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The evolution of early hominin food production and sharing

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How did humans evolve from individualistic to collective foraging with sex differences in production and widespread sharing of plant and animal foods? While current evolutionary scenarios focus on meat, cooking, or grandparental subsidies, considerations of the economics of foraging for extracted plant foods (e.g., roots, tubers), inferred to be important for early hominins (∼6 to 2.5 mya), suggest that early hominins shared such foods with offspring and others. Here, we present a conceptual and mathematical model of early hominin food production and sharing, prior to the emergence of frequent hunting, cooking, and increased lifespan. We hypothesize that extracted plant foods were vulnerable to theft, and that male mate guarding protected females from food theft. We identify conditions favoring extractive foraging and food sharing across mating systems (i.e., monogamy, polygyny, promiscuity), and we assess which system maximizes female fitness with changes in the profitability of extractive foraging. Females extract foods and share them with males only when: i) extracting rather than collecting plant foods pays off energetically; and ii) males guard females. Males extract foods when they are sufficiently high in value, but share with females only under promiscuous mating and/or no mate guarding. These results suggest that if early hominins had mating systems with pair-bonds (monogamous or polygynous), then food sharing by adult females with unrelated adult males occurred before hunting, cooking, and extensive grandparenting. Such cooperation may have enabled early hominins to expand into more open, seasonal habitats, and provided a foundation for the subsequent evolution of human life histories.

food sharing | human evolution | extractive foraging | cooperation | pair-bonds

Significance

Human foragers share food extensively. Influential scenarios for the evolution of hominin food sharing focus on hunting, scavenging, cooking, or grandparental subsidies. However, evidence that the diets of early hominins such as *Australopithecus* included nutrient-dense extracted foods, long before reliance on meat, fire, or increased lifespan, suggests the possibility that early hominins shared extracted foods. Here, we present a conceptual and mathematical model of the evolution of food production and sharing in early hominins, across diverse mating systems. Male mate guarding protects females from food theft, promoting extractive foraging by females. This increased foraging efficiency motivates females to share food with males when pair-bonds exist. Female provisioning of males may have catalyzed the evolution of uniquely hominin traits.

Human hunting and gathering is a collective strategy involving sex differences in production and exceptional cooperation (1–3). This subsistence pattern is likely a cause and consequence of unique human life history traits (2, 4–6). Among contemporary foragers, hunting and fishing—mainly by men—provide a majority of the calories consumed (5, 7). Much attention has thus focused on the evolution of food sharing by males (4, 8, 9). But extracting, preparing, and sharing plant foods—which among contemporary foragers are performed mainly by women—also constitute key economic strategies that differ strikingly from those observed in other primates (10–14). Forager diets at high latitudes consist largely of meat and fish obtained by men [(15), but in warmer climates, where early hominins evolved, women contribute substantially to the diet median 30.5% of calories provided by adults; range: 15.9 to 57.0%, $n = 9$ populations; (16)]. Meat is unlikely to have constituted a large part of the diet for early hominins, such as *Australopithecus*. Early hominins probably lacked sophisticated projectile weapons for hunting (e.g., stone-tipped spears), for which the earliest evidence dates to ∼500,000 ya (17). Recent studies have also challenged long-held views that an increase in meat eating accompanied the origin and subsequent evolution of the genus *Homo* (18).

Early hominin teeth and jaws appear adapted not for eating meat, but instead for processing plant foods (19, 20). Studies of dental morphology, paleoecology, and stable isotope signatures suggest that the underground storage organs (USOs) of plants (e.g., roots, tubers, corms, bulbs, rhizomes) were important foods for early hominins (14, 21–24). Modern foragers use simple tools (e.g., digging sticks) to obtain deeply buried USOs (22). Such digging is a form of extractive foraging, i.e., obtaining foods embedded in substrates. Other extracted foods important for contemporary foragers and likely accessible to early hominins include hard-shelled nuts that can be smashed open with stones (11). Compared to nonhuman primates, humans engage in an exceptional degree of extractive foraging and active sharing of extracted foods (25). Given that extracted foods are inferred to have been important components of early hominin diets (26), and are shared by contemporary foragers, here, we examine how reliance on these foods may have promoted food sharing in early hominins.

Extracting foods provided competitive advantages for early hominins, because these foods are abundant in open habitats and effectively hidden and protected from most

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African herbivores (21, 22). Extracted foods can be large and energy-dense, making sharing economically feasible (14). Unlike nonhuman primate females, who collect (e.g., leaves or fruits) rather than extract most foods and rarely share with others besides their own offspring (27), forager women regularly share foods they acquire with nuclear kin and others, e.g., refs. 14, 26, and 28. Sharing with offspring provides direct fitness benefits and requires little additional explanation (29). What remains unclear in current scenarios of early hominin food sharing are the conditions favoring the evolution of sharing between unrelated adults, which we address here. Because extraction and sharing of plant foods is rare among nonhuman primates and produces scant archaeological evidence, we employ mathematical modeling to identify socioecological factors promoting these activities among early hominins, and perhaps even their ape ancestors.

Efforts to explain the origin of hominin plant food sharing focus on surplus production by grandmothers (14, 30) and cooking, particularly by females (13). Grandmothers can increase their fitness by provisioning descendants (31). Such investments by postreproductive females have been argued to play a major role in the evolution of human life histories, perhaps by the time of *Homo erectus* (14). However, the timing of the increase in human longevity remains unknown (5). In any case, women extract and share plant foods throughout adulthood. Diets proposed for early hominins (∼6 mya) include foods that potentially promoted sharing among adults, even if these hominins resembled other nonhuman primates in having few females that experience postreproductive senescence (32).

Cooking likely impacted human evolution profoundly (13, 33), but hominins probably relied on extracted plant foods long before controlling fire (22). We thus consider the possibility that sharing of extracted plant foods originated in hominins before meat and cooking predominated hominin diets.

Conceptual Model. Findings from paleoclimatology, paleoanthropology, primatology, and human behavioral ecology provide a motivating framework for our model (Fig. 1). Key factors explaining the evolution of extractive foraging and sharing of plant foods are categorized broadly as ecological and social (toward the *Left* and *Right* of Fig. 1, respectively).

Ecological change. The ape ancestors of hominins likely lived in forests and consumed mostly easy-to-acquire, collected plant foods requiring little extrasomatic processing, similar to present-day *Pan* and *Gorilla* (34). Starting in the late Miocene, the African climate became cooler and drier (Fig. 1*A*), which by the Pliocene resulted in the gradual retreat of forests and expansion of open woodlands and grasslands [Fig. 1*B* (35)]. In these more open habitats, the leaves and fruits that forest-dwelling apes relied upon became seasonally scarce. Studies of hominin dental morphology and stable isotope signatures, and of modern nonhuman primates and human hunter-gatherers suggest that early hominins increasingly relied on hidden and/or protected foods including USOs, nuts, and fruits with hard shells, such as baobabs, Fig. 1*C* (11, 15, 22, 34).

While baboons (*Papio* spp.) and other monkeys adapting to open habitats retained quadrupedal posture and locomotion, early hominins evolved bipedality (Fig. 1*D*), perhaps for feeding on the small trees and shrubs that predominate in open habits (36), for wading to obtain protein-rich aquatic foods (37, 38), or other reasons. Evolution of more effective bipedality increased hominins' ability to travel between widely dispersed food sources (39–41) and freed the hands to use more complex tools and more efficiently carry food (42).

In more open habitats, lower abundance of fruits and leaves and greater abundance of hidden, protected plant foods increased the relative value of extractive foraging (Fig. 1*E*). Accessing hidden, protected foods is an important primate adaptation for surviving in open habitats. For example, yellow baboons (*Papio cynocephalus*) in savannas spend roughly 30% of their feeding time using their hands to dig corms of grasses and sedges (43). Tools such as sticks and stones are needed to access more deeply buried USOs and hard-shelled fruits and nuts. Some chimpanzees (*Pan troglodytes*) use stones to crack nuts (44) and sticks to dig for USOs (45). Chimpanzees extract food much less often than humans, but their capacity to do so suggests that early hominins

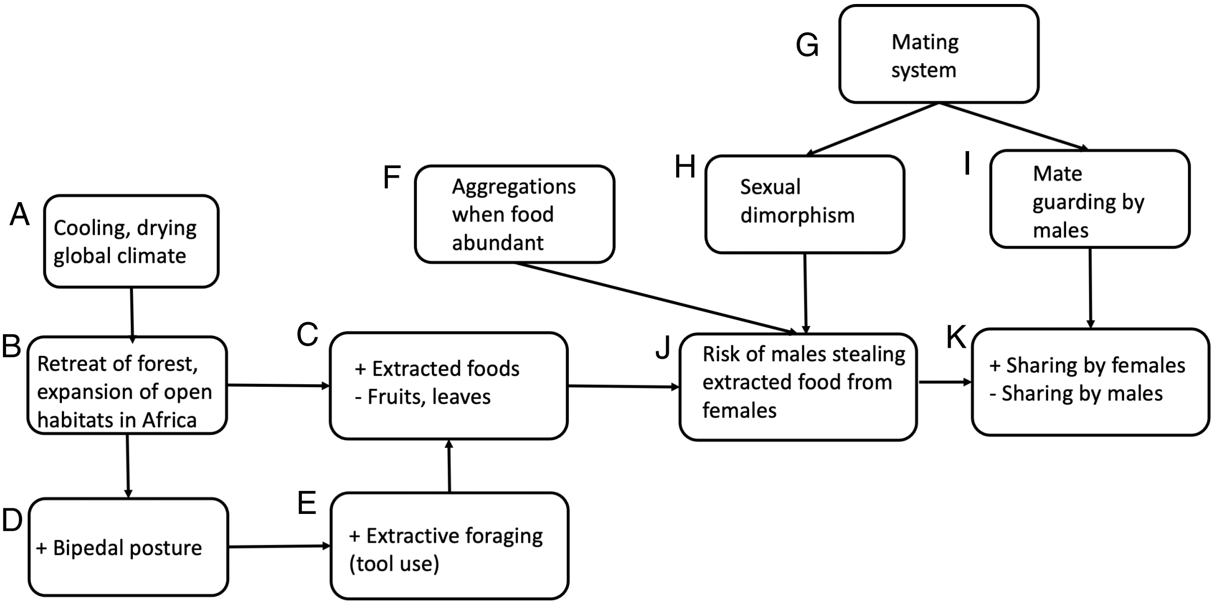

Fig. 1. Conceptual framework for the origins of extractive foraging and food sharing by hominins. For descriptions of each component of the framework (*A*–*K*) see the main text.

also used such tools, particularly when other preferred foods were scarce, starting them down a path toward more extensive food extraction and reliance on culturally transmitted knowledge, e.g., ref. 46.

Mating system. Extractive foraging for plant foods likely emerged early in hominin evolution, but under what conditions hominins may have shared these foods is unknown. Like chimpanzees and bonobos (*Pan paniscus*), early hominin mothers likely shared more difficult-to-acquire foods with their offspring (10, 12, 29). When cracking nuts, female chimpanzees share nut meat with their young offspring (47). When and why hominins evolved to share plant foods with nonkin, including mates, remains largely unexplored. Food sharing among modern foragers regularly occurs within the context of pair-bonds (usually monogamous), sex differences in food production, exchange between sexual partners, and dietary reliance on plant and animal foods, e.g., refs. 48 and 49. Several efforts to explain the origins of hominin food sharing have thus focused on the context of mating relationships, as a means by which males either invest in offspring in exchange for paternity certainty (8), or by which both sexes provide complementary resources in a reciprocal fashion to maximize the pair's economic efficiency and fitness (2, 9, 16). An opposing view argues that males hunt and share meat to increase extrapair mating opportunities by broadcasting signals of phenotypic quality (50, 51). These scenarios often propose simultaneous changes in mating system and food sharing, mediated either by male provisioning of mates and offspring (2, 5, 8), group-wide signaling of male quality (50), or cooking by females (13). However, evolutionary sequences consisting of a sequential series of small changes are more likely to occur than simultaneous, large changes in multiple traits (52, 53). We thus explore a sequence of events that does not require simultaneous evolutionary changes of both mating system and sharing behaviors.

Mating systems of early hominins and their ape ancestors are unknown (54); *Discussion*. Nonhuman apes today exhibit one of three systems: Gibbons and siamangs are mostly monogamous; gorillas are mostly polygynous, and the rest are promiscuous (55). In our model, we explore each of these three mating systems, which can affect food production and sharing in multiple ways, including the risk of food theft, and the benefits that male presence bestows on females.

Food theft. If the mating system favors male investment in contest competition, as typically occur in promiscuous and polygynous systems, e.g., ref. 56, males can evolve to be much larger than females (54). Such body size sexual dimorphism enables males to take food from females with impunity (Fig. 1 *H* and *J*), as occurs in chimpanzees (57) and hamadryas baboons (*Papio hamadryas*) (58). Given evidence of substantial body size sexual dimorphism for many hominin species, Wrangham et al. (13) proposed that when hominins began cooking (∼1 to 2 mya), females established pair-bonds with specific males to prevent other males from stealing what they cooked. But long before hominins began cooking, the extracted plant foods upon which they relied were vulnerable to theft, as is observed among modern nonhuman primates.

We consider "theft" to include food transfers resulting from a range of behaviors, including supplanting individuals at feeding sites, harassment, cofeeding, and taking scraps. Harassment, which can promote food transfers by imposing costs on the possessor, is expected to pay off when foods are larger, divisible, and difficult to monopolize (59). Compared to collected foods, extracted plant foods face greater vulnerability to theft for three reasons: i) they have higher energy density, making the payoff for theft higher; ii) when contained in larger packages, they can be more easily divided, thus making them more vulnerable to scrounging; and iii) because they take time and effort to extract, there are more opportunities to steal the labor undertaken to acquire them. For example, among olive (*Papio anubis*) and yellow baboons, higher-ranking individuals commonly supplant lower-ranking individuals when feeding on the pea-sized corms of grasses and sedges, which are buried just below the surface (60, 61). Modern African hunter-gatherers acquire more deeply buried USOs that, compared to corms, are bigger, contain more energy, and take longer to acquire (15, 22). These characteristics may have made such foods even more vulnerable to supplanting, scrounging, and other forms of theft (Fig. 1*J*). Risk of theft would depend not only on whether a given food item is extracted or collected but also on the degree of body size sexual dimorphism (Fig. 1 *H* and *J*) and the extent to which individuals aggregated at feeding sites (Fig. 1*F*), with larger aggregations increasing risk.

Male presence. The nature and magnitude of benefits that early hominin females would receive from male presence are expected to differ across mating systems. The presence of long-term pair-bonds determines whether a female can expect to benefit from one vs. several males. First, as Wrangham et al. (13) propose for cooking, food theft risk reduces incentives for females to produce surpluses from extractive foraging, including for offspring (Fig. 1*J*). But if males guard females from mating attempts by rival males, as occurs widely in primates (62), then guarding males also would thwart potential food thieves and enhance female willingness and ability to extract plant foods (Fig. 1 *I* and *K*). Benefits females accrue from mate guarding should be greater in species with pair-bonds (monogamous or polygynous), where males guard females throughout their reproductive cycle, instead of guarding females only when they are receptive to mating (63, 64). Second, in addition to facilitating female extractive foraging, mate-guarding males can also provide benefits to females through support in intergroup conflict (65–67), territorial competition (68, 69), and protection from predators (70) and infanticide (71, 72), Fig. 1*I*). When mate guarding, males may suffer costs because they cannot simultaneously forage at maximum efficiency and fend off rival males. In both baboons (73) and chimpanzees (74), mate-guarding males suffer reduced foraging efficiency.

Mathematical Model

Our model addresses how the relative value of extracted foods and risk of food theft affect the evolution of food production and sharing in three possible early hominin mating systems, prior to the emergence of frequent grandparental subsidies, scavenging, hunting, and cooking. We model a population in which genetically unrelated males and females in each generation interact in groups with N males and N females each. In each sex, there are two evolving traits: foraging behavior and food sharing with the opposite sex. Evolution occurs on two distinct time scales. On the time scale of an individual's lifespan, foraging strategies are individually learned and an optimal foraging strategy is learned quickly enough for the learning period to be ignored in the analysis. On a longer time scale, food-sharing strategies are transmitted vertically across generations (either biologically or culturally), and we identify evolutionarily stable sharing strategies.

There is a mating system in place, which does not evolve. We compare optimal foraging and evolutionarily stable sharing strategies in promiscuous (i.e., pair-bonding is absent), monogamous (i.e., each male has one pair-bonded mate), and polygynous (i.e., some males have $k \geq 2$ pair-bonded mates while others have none) systems. To ensure transparent comparisons across mating systems, the foraging technology and the risk of food theft are modeled identically across them. While these assumptions would certainly warrant closer examination in future research, this approach allows us to study in detail the effects of the following two key differences between promiscuous and nonpromiscuous mating systems.

First, across systems, female reproductive success (RS) is an increasing function of both own energy intake and the intake of some male(s), since male presence protects her offspring from dangers such as predators and infanticidal males. This complementarity between male and female energy levels is the driving force behind the benefits from sharing. The fundamental difference between promiscuous and nonpromiscuous systems is that, in the former, the females do not benefit from presence of a specific male, while in the latter they do.

Second, in the two systems with pair-bonding, males guard their (pair-bonded) female(s) continuously, in all reproductive states as in hamadryas baboons and gelada monkeys (*Theropithecus gelada*), (64), rather than just when females are sexually receptive, as in olive and yellow baboons and chimpanzees. Efficient mate guarding requires attention, which reduces the amount of time that a male can spend on extractive foraging. Continuous mate guarding drives the results for two distinct reasons: 1) Mate guarded females are somewhat protected from food theft, thus enhancing their return from extractive foraging; and 2) mate guarding limits a male's time budget available for foraging, thus driving a pair-bonded female to share food with her paired male.

Our model includes traits presumed to have resulted from sexual selection—particularly body size sexual dimorphism, and mate guarding—but rules out sexual selection as a driver of the evolving traits, not because we believe that it is irrelevant, but because this approach enables us to study the nontrivial trade-offs that appear absent of sexual selection.

Foraging Behavior. Each female divides her foraging time budget of 1 (this is net of time spent on mating, sleeping, etc.) between collecting easily accessible foods of lower nutritional value F (i.e., leaves and fruits) and extracting more-difficult-to-acquire foods of higher nutritional value H (e.g., nuts and tubers). A female who spends $a \in [0, 1]$ on extracting and $1 - a$ on collecting, and who lives in a group where males spend time g on mate guarding, acquires total energy:

$$x = x(a, g) = (1 - a)^{1/2}F + a\left[1 - (1 - g)\theta\right]H. \qquad \textbf{[1]}$$

The first term is the total energy of collected foods acquired by spending time $1 - a$ on this activity; the square root of $1 - a$ captures the decreasing marginal returns to time spent on this activity, (e.g., the more time the female spends consuming leaves in a given location, the farther she will have to travel to collect even more leaves). The second term is the total energy of extracted foods the female acquires by spending the share a of her time on this activity. The parameter $\theta \in [0, 1]$ is the share of extracted foods that males other than her pair-bonded mate attempt to steal; this food theft intensity is a nonevolving parameter. The food theft risk is, however, reduced by the indirect protection provided by her pair-bonded mate's guarding, captured by the term $(1-g)$ that multiplies θ; the food theft risk is fully eliminated when the male uses the maximal amount of mate guarding $g = 1$. By being close to the female while she forages, a mate guarding male protects her from food theft by other males. The returns to extracting are constant to reflect the idea that once an individual starts extractive foraging (e.g., digging for tubers), either there are food items to be found or not, i.e., a can be interpreted as the probability of finding extracted foods.

Each male also decides how much time to devote to extracting or collecting. From his time budget of 1, he spends g on mate guarding, θ on food theft (if there is extracted food to be stolen from females), and b on extracting, thus generating the following total energy from foraging:

$$y = y(b, g) = (1 - \delta_a\theta - g - b)^{1/2}F + bH, \qquad \textbf{[2]}$$

where $\delta_a = 1$ if there is some extracted food to be stolen from females, and $\delta_a = 0$ otherwise. Both sexes are equally efficient at collecting and extractive foraging, and they have the same total time budget net of activities not considered in the model. However, males have less time for foraging than females due to mate guarding and/or food theft, and females are subject to food theft while males are not.

We will write a_g^* and b_g^* for the optimal foraging strategy for females and males, respectively, and $x_g^* \equiv x(a_g^*, g)$ and $y_g^* \equiv y(b_g^*, g)$ for the total amounts of energy evaluated at these optimal strategies.

Food Sharing and Reproductive Success. A female gives the share $s \in [0, 1]$ of her extracted and collected food (that remains following food theft) to some male(s). Likewise, a male gives the share $t \in [0, 1]$ of his extracted and collected food to some female(s). Together with the collecting and extracting behaviors, food theft by males and food sharing by both sexes determine the total amount of energy available in the group and how this energy is distributed among adults. Transfers from mothers to offspring are not modeled explicitly; instead, we assume that part of a female's energy is transferred to her offspring, either through milk or solid food.

Both food theft by males and food sharing by females entail a redistribution of energy from females to males; a key difference is that food sharing occurs only if it is beneficial for females, while food theft harms females. We will see that females sometimes have an interest in sharing food above and beyond the energy that males obtain by stealing food.

The promiscuous mating system [i.e., no pair-bonds]. Because males guard females only when females are sexually receptive (if at all), males provide negligible protection for female foraging efforts ($g = 0$). An adult has no favored partner, so we posit that if a female shares, she gives the same amount to all the N males in her group, and if a male shares he gives the same amount to all the N females in his group. After food transfers occur—both through theft and sharing—the net amount of energy a focal female who shares $\hat{s}$ of her food x_0^* has at her disposal in a group where there is one focal male who shares $\hat{t}$ and $N - 1$ males who share t of their food y_0^*, is:

$$\hat{X}(\hat{s}, \hat{t}; t) = (1 - \hat{s})x_0^* + \left(\frac{\hat{t}}{N} + \frac{(N-1)t}{N}\right)y_0^*. \qquad \textbf{[3]}$$

Similarly, the total amount of energy of a focal male who shares $\hat{t}$ of his food y_0^* in a group where one focal female shares $\hat{s}$ and $N - 1$ resident females share s of their food x_0^*, is:

$$\hat{Y}(\hat{t}, \hat{s}; s) = (1 - \hat{t})y_0^* + \left(\frac{\hat{s}}{N} + \frac{(N-1)s}{N}\right)x_0^* + \theta a^* H. \qquad \textbf{[4]}$$

The last term is energy obtained through stealing a share $\theta \in [0, 1]$ of the food extracted by one female, a^*H.

Each female transmits her sharing trait faithfully to all her female offspring, except for the rare case in which a genetic mutation (or a cultural innovation) arises spontaneously. Assuming that the sex ratio is balanced at birth and independent of the mother's sharing behavior, a female's RS equals (half of) the expected number of her offspring that survive to sexual maturity. Taking the number of offspring to depend on the female's own energy, and the survival probability to depend also on male presence, and hence on their energy, in a population where resident females share s and resident males share t, the RS of a mutant female who shares $\hat{s}$ takes the following form (we omit the factor 1/2, which is irrelevant for the results, since it does not affect the sign of the gradient):

$$\hat{w}(\hat{s}, s; t) = \hat{X}(\hat{s}, t; t) \cdot pN \cdot \hat{Y}(t, \hat{s}; s). \qquad [5]$$

The first term is the female's energy. The last term is the average male's energy in the group, and $p \in [\frac{1}{N}, 1]$ measures how much the female benefits from services provided by the group's males, such as protection against predators and infanticidal males. For example, $p = 1/N$ means that she may expect one male to protect her, should her offspring be attacked by predators or infanticidal males; at the other extreme, if $p = 1$, she benefits from the services of all males in the group.

Turning now to males, they are identical in all respects (except for their propensity to share), and sharing is not a sexually selected trait. Moreover, a male does not preferentially interact with the female he mates with. Accordingly, it is natural to assume that each male transmits his sharing trait to a share $1/N$ of the N females' male offspring. Hence, a focal mutant male, who shares $\hat{t}$ in a population where females share s and resident males share t, achieves RS (again, we omit the factor 1/2 that would account for the fact that a male transmits his trait to his male offspring only):

$$\hat{v}(\hat{t}, t; s) = \frac{1}{N} \cdot N \cdot \hat{X}(s, \hat{t}; t) \cdot p \left[\hat{Y}(\hat{t}, s; s) + (N-1)\hat{Y}(t, s; s) \right]. \qquad [6]$$

Monogamous and polygynous (i.e., pair-bonded) mating systems. In a polygynous system some males (exactly N/k of them) are each pair-bonded with a fixed number of k females each, while the remaining males are mateless. Monogamy is the special case where $k = 1$ and no males are mateless. Of the energy x_g^* that remains for a female upon her optimal foraging and the food theft accomplished by males other than her pair-bonded male, she shares only with her pair-bonded mate (if at all). Likewise, of the energy y_g^* that a male has upon his optimal foraging, he shares only with his pair-bonded females (if at all). The total amount of energy that a focal female who shares $\hat{s}$ has at her disposal, given that her pair-bonded male spends time g mate guarding and shares $\hat{t}$ equally among his k pair-bonded females, thus equals:

$$\hat{X}(\hat{s}, \hat{t}) = (1 - \hat{s})x_g^* + \frac{\hat{t}y_g^*}{k}. \qquad [7]$$

The total energy that a focal male who shares $\hat{t}$ has at his disposal, given that a focal female in his group shares $\hat{s}$ while his other pair-bonded females share s, equals:

$$\hat{Y}(\hat{t}, \hat{s}; s) = (1 - \hat{t})y_g^* + [(k-1)s + \hat{s}]\, x_g^* + \frac{N-k}{N-1}(1-g)\theta a_g^* H, \qquad [8]$$

where we assume that the extracted food that gets stolen from the females who are not his pair-bonded females, $(N-k)(1-g)\theta a_g^* H$, is shared equally between him and the other $N-2$ males who steal from these females.

In a population where resident females share s and resident males share t, the RS of a mutant female who shares $\hat{s}$ takes the following form (again we omit the factor 1/2):

$$\hat{w}(\hat{s}, s; t) = \hat{X}(\hat{s}, t) \cdot q\hat{Y}(t, \hat{s}; s). \qquad [9]$$

In contrast to the promiscuous system, here, the female only receives male services of protection from predators and infanticidal males from her pair-bonded male. The parameter $q \in [\frac{1}{k}, 1]$ measures how much she benefits from these services. For example, $q = 1/k$ means that she may expect her male to be able to protect only one of his pair-bonded females when the group is attacked by predators; at the other extreme, if $q = 1$, the male can protect them all.

Turning now to a focal mutant male, his RS depends on the polygyny rate k in the following manner (again we omit the factor 1/2):

$$\hat{v}(\hat{t}, t; s) = [1 - \phi(1-g)]kq\hat{X}(s, \hat{t})\hat{Y}(\hat{t}, s, s) + \phi(1-g)\frac{N/k - 1}{N-1}kq\hat{X}(s, t)\hat{Y}(t, s, s). \qquad [10]$$

ϕ is the share of her copulatory acts that a female concedes to extrapair matings. The first (respectively second) term is the number of offspring of the focal male's pair-bonded (respectively nonpair-bonded) females for which he is the biological father. The second term is independent of the focal male's sharing strategy, however, for a male shares only with his pair-bonded females, and females concede extrapair matings without regard to the males' sharing strategies (since we rule out sexual selection as a driving force; *SI Appendix*, Remark 1).

Evolutionary Stability. In order to find the evolutionarily stable pair of food-sharing strategies (s^*, t^*), we assume that genetic mutations (or cultural innovations) in s and t are rare enough for there never to be more than three types in the population: the resident female type adopting strategy s, the resident male type adopting strategy t, and either some mutant female type adopting strategy $\hat{s}$ or some mutant male type adopting strategy $\hat{t}$. Hence, at an evolutionarily stable pair of sharing strategies (s^*, t^*), a mutant female's RS is maximized for s^*, given that all females share according to s^* and all other males according to t^*, and a mutant male's RS is maximized for t^*, given that all other females share according to s^* and all males according to t^*:

$$\begin{cases} s^* \in \arg\max_{\hat{s} \in [0,1]} \hat{w}(\hat{s}, s^*; t^*) \\ t^* \in \arg\max_{\hat{t} \in [0,1]} \hat{v}(\hat{t}, t^*; s^*). \end{cases} \qquad [11]$$

It turns out that this system of equations is also sufficient for (s^*, t^*) to be evolutionarily stable, for in our model $\hat{w}$ and $\hat{v}$ are both strictly concave functions (*SI Appendix*, Lemmas 1 and 2).

Results

Pair-Bonds Depress Male but Promote Female Extractive Foraging. The amount of time that males and females spend acquiring different foods depends on 1) the relative value of extracted vs. collected foods (H/F); 2) risk of food theft (θ); and 3) whether males mate guard (g). Fig. 2 shows, for three different values of g, the optimal extractive foraging time for

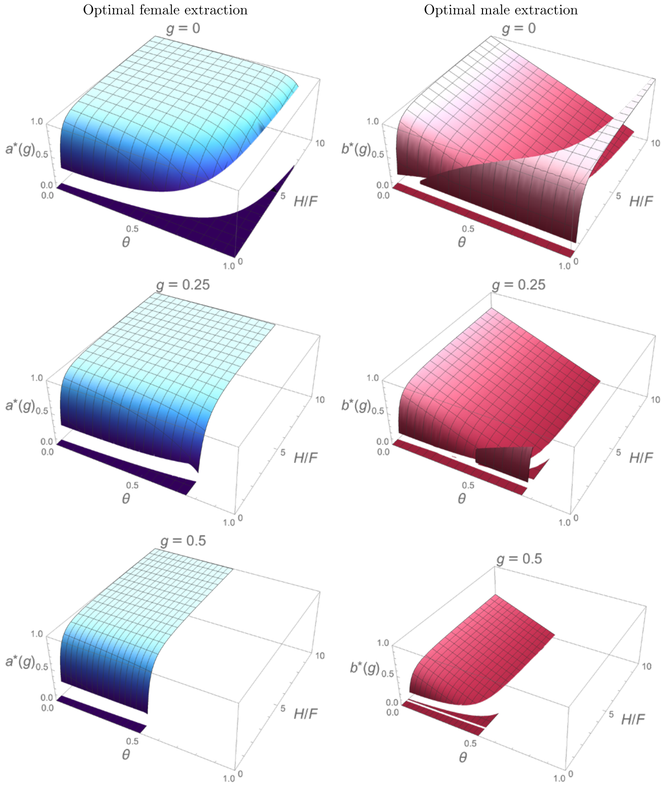

Fig. 2. Optimal strategies of extractive foraging by sex. The *Left* (respectively *Right*) column of figures shows, for three different values of mate guarding, g (from *Top* to *Bottom*, $g = 0, g = 0.25$, and $g = 0.5$), the optimal amount of time that females $a^*(g)$ respectively males ($b^*(g)$) spend on extractive foraging, as a function of food theft, θ, and the relative energetic profitability of extracted vs. collected foods, H/F. Parameter regions shown in white are irrelevant, due to the time budget constraint $\theta + g + b^*(g) \leq 1$.

each sex, as a function of H/F and θ. As might be expected, both sexes engage in extractive foraging only when the value of extracted foods sufficiently exceeds that of collected foods. However, a high ratio H/F is not sufficient for extractive foraging to occur. First, females reduce extractive foraging time as risk of food theft increases, particularly at lower values of H/F and in the promiscuous system where they are not indirectly protected from food theft by a mate guarding male ($g = 0$). In nonpromiscuous systems, where $g > 0$, females are somewhat protected from food theft by other males thanks to the mate guarding by their pair-bonded male, which induces higher levels of female extractive foraging. Second, food theft and mate guarding are time-consuming activities that reduce extractive foraging time for males. The exception to this rule appears in the promiscuous system ($g = 0$) when the food theft risk θ is so high that females do not extract. Then, males heavily engage in extractive foraging once H/F is large enough (*SI Appendix*, Propositions 6 and 8).

Pair-Bonds Depress Food Sharing by Males but Promote Food Sharing by Females. In the promiscuous system females do not share food with males for any parameter values (Fig. 3; *SI Appendix*, Proposition 7). A female has an incentive to share only if the cost of giving up her own energy intake is outweighed by the benefit obtained from strengthening the services of protection (from predators and infanticidal males) and resource defense she gets from the males. Because she cannot count on a specific male to provide these services, she shares with all the males if she shares at all. The average benefit she obtains from male services is thus always smaller than the cost associated with the loss of energy she incurs by sharing. In a sense, the services provided by the males are a public good for the females, and the lack of sharing by females is akin to underprovision of this public good.

Now, since males do not spend substantial time mate guarding in a promiscuous system, and because they steal food from females whenever females engage in extractive foraging, the males typically end up with at least as much energy as females. Hence, in the promiscuous system, it is instead males that share food with females, as long as the relative value of extracted foods (H/F) is not too low.

In contrast, when pair-bonds exist females share food with males under a broad range of conditions including varying H/F values (Fig. 4 and *SI Appendix*, Propositions 5, 9, and 10). Two factors explain this. First, the benefit from giving up own energy intake in order to strengthen the services provided by males is not diluted among N males, as in the promiscuous system. In both monogamous and polygynous systems, the female concentrates her sharing on her pair-bonded male, whose presence she can fully count on. Second, since the male spends time g on mate guarding, a female acquires more energy than the male, and the complementarity between her energy and that of her pair-bonded male then leads her to share.

To highlight the role played by mate guarding, in Fig. 4 we include the outcome in the hypothetical case that monogamous males would not guard their pair-bonded female(s) ($g = 0$). Comparing this with the case with mate guarding ($g = 0.25$), we see that females rarely share food if males do not mate guard. A noticeable difference between polygynous and monogamous systems is that under monogamy, energy flows from the male to his pair-bonded female for some parameter values even when he engages in mate guarding. This is true when food theft intensity

	No extraction	Only ♂ extract	Only ♀ extract	♀ and ♂ extract
No sharing	🟦	🟦	🟦	⬜
Only ♀ share	🟥	🟧	🟥	⬜
Only ♂ share	🟩	🟩	🟨	⬜

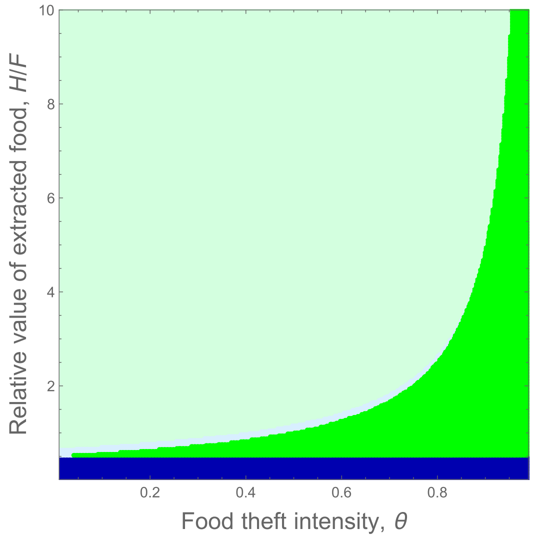

Fig. 3. Sex differences in food production and sharing in the promiscuous mating system. The plotted regions correspond to the combinations of three possible types of evolutionarily stable sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend.

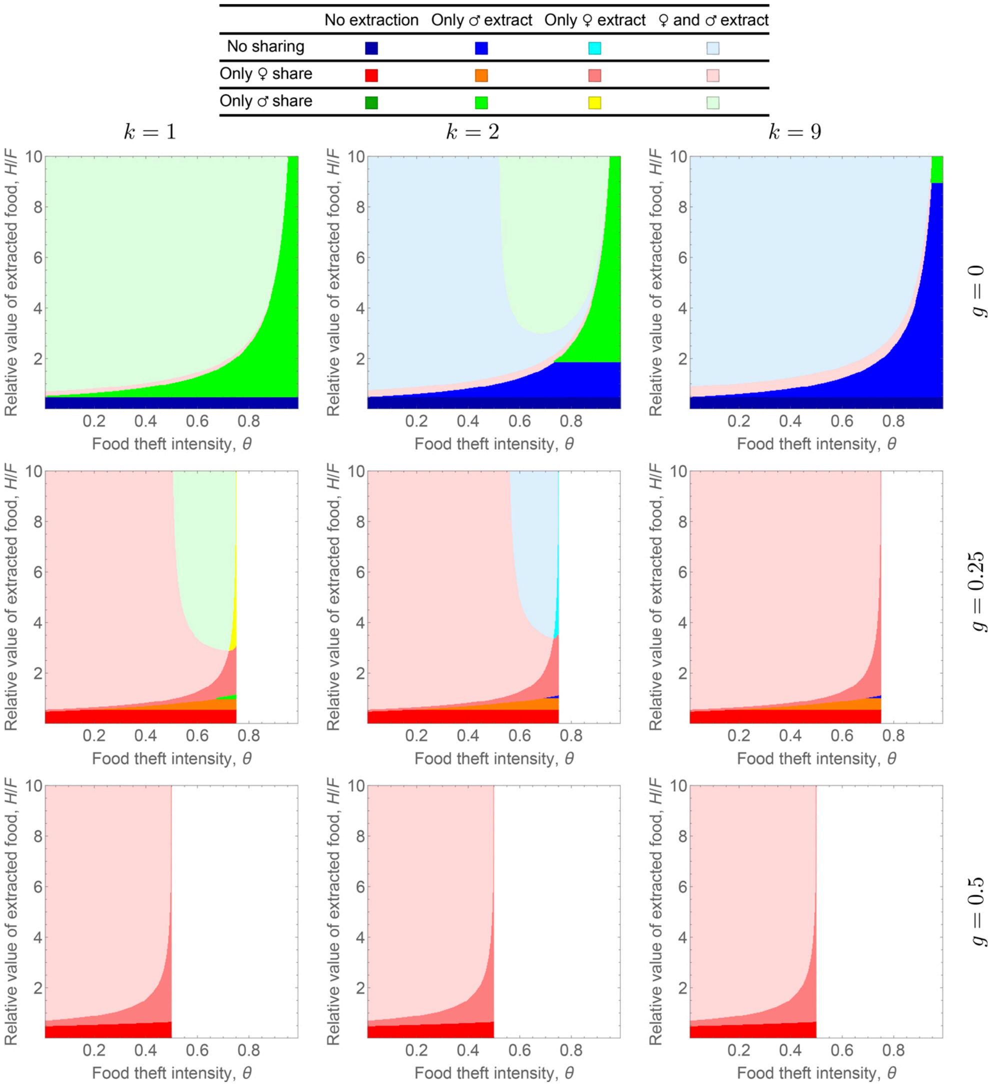

Fig. 4. Sex differences in food production and sharing in monogamous and polygynous mating systems. The plotted regions correspond to the combinations of the three possible types of evolutionarily stable sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend. Note that the combination "No extraction" and "Only males share" does not arise for any parameter values. $N = 18$.

(θ) is high enough for him to accumulate excess energy compared to his pair-bonded female.

Sex Differences in Food Production and Sharing by Females Occur Only When Pair-Bonds Exist. Female investment in extractive foraging and female food sharing with males tend to go hand in hand. This suggests a possible rationale for this combination of sex differences in food production and sharing. For a complete lack of male extractive foraging to arise, the relative energetic value of extracted vs. collected foods, H/F, must be large enough but not too large, and the food theft intensity, θ, should be sufficiently large (Cases A2 and C3 in *SI Appendix*, Proposition 8 and Fig. 4). These two conditions compel females to extract food, as long as the indirect protection from food theft that mate guarding entails is sufficiently pronounced (i.e., g is large enough), while males are kept busy by mate guarding and food theft. The little time that remains from a male's time budget is not worth investing in extractive foraging since extracted foods are not sufficiently rewarding (this is why H/F cannot be too large for the complete lack of male extractive foraging to arise). The same conditions favor female-only sharing because the amount of food obtained by a female via extractive foraging is larger than the amount of food collected and stolen by males (*SI Appendix*, section C.3); thus, females have a surplus that can be shared with their pair-bonded male. This tendency is more general, however: 1) the combination of female investment in extractive foraging and female food sharing arises only in a nonpromiscuous system, since females never share in the promiscuous one; and 2) female investment in extractive foraging is more pronounced in the nonpromiscuous systems, due to the time that males invest in mate guarding in these systems (Fig. 1).

Ecological and Social Factors Affect Fitness Advantages Conferred by Sex Differences in Food Production and Sharing. We now assess how a change in the energetic value of extracted vs. collected foods (H/F), which presumably increased starting in the late Miocene (Fig. 1 *A*–*E*), influences the relative efficiency of promiscuous and nonpromiscuous mating systems; by "efficiency," we mean the average female RS obtained for a given amount of time spent foraging.

Thus, Fig. 5 compares variation in female RS given optimal foraging and evolutionarily stable sharing strategies under the

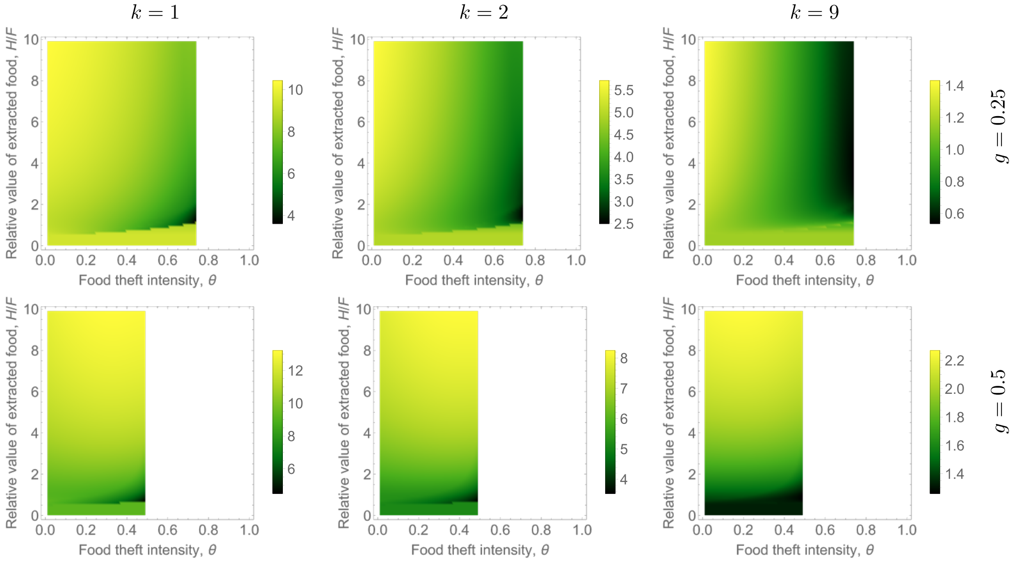

Fig. 5. Comparison of reproductive success between promiscuous vs. monogamous (*Leftmost* column) and polygynous mating systems (*Middle* and *Rightmost* columns). Shading represents the ratio of the reproductive success per unit of adult time spent foraging evaluated at the evolutionarily stable state in either monogamous or polygynous systems (numerator) over the fitness per unit of adult time spent foraging in the promiscuous system (denominator), i.e., $\frac{\hat{w}(s^*, s^*; t^*)/(2 - \delta\theta - g)}{\hat{w}_P(s_P^*, s_P^*; t_P^*)/(1 + N(1 - \delta\theta))}$, where the index P indicates the promiscuous system, for $\hat{w}_P(s_P^*, s_P^*; t_P^*)$, Eq. **5** and the absence of index indicates the polygynous or monogamous systems for $\hat{w}(s^*, s^*; t^*)$, Eq. **9**; we used the values $p = 1/N$ and $q = 1$ so that each female gets services (protection from predators and infanticidal males) provided by one male in each system. The shading scale is panel-dependent; see the panel-specific legend to the *Right* of each panel. $N = 18$.

promiscuous ($g = 0$) vs. monogamous and polygynous systems with mate guarding. Group size N and food theft intensity θ are assumed to be identical in the three systems. To obtain a meaningful comparison, we evaluate female RS per unit of adult time spent foraging. In the promiscuous system, each offspring in each group of $2N$ adults benefits from the foraging time budget of its mother plus that of the N males Eq. **5**. Hence, we divide female RS by $1 + N(1 - \delta\theta)$. In the nonpromiscuous systems, each offspring in each unit of one male and k females benefits from the foraging time budget of its mother plus that of the male Eq. **9**. Hence, we divide female RS by $2 - \delta\theta - g$. Finally, for a meaningful comparison we further assume that each female can benefit from male services (i.e., protection from predators and infanticidal males) provided by one male, by setting $p = 1/N$ in the promiscuous system and $q = 1$ in the nonpromiscuous systems.

We highlight two findings in Fig. 5. First, an increase in the relative energetic value of extracted vs. collected foods (H/F) generally has a nonmonotonic effect on the advantage that pair-bonds (*cum* mate guarding) confer on female RS compared to the promiscuous system. As H/F reaches values triggering extractive foraging (i.e., for values of H/F slightly below 1; Fig. 2), there is first a reduction in the fitness advantage of the nonpromiscuous system over the promiscuous one. However, as H/F increases further, the fitness advantage of the nonpromiscuous system over the promiscuous one increases. For high enough values of H/F, this fitness advantage becomes even more pronounced than for values of H/F where no extractive foraging occurs. The only exception to this rule appears when food theft intensity θ is high and mate guarding is low, $g = 0.25$.

Second, thanks to its effect on extraction and sharing, a higher level of mate guarding g in the nonpromiscuous system enhances its fitness advantage over the promiscuous system (the ratio is higher in the *Bottom* than in the *Top* row of Fig. 5), which is particularly evident when comparing the fitness advantage for the highest values of H/F with those for which no extractive foraging occurs.

Discussion

Our model identifies a range of conditions promoting extractive foraging (Fig. 2) and food sharing (Figs. 3 and 4) by unrelated early hominin adult males and females. Both sexes extract foods when this yields higher returns than collecting foods such as fruits and leaves. When risk of food theft is moderately high, males devote little time to extraction, because they instead steal food from females. When risk of food theft is extremely high, females stop extracting foods but males begin extracting, because females no longer produce anything to steal.

Hominin mating systems profoundly affect food sharing strategies. Under promiscuous mating, males share with females under a broad range of conditions, but females do not share with males (Fig. 3). With pair-bonds (monogamous or polygynous), food sharing tends to flow from females to their pair-bonded males (Fig. 4). Pair-bonded males rarely share with females, except when they spend little time mate guarding, (e.g., Fig. 4, $g = 0$, $k = 1$), or when the value of extracted foods is extremely high, (e.g., Fig. 4, $g = 0.25$, $k = 1$, $\theta > 0.5$). The overall pattern of results differs greatly between systems with vs. without pair-bonds, but differs little as the number of females per male (k) increases from 1 to 9.

Hominin females share with their pair-bonded males even when no theft occurs ($\theta = 0$), provided males invest in mate-guarding. Compare, for example, the rows corresponding to $g = 0.25$ and $g = 0$ in Fig. 4. Why would females share with males if there is no risk of theft? Males provide other benefits to females, including protection from infanticide and predators, but in providing these benefits, they pay costs of mate-guarding. Females then gain fitness benefits by giving some food to males to offset their mate-guarding costs.

These results suggest that sharing between unrelated adults may have emerged early in hominin evolution, before scavenging, hunting, or cooking became important for subsistence, and may thus have ancient roots. These results also differ from existing scenarios in which sharing by males and females emerges simultaneously, when males began hunting as (5) seem to imply. Our model shows that hominin females could benefit from sharing food with males, even if males shared no food with them.

In our model, hominin females do not share under promiscuous mating, but only when pair-bonds already exist. This contrasts with the proposal that pair-bonds emerged as a consequence of food sharing by females (13). We did not attempt to model a transition from promiscuity to pair-bonds. However, because each step in an evolutionary sequence should provide fitness benefits, our results suggest that pair-bonds would need to exist before adult females would be willing to share food with unrelated adult males.

We find, under a broad range of conditions, that with profitable extractive foraging, hominin females have higher fitness with pair-bonds than promiscuity (Fig. 5). This advantage is higher as the relative value of extractive foraging increases. This suggests that if pair-bonds existed in early hominins, the presence of mate-guarding males protected extractive foraging by females, thus enabling them to persist in habitats that were becoming increasingly unsuitable for other apes, and even to occupy landscapes not previously used by apes.

The next sections highlight empirical evidence from paleoanthropology and primatology relevant to our model's assumptions, results, and predictions, as well as suggestions for future research, and discuss our model in relation to other scenarios explaining the origins of hominin food sharing.

Evidence from Paleoanthropology and Primatology. Our model predicts that extractive foraging and sharing of plant foods by females characterized early hominins if the following conditions (Fig. 1) were met: 1) extractive foraging was sufficiently profitable, compared to collecting fruits and leaves (Fig. 1*C*); 2) extractive foragers faced a risk of theft (Fig. 1*J*); 3) sexual pair-bonds existed (Fig. 1*G*); and 4) mate guarding by males protected female foraging efforts, and/or provided sufficient benefits to females to make it worthwhile for females to subsidize males (Fig. 1*H*). We now consider the available evidence for each of these conditions.

Profitability of extractive foraging. There is no modern primate that perfectly captures the variability underlying early hominin feeding strategies, and we currently lack detailed knowledge of early hominin diets. However, as the climate of late Miocene Africa became cooler and drier, fruits and leaves became seasonally scarce in many habitats (75, 76). Seasonal scarcity of such resources is thought to be the main factor limiting distribution of nonhuman apes in Africa today (77). Large, deeply buried tubers are abundant in habitats similar to those reconstructed for early hominins, and likely provided an important source of food during dry seasons, when fruits and leaves were scarce (22, 78). Among modern hunter-gatherers such as the Hadza of Tanzania, meat, honey, and berries are preferred over tubers (78). However, early hominins likely lacked regular access to meat and honey, and berries would be limited in availability during some seasons. Other foods that require extensive processing, such as baobab fruits and mongongo nuts (79), are highly prized by foragers (78, 79). While early hominins surely did not process foods as extensively as modern humans, observations of chimpanzees cracking nuts (80) and evidence of digging for USOs (45) suggest that early hominins also obtained such foods. Agent-based spatial simulation models using parameters from empirical data in East Africa suggest that addition of tubers to Plio-Pleistocene hominin diets (made possible through the use of simple digging sticks) significantly increased the probability that hominins met daily energetic requirements year-round (81). Moreover, nutritional analysis of certain USOs, e.g., rhizomes of *Cyperus papyrus* that are commonly eaten raw by local people in sub-Saharan Africa reveals a higher carbohydrate, fat, and energy content per unit weight (25 g, 0.4 g, and 104 kcals, respectively, per 100 g) than the domesticated potato *Solanum tuberosum* (82). Taken together, it thus seems likely that hominins relied to a considerable extent on extracted foods characterized by variable processing demands, which were more profitable than collected foods under many circumstances, particularly in seasons with few available fruits and leaves. This scenario is consistent with prior proposals stating that the adaptive radiation of early hominins was due in large part to competition over and differential exploitation of fallback foods (83).

Future studies of fossil hominins may provide more details of diet, such as evidence from protein residues and phytoliths. Studies comparing nutrient composition and foraging efficiency for collected vs. extracted foods eaten by African apes and hunter-gatherers would also be informative.

Vulnerability of extracted foods to theft. Whether hominins faced risks of food theft during extractive foraging likely depended on features of specific food items, such as their nutritional quality and whether they could be monopolized. Behavioral observations of nonhuman primates provide useful insights.

In *Pan*, female food acquisition varies depending on risk of theft. Gilby et al. (57) argue that females hunt less frequently in chimpanzees than in bonobos because chimpanzee males outrank females and steal from them with impunity, whereas bonobo females often outrank males and face little risk of food theft. When chimpanzees crack nuts, offspring beg for nut meat from their mothers (47), but other individuals do not attempt to steal nut meat, perhaps because nuts are abundant (Wittig, Personal Communication). Chimpanzee food theft thus mainly consists of males stealing animal products from females.

In baboons, however, competition for extracted plant foods appears to be intense. The rate of supplanting in female olive baboons is an order of magnitude higher for corms vs. other foods (60). Yellow baboons also frequently supplant one another when extracting fever tree gum (43). Baboons that are able to obtain a large bolus of fever tree gum sometimes attract scrap feeders that congregate in a manner "reminiscent of the behavior of animals around a prey carcass" (43).

Early Hominin mating systems. We modeled food production and sharing dynamics in three different mating systems because inferring the mating system of extinct species poses many challenges. Nonetheless, several relevant sources of evidence exist, which on balance suggest that a polygynous mating system is most likely. First, two features of primates that are preserved in the fossil record and correlated with the mating system are sexual dimorphism in body size and canine height. In primates, males are larger and have longer canines than females in polygynous and promiscuous systems with intense male contest competition (54). Fossil evidence shows that in early hominins (84) and in many apes that lived before hominins evolved (85), males were larger than females, to a greater extent than in either modern humans or chimpanzees (86 for an opposing view). If estimates that hominin males were substantially larger than females are correct, this suggests a mating system in which males needed to be large to compete successfully—more like polygynous gorillas than monogamous gibbons or promiscuous chimpanzees (87). In contrast to this evidence of substantial body size sexual dimorphism, canine size differed only moderately between the sexes (54). Some argue that this indicates that monogamy characterized hominins (88). Others, however, have argued that bipedal hominins fought with their hands and perhaps also weapons, rather than their teeth (42), which freed hominins to optimize their teeth and jaws for feeding efficiency (89).

Second, a key indicator of the mating system in extant primates is the presence of swellings of the anogenital skin, which provides a graded signal of fertility and is more common in multimale mating systems (90). Gibbons exhibit small sexual swellings and female gibbons infrequently mate with multiple males (91). The presence of large sexual swellings in chimpanzees and bonobos, but not other apes, suggests that frequent multimale mating and associated sexual swellings are derived features of *Pan*. Parsimony suggests that sexual swellings increased in size in *Pan* in response to a newly evolved multimale mating system (90, 92).

Third, some of the largest genetic changes inferred to have occurred in *Pan* since the divergence of *Pan* and *Homo* are associated with features of male reproduction, including sperm production (87, 93). This suggests that *Pan* underwent major changes in mating behavior. If the last common ancestor of *Pan* and *Homo* had a one-male mating system, then male–female bonds would be an ancestral trait for hominins.

Effects of pair bonds. Our model tests a prediction from ref. 13 that in hominins, alliances between the sexes were a central factor promoting female food production. This previous model proposes that females formed pair-bonds with males to prevent theft of the foods they cooked, whereas in our model, sharing evolves as a consequence of the mating system. If, as noted above, polygyny was an ancestral hominin trait, then pair-bonds may have supported the emergence of extractive foraging and food sharing, rather than evolving due to these behaviors.

In our model, when pair-bonds exist, female fitness depends directly on the male's energy $(\hat{Y}(t, \hat{s}; s))$. This term captures the benefits that females can obtain from male services, including protection from infanticide and predators, and help during intergroup conflict. We assume that those benefits are higher when pair-bonds ensure that a female has a single male committed to her well-being: In populations without pair-bonds, this term is discounted by the number of males in the group. As long as a female's fitness depends directly on the well-being of a particular male, she has strong incentives to invest in him, such as through feeding him. The validity of these assumptions could be tested with studies of living primates, including comparisons of closely related species with and without pair-bonds, such as olive and hamadryas baboons.

The extent to which male mate guarding protects females from food theft is a question that requires further testing in living primates. Males have been proposed to serve as “hired guns” in many primate societies (65, 94, 95), in which male efforts to defend mates from rival males provide protection of food resources as a by-product. For example, female chimpanzees reproduce more quickly when the size of the territory defended by males is larger (68). Swedell (58) notes that female hamadryas baboons, in striking contrast to other baboons, rarely compete over access to food. The presence of leader males in these societies may buffer females from feeding competition from other females. Nonetheless, hamadryas males often displace their mates at food sources (58, 96). Among olive baboons, feeding competition is the most common context of aggression between males and their female “friends” (97). Whether females gain net feeding benefits from associating with males is an open question.

The role of males in improving females' access to specific foods requires further study. Detailed observations of species living in multilevel societies, such as gelada monkeys and hamadryas baboons, in which the sexes form enduring breeding bonds, would be relevant.

Comparison with Existing Evolutionary Scenarios of Human Food Sharing. Our model differs from prior scenarios in its combination of focusing on i) sharing of plant foods rather than meat (cf., refs. 5 and 98); ii) sharing by females rather than males (cf., refs. 4 and 8, 9); iii) sharing by all adult females rather than a focus on grandmothers as donors (cf., refs. 30 and 14), and by unrelated adults; iv) sharing before the invention of cooking (cf., refs. 13); and v) sharing as a consequence of mating system, rather than as a cause of changes in the mating system (cf., ref. 13). We view our findings as complementary to many of these previous scenarios. Insofar as sharing plant foods promoted the evolution of cooperative psychological traits, such as impulse-control and other-mindedness, the sharing of plant foods by early hominins may have promoted the evolution of other traits, such as sharing meat, cooking, and grandparenting.

Some have argued that men share to gain status and increase mating opportunities (50). We do not attempt to model mate choice decisions in the present model, as doing so would complicate the model without altering the key mechanism at work here. Additionally, we do not attempt to model details of individual life-history, such as maternal tradeoffs between current and future reproduction, which have been proposed as critical to the emergence of grandmothering as a hominin strategy (6, 30). Incorporating details of mating decisions and life history traits would be excellent topics for future studies.

Hunting and Meat Sharing. In our model, males share extracted foods only in promiscuous systems. This may seem surprising, given that in modern foragers—which are mostly characterized by monogamy and polygyny—males share extensively with females. However, here, we have not attempted to model large-scale hunting or scavenging. The parameter H could be interpreted to represent meat, but only meat which 1) can be caught by one individual and 2) does not require more time investment than digging. Thus H could represent opportunistic captures of prey, such as occurs when baboons catch hares and antelope fawns, or even products extracted from animal carcasses, such as bone marrow or brains (99). Indeed, in our model, promiscuous mating results in a similar pattern to what is observed for hunting and meat sharing in chimpanzees: Males hunt and share meat with females, whereas females rarely hunt, because they risk having their prey stolen by males (57). However, H does not capture kills that would require extensive coordination and/or engage in hunting “outings” that might end up being fruitless.

Our model explores the hypothesis that female plant food extraction and sharing evolved before males began hunting in a coordinated manner. Our model is thus complementary to existing models focusing on male hunting and meat sharing, which began to reliably occur later in hominin evolution. The model presented here does not contradict that of Alger et al. (9), who propose a model of the evolution of paternal provisioning at a later stage of hominin evolution, when collective hunting by males would already have been in place.

Early hominins likely did not have the complex technology (e.g., spears) often needed to kill large game. Moreover, in modern humans, the sexes often forage separately. Early hominins presumably lacked language, and thus lacked sociolinguistic means to monitor mating behavior. Before the evolution of language, separate foraging by the sexes would impose severe trade-offs between hunting and mate guarding, and therefore seems incompatible with maintaining pair-bonds.

Another key difference between our model and the embodied capital model (5) is that, in our model, degrees of dietary reliance on and sharing of extracted foods are decoupled from cognitive capacities. We show that as the relative profitability of extractive foraging increases (due to exogenous ecological changes), females have higher fitness in mating systems with pair-bonds than under promiscuity (Fig. 5). This suggests that if pair-bonds existed in early hominins or their ape ancestors, increased female foraging efficiency caused by male mate guarding enabled early hominins to occupy environments not previously used by other apes, and/or persist in habitats that were becoming increasingly unsuitable for other apes. This habitat expansion is not dependent on having larger brains, and our findings accord with existing fossil evidence indicating that early hominins occupied diverse habitats long before observed increases in hominin cranial capacity.

Surplus Production. A question arising from our study is, if female fitness generally depends on male energy, and if females benefit to a greater extent when pair-bonded with a particular male—then why don't females more often share food with males? As noted in a review of food sharing in primates (27), "Sharing from females to males was too rare to test." The answer may be that primates rarely produce surplus food efficiently, and that extractive foraging may provide a means to produce surpluses at low marginal costs. Indirect evidence that chimpanzees sometimes dig 3 to 25 cm for USOs (45) suggests that early hominins, with more human-like manual dexterity (100), would be able to dig deeper, e.g., 25 to 50 cm deep among Hadza (101), producing surplus food routinely, much as hunter-gatherers do today (14). With effective skills, obtaining a USO large enough to share with others may require little more effort than digging a smaller one.

Primates accessing food stored by humans provide informative anecdotes of what happens to sociality upon discovery of methods for acquiring nutrient-dense foods. At Gombe National Park, many baboons have learned to open doors of park and research staff by turning door handles, and thereby gain access to food stored in their houses. In response, people began locking their doors, but leaving the key in the lock, because risk of theft by humans in this small community is low. One female baboon, Harina, learned to unlock doors by turning the key. She was then followed by males who took advantage of her door-opening skills (MLW, personal observation).

Looking beyond primates, in lions (*Panthera leo*), group hunting permits large prey capture. Females share food with males which are 40% larger than females (102), and benefit from male services, such as territory defense and protection from infanticide (103), and so benefit from investing in males, much as we propose for hominins.

Conclusions

We propose that food sharing occurred between unrelated adults in early hominin populations prior to reliance on grandparental subsidies, and before meat and cooked foods predominated the diet. If early hominins had pair-bonds, either monogamous or polygynous, females would have gained fitness benefits from sharing with their pair-bonded males, provided they had access to food surpluses. In this case, the invention of digging sticks and other simple tools provided the keys needed to open a storehouse of energy surpluses.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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