatively greater value on a male's genetic quality than on offered parental investment during mate choice. Factors affecting the marginal benefits derived from additional male parental investment (such as the compatibility of offspring care with food production) are likely to affect both the direct fitness benefits of male investment, as well as female choice criteria regarding the relative weight of investment offers versus genetic quality. These two effects should mutually reinforce each other. When male parental investment is relatively less important, on the other hand, the result may be promiscuity (as in *Pan*) or polygynous mating without significant male parental investment (as in most nonhuman primates, with the exception of callitrichids).

It is relevant to note that male coercion may limit the scope of female choice, particularly among chimpanzees (Muller et al. 2011; Muller, this volume). This phenomenon probably reinforces the effect of a care-compatible optimal diet on the outcome of uncooperative sex roles in chimpanzees. The scope for female choice may be greater where coalitions can be formed against aggressive males, as in bonobos (Furuichi 2011; Hare et al. 2012; Jaeggi et al. 2016). In the case of humans, the scope for female choice is highly variable. A lack of direct female control over partner choice and marriage is clearly manifest in some human societies, particularly those relying on defensible, durable, and inherited resources (Boone 1986; Borgerhoff Mulder 1992). Among contemporary foragers, the evidence discussed below shows that females exert considerable choice in mating decisions for their own benefit (Draper 1975; Marlowe 2004; Pillsworth 2008; Gurven et al. 2009), with the important exception of rape, which occurs at apparently low levels ubiquitously (Burbank 1992; Marlowe 2010; Muller, this volume).

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Two additional considerations have important implications for the theory of mating effort and parental investment in chimpanzees and humans. First, there is evidence in both species that male support for females or their offspring can be motivated in part by mating effort (Anderson et al. 1999; Kaburu and Newton-Fisher 2015). Second, there has been considerable debate in the literature on humans over whether the production and sharing of food by men are motivated by payoffs to parental investment per se, or increased access to fertility through signaling or trade (Hawkes and Bliege Bird 2002; Gurven and Hill 2009, 2010; Hawkes et al. 2010, 2014; Wood and Marlowe 2013, 2014). The empirical data on contemporary chimpanzees and human foragers are discussed in light of these theoretical considerations in the following two sections.

Chimpanzees

Despite highly dimorphic reproductive behavior, there are typically small differences between chimpanzee females and males in diet and foraging behavior. As in most species in which female reproduction is limited by access to food and males are larger than females, female chimpanzees are expected to consume relatively more high-quality foods—ripe fruit, insects, and nuts, rather than lower-quality leaves and unripe fruit—compared to males (Gaulin 1979; Sailer et al. 1985). Because chimpanzee males more frequently participate in hunts and have greater access to and control over carcasses, however, male chimpanzees tend to eat greater quantities of meat (0–3 percent of total diet) (Teleki 1973; Boesch and Boesch-Achermann 1989; Tennie et al. 2008; Wood and Gilby, this volume). Dimorphism in diet could also be affected by tendencies for females to occupy and defend core areas, and for males to range more widely across the breadth of territories (Williams et al. 2002; Emery Thompson et al. 2007; Murray et al. 2007).

The reproductive roles of female and male chimpanzees are strikingly different. Females bear the full cost of reproduction and parental investment after fertilization, including gestation, lactation, carrying, care, food transfers (mostly passive), and maintaining access to core feeding areas (Emery Thompson et al. 2007, 2012; Murray et al. 2007; Jaeggi and van Schaik 2011). Male chimpanzees cooperate to defend territories capable of supporting the reproduction of multiple females (Wilson et al. 2014) and compete for access

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to estrous females within linear dominance hierarchies (Wroblewski et al. 2009).

The promiscuous mating system of chimpanzees yields diffuse expectations of paternity certainty across males in a group (Chapais, this volume). Females actively seek matings with multiple males and advertise their fertility through sexual swellings (Stumpf and Boesch 2006). While this may have a protective effect against infanticide, it also produces minimal inclusive fitness motivation for parental investment by males. Thus, there is little evidence of direct paternal investment in terms of direct care or food provisioning, with the potential exception of males adopting orphaned offspring (Boesch et al. 2010).

The cooperation of chimpanzee males in the defense of territory against other groups can be considered a form of blanket protection to females and their offspring, particularly if territorial takeovers entail a threat of direct attacks or infanticide (Watts et al. 2002; Mitani et al. 2010; Wilson et al. 2014). Individual males may also sometimes protect females from others' aggression within communities. Recently immigrated females may preferentially associate with adult males in order to be protected against the aggression of resident females (Kahlenberg et al. 2008), which can also lead to infanticide (Townsend et al. 2007).

Within chimpanzee communities, rates of association and affiliative interactions (e.g., grooming) are greatest within male-male dyads—who rely on alliances with each other for rank and territorial defense—followed by female-male dyads, then female-female dyads (Watts 1998, 2002; Stumpf and Boesch 2006; Machanda et al. 2013). There is evidence that this pattern changes when female choice is more pronounced—for example, when female-female coalitions protect against male coercion, as in bonobos (White and Wood 2007; Tokuyama and Furuichi 2016).

Adult female-male associations in chimpanzees sometimes reflect kinship, principally between mothers and sons (Pusey 1983). Mother-son bonds in adulthood are especially important in bonobos, where male-male bonds are weak or absent; here, males rely on maternal support for acceptance by dominant females, and for access to high rank, resources, and mating opportunities (Surbeck et al. 2011). Given dominant patterns of male philopatry and female dispersal, however, there are relatively few opportunities for female and male relatives (other than mother and offspring) to interact or even fully recognize each other as kin (Wroblewski 2010; Chapais this volume).

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Female-male interactions are shaped in large part by the dynamics of the mating system. There is some evidence that preferred—older, parous, higher-ranking, and/or estrous—females receive higher rates of affiliative behavior from males (e.g., association and spatial proximity: Muller et al. 2006; Machanda et al. 2013; grooming: Kaburu and Newton-Fisher 2015; meat sharing: Gomes and Boesch 2009; Wood and Gilby this volume). Ironically, preferred females also experience higher rates of aggression from males as a form of mate guarding, particularly during estrus (Muller et al. 2007, 2011).

There is evidence for pair-specific heterogeneity in frequencies of copulation, paternity, and interaction within groups, which may be motivated by preferences of one or both individuals (Newton-Fisher et al. 2010; Gomes and Boesch 2011), or which may simply arise as a by-product of other factors, such as overlapping spatial patterns (Langergraber et al. 2013; Machanda et al. 2013). Male chimpanzees sometimes attempt to draw or coerce estrous females away from other males for periods of “consortship” (Watts 1998; Wroblewski et al. 2009), yet there is no evidence that particular dyads form consortships more than expected by chance. Several males may cooperate to consort with females and exclude other males (Watts 1998), a pattern also observed in dolphins (Connor et al. 2001).

There are important differences across sites and across time in the form and intensity of male-female relationships in chimpanzees and bonobos (Langergraber et al. 2013). For instance, levels of female sociality (i.e., time associating with others, mating activity, and frequency and duration of sexual swellings) increase with food availability and decrease with feeding competition (van Schaik 1989; Chapman et al. 1994; Hohmann and Fruth 2002; Mitani et al. 2002; Stumpf 2007). With greater food availability, females can afford to be more sexually active—increasing the ratio of receptive females to males—and more sociable, which broadens the scope for forming long-term bonds and alliances with both females and males (Stumpf 2007; Jaeggi et al. 2016). Thus, the ratio of males to females with maximal sexual swellings ranges from two to three among bonobos and Tai chimpanzees, to twelve at Gombe (Stumpf 2007). The percentage of time that females spend away from other adults averages 30 percent across chimpanzees, but varies considerably across site: females at Tai, for example, average only 4 percent, while bonobos average 2–3 percent (Stumpf 2007). By reducing male-male competition over estrous females and increasing female social capital, greater food availability thus increases the potential for female choice and may even

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lead to dominance over males, as in bonobos (Stumpf and Boesch 2006; White and Wood 2007; Hare et al. 2012; Jaeggi et al. 2016).

Humans

Patterns of cooperation between the sexes in human societies stand in stark contrast to those of *Pan*. The sexual division of labor is a ubiquitous and well-documented feature of all traditional human societies (Murdock and Provoost 1973). There is an extensive division of labor by sex—illustrated in Figure 15.1 for the Tsimané—including not only direct childcare and energy production, but also food processing, collecting firewood and cooking, construction of housing, and manufacture of tools (Marlowe 2007). The behavior of females and males reflects complementary adjustments to the investments of the opposite sex and the needs of offspring. This allows each sex to intensively learn the skills necessary for one role, and disregard the skills of the other (Kaplan et al. 2001).

Compatibility of labor with simultaneous childcare is an important predictor of women’s activities (Minge-Klevana 1980; Hurtado et al. 1985, 1992).

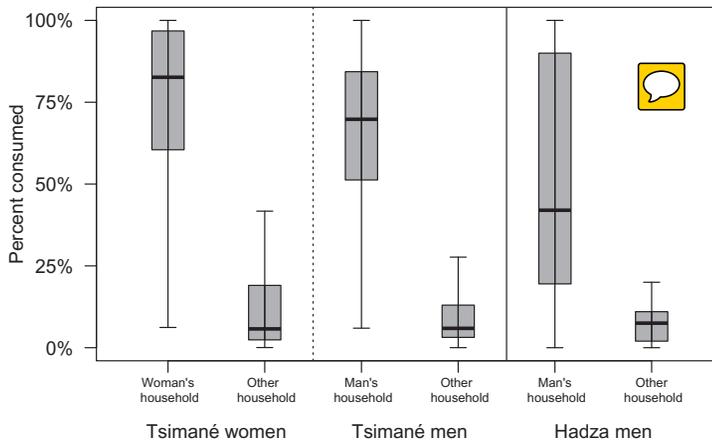


FIGURE 15.1. The sexual division of productive labor among Tsimané women (dark gray) and men (light gray). The horizontal axis denotes percent of time in each activity devoted by women versus men. Values are derived from 11,971 spot observations (adapted from Gurven et al. 2009).

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Among the Aché who did not maintain permanent camps with safe places for children, women spent more than 90 percent of daytime hours in tactile contact with children under age three (Hurtado et al. 1985). Even in safer environments where cleared spaces are maintained, as among the Tsimané, children are actively cared for by their mothers 30 percent of their waking hours (Winking et al. 2009). While mothers are the predominant caregivers in apparently all forager societies, fathers also engage in some direct care, though there is significant variation in direct paternal care across groups: Aka fathers provide around 22 percent of the care received by young children as measured by time investment, while !Kung, Hadza, Efe, Agta, and Tsimané fathers provide 1.9–7 percent (Griffin and Griffin 1992; Hewlett 1992; Marlowe 1999; Hewlett and Macfarlan 2002; Winking et al. 2009).

The weight of evidence suggests substantial economic contributions to familial and offspring well-being from both mothers and fathers. Across a sample of ten foraging societies, females produce a mean of 32 percent of all calories and 12 percent of all protein, while males produce 68 percent of all calories and 88 percent of all protein (Kaplan et al. 2000). There are no foraging societies reported in which men are not important providers of animal protein and lipids (Kaplan et al. 2000; Marlowe 2005; Kelly 2013). While there is a consistent specialization of females and males in complementary forms of production, there is also considerable variability across foragers depending on conditions. Hunting by women, for example, has been well described for the Aka and Agta, where hunting methods (nets among the Aka; bows, arrows, and dogs among the Agta) were less incompatible with pregnancy and childcare, small and medium game were relatively abundant near camps, and (among the Agta) there were considerable gains from trading meat for carbohydrates (Goodman et al. 1985; Noss and Hewlett 2001; Gurven and Hill 2009).

Among the Tsimané, mothers, grandmothers, fathers, and grandfathers all contribute substantial net transfers of food to dependent young. Fathers' rate of net provisioning to children is roughly twice that of mothers, while grandfathers give around 25 percent more to grandchildren than do grandmothers (Hooper et al. 2015). The importance of offspring need in motivating Tsimané women and men's work effort is illustrated in Table 15.1: women produce 310 additional calories through horticulture per day for each child over three, while men produce 240 additional calories through hunting for each additional child. As shown in Figure 15.2, 65–75 percent of Tsimané par-

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TABLE 15.1. Tsimané economic production as a function of dependent offspring (multilevel regression with community-level random effects).

Predictor	Hours per Day			Calories per Day		
	<i>B</i>	β	<i>p</i>	<i>B</i>	β	<i>P</i>
A. Women’s horticultural effort and productivity (n = 253)						
(Intercept)	-0.116	-0.061	0.746	-171.1	-0.134	0.965
Age	0.070	1.030	0.010	117.4	0.326	0.446
Age ²	-0.001	-0.665	0.078	-0.2	-0.037	0.935
Offspring 0–2	-0.180	-0.175	0.004	-828.3	-0.153	0.017
Offspring 3–19	0.043	0.130	0.087	313.7	0.182	0.033
B. Men’s hunting effort and productivity (n = 281)						
(Intercept)	-0.060	0.228	0.798	-1,205.8	0.196	0.206
Age	0.054	0.657	0.020	162.3	0.770	0.019
Age ²	-0.001	-0.407	0.148	-2.4	-0.664	0.039
Offspring 0–19	0.065	0.204	0.002	240.5	0.295	<0.001

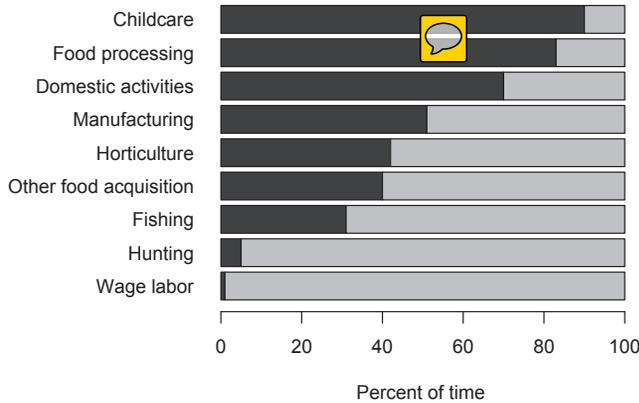


FIGURE 15.2. Estimated percent of food consumed by members of an adult producer’s household versus members of other households, for Tsimané women and men and Hadza men. The values received by other households represent the mean received by households that ever received food from the producer (for the Tsimané) or that resided in the same camp (for the Hadza). Tsimané values reflect sums over 93 (± 40 SD) days from 371 women and 490 men (Hooper et al. 2015), while Hadza values reflect 98 distribution events from 44 men (adapted from figure 5 in Wood and Marlowe 2013).

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ents' production is consumed within the nuclear family. Among the Hadza, who share food more widely, men's families consume around 40 percent of the food they produce (Wood and Marlowe 2013).

Consistent with an emphasis on providing direct care with the economic support of husbands and other kin, female foragers significantly decrease time spent foraging with the presence of young children. Among the Aché and Hiwi, nursing women show significant reductions in production rates and time allocated to production (Hurtado et al. 1985, 1992). Hadza mothers with nursing infants likewise show reduced foraging effort and productivity, while married men and fathers are significantly more productive than unmarried and childless men (Marlowe 2003, 2010; Wood and Marlowe 2013). Table 15.1 shows that Tsimané women produce roughly 830 fewer calories per day for each child under three. Shuar women who are pregnant or lactating show reduced physical activity, while their husbands are relatively more active (Madimenos et al. 2011). The ability of female foragers to decrease their burden of work during lactation pays off in survival and fertility; among other primates, in contrast, lactation is often the most vulnerable part of the adult life course, because females must work to support the nutritional needs of both themselves and their nursling (Lancaster and Kaplan 2009).

A number of accounts have emphasized the role of male-male competition, mate guarding, and infanticide avoidance in the origins of human pair-bonds (Blurton Jones et al. 2000; Hawkes and Bliege Bird 2002; Coxworth et al. 2015); these factors have also been associated with variation in pair-bonding in other primates and mammals (van Schaik and Kappeler 1997; Palombit 1999; Lukas and Clutton-Brock 2013; Opie et al. 2013). Chapais has proposed that polygynous—but basically uncooperative—pair-bonds may have been present as a result of these factors in hominins preceding *Homo*, with implications for paternity certainty and alliance formation (Chapais 2008, this volume). Muller and Pilbeam (this volume) discuss the evidence bearing on whether polygynous pair-bonds (as in gorillas) or promiscuity (as in chimpanzees) were characteristic of the common ancestor of *Pan* and *Homo*.

Despite generally high levels of paternal investment in human foragers compared to other mammals, cases of desertion, infidelity, and disinvestment by men are also clearly common (Winking et al. 2007; Marlowe 2010; Stieglitz et al. 2012, 2014). Disinvestment becomes more likely where there are relatively low costs and high potential benefits to extrapair mating effort, and mothers and other kin can more easily compensate for the loss of

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men's contributions. The data show that dissolution of pair-bonds and spousal abuse are most frequent early in marriages, and that marriages tend to be quite stable once more than two children are born to the same parents (Early and Headland 1998; Kaplan et al. 2001, 2010; Marlowe 2010; Stieglitz et al. 2011).

While there is some evidence of motivations for men to produce and provision women or their offspring to secure mating opportunities, either within or outside current pair-bonds (Anderson et al. 1999; Smith et al. 2003), mating effort alone appears insufficient to account for the magnitude of fathers' contributions to their families as described for contemporary foragers and forager-horticulturalists (Hewlett and Macfarlan 2002; Hill and Hurtado 2009; Howell 2010; Wood and Marlowe 2013; Hooper et al. 2015). As such, the pattern of cooperative pair-bonding and biparental care observed in humans is probably best understood in light of returns to biparental investment. Ultimately, the origins of cooperative pair-bonds in humans may have more in common with birds than with other primates and mammals.

Further Implications for the Biodemography of *Homo* and *Pan*

Complementarities between female and male parental roles structure patterns of pair-bonding, marriage, and reproduction in human foraging societies. In a cross-cultural sample of 145 foraging groups, the modal percentage of monogamous marriages is 96–100 percent, and in the majority of societies, fewer than 10 percent of marriages are polygynous (Binford 2001). As a result, female and male reproductive schedules tend to be closely linked: age-specific fertility and expected future fertility for women and men are similar in shape, with the male curves shifted three to five years to the right (i.e., higher ages) and having a slightly longer tail (Tuljapurkar et al. 2007). The demographic linkage between female and male foragers is also manifest in the tendency for males to cease reproducing when their wives reach menopause. Among the Tsimané and Aché, only 10 percent and 17 percent of men reproduce again after their wife (or first wife) reaches menopause, respectively (Hill and Hurtado 1996; Kaplan et al. 2010).

Because chimpanzees and bonobos lack cooperative pair-bonds, the life histories of reproduction are likely to be substantially more dimorphic compared to human foragers. Chimpanzees—like most mammals with vanishing

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levels of paternal investment and high male reproductive skew—perpetuate and endure high levels of male-male competition, which can lead to later onset and earlier termination of reproduction and higher mortality among males compared to females—males live faster and die younger (Clutton-Brock 1991; van Noordwijk and van Schaik 2004; Clutton-Brock and Isvaran 2007). In bonobos, too, males have substantially lower life expectancy than females, at least in captivity (Jeroen Stevens, personal communication), which seems to point to a similarly dimorphic life history.

The importance of alliances for achieving rank in chimpanzees may somewhat reduce this effect compared to species with more solitary forms of competition, as older, politically connected males can continue to enjoy reproductive success (de Waal 1982; Duffy et al. 2007; Wroblewski et al. 2009). While published data on age-specific fertility and mortality rates in wild chimpanzees are still sparse, these predictions can soon be tested given a growing number of studies on genetic paternity (Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010).

In Chapter 10, Chapais describes the role of human pair-bonding in expanding the scope of cooperative alliances through both affinal and consanguineous kinship. As Chapais indicates, while the chimpanzee pattern of migration at puberty halves the potential extent of one's kin network, human marriage doubles it. Indeed, data from contemporary foragers and forager-horticulturalists indicate that cooperative pair-bonds provide a nucleus for networks of support across extended families. These families show patterns of investment in offspring by nonparents across three generations—grandparents, uncles, aunts, and siblings (Gurven et al. 2000; Hooper et al. 2015)—which have been described as a system of cooperative breeding (Kramer 2005; Sear and Mace 2008; Hill and Hurtado 2009; Hrdy 2009). The support that mothers and offspring receive from spouses, parents, and other members of the extended family described above likely underlies the relatively shorter interbirth intervals and higher fertility of humans compared to other great apes (Hrdy 2009; Isler and van Schaik 2012a, 2012b).

Conclusion

We have an increasingly clear picture of the modal equilibrium pattern of behavioral and biodemographic characteristics in human foragers and wild

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chimpanzees. The coevolutionary sequence that gave rise to these modal patterns, on the other hand, remains more difficult to illuminate (Foley and Gamble 2009).

We suggest that knowledge of shifting natural environments can provide an anchor for theorizing social and behavioral change among the great apes from the Miocene to the present. Given the time scales involved, and the expected transience of unstable constellations of traits, models will improve by specifying the conditions that support the evolutionary stability of the equilibrium distribution of traits and behaviors in each step of the historical sequence. The ecological factors emphasized here are the returns from extracted, scavenged, and hunted food, and the returns to economic and reproductive specialization between the sexes.

The paleoanthropological and archaeological signatures of the variables highlighted in this chapter include evidence of subsistence technology and practices (Wrangham 2009; Ferraro et al. 2013; Estalrich and Rosas 2015; Roach and Richmond 2015), diet (Balter et al. 2012; Wood and Gilby, this volume; Carmody et al. this volume), sexual dimorphism (Plavcan 2012), brain size (Holloway et al. 2004), and developmental rates (Bermúdez de Castro et al. 2010; Zollikofer and Ponce de León 2010). Current evidence is generally consistent with (in that it does not refute) the mainstream view that cooperative pair-bonding and the sexual division of labor arose with the genus *Homo* ca. 2–3 Ma (Lovejoy 2009). Evidence of meat eating and uncertainty surrounding the extent of sexual dimorphism in *Australopithecus*, however, may push these possibilities farther back in time (McPherron et al. 2010); contradictory developmental evidence, however, could push them later, toward the origin of modern *Homo sapiens* (Ramirez Rozzi and Bermudez de Castro 2004; Dean 2006; Ruff and Burgess 2015). In this context, it might be useful to consider a gradual evolution of meat-eating in hominins (Thompson et al. in revision), starting with chimpanzee-like opportunistic hunting of small game, the consumption of bone marrow using percussive technology (at which females excel: Boesch and Boesch 1981) once chimpanzee-like cognition increasingly encountered animal bones left by carnivores in more open habitats, to habitual scavenging, cooperative hunting with spears, and eventually solitary hunting with projectile weapons; the first stages of this sequence would already have provided females and their infants with better nutrition, allowing the evolution of larger brains, but only the latter stages would have required a sexual division of labor. New

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empirical methods combined with the development of explicit, testable theoretical models will provide greater certainty regarding the natural histories of the mating systems and linked life histories of *Pan* and *Homo* in coming years.

Endnotes

1. The term forager is used to refer to “pure” foragers (i.e., people subsisting almost entirely from hunting and gathering, such as the Aché, Hadza, or !Kung). Forager-horticulturalists (such as the Shuar or Tsimané) may derive the bulk of their calories from cultivated foods, but share with contemporary foragers a reliance on hunting or fishing for animal protein and fats, communal property rights, and relatively egalitarian, small-scale sociopolitical organization.

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