



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

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

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.

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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. 1A), which by the Pliocene resulted in the gradual retreat of forests and expansion of open woodlands and grasslands [Fig. 1B (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. 1C (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. 1D), perhaps for feeding on the small trees and shrubs that predominate in open habitats (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. 1E). 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

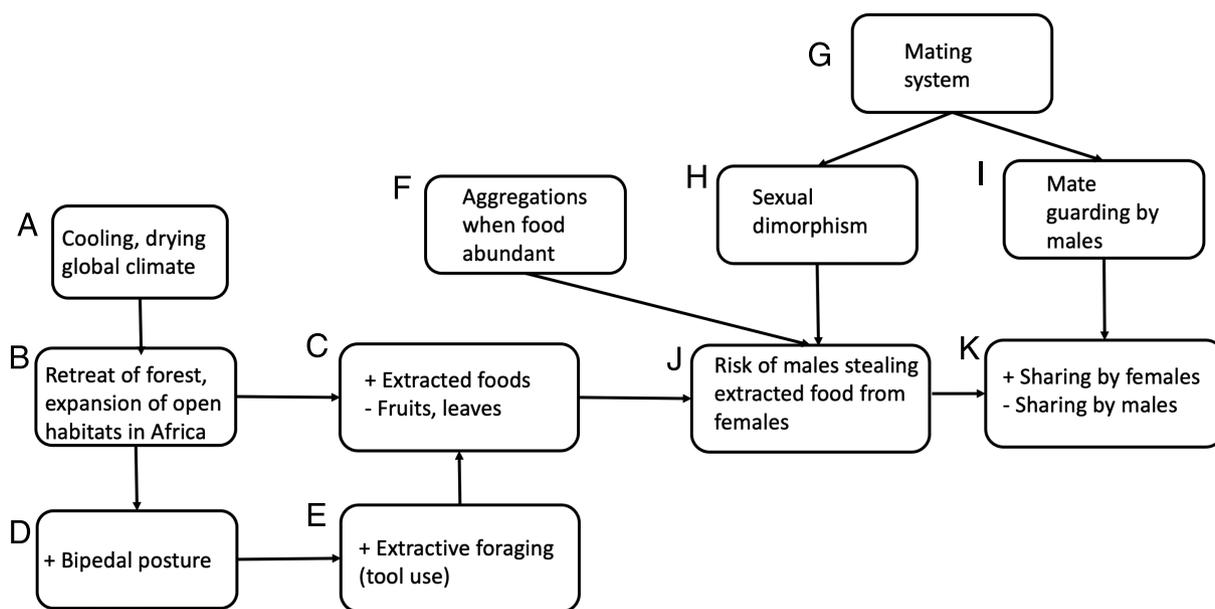


Fig. 1. Conceptual framework for the origins of extractive foraging and food sharing by hominins. For descriptions of each component of the framework (A–K) see the main text.

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:

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

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:

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

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:

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

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:

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

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):

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

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):

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

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:

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

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:

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

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 $1/2$):

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

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 $1/2$):

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

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^* :

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

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

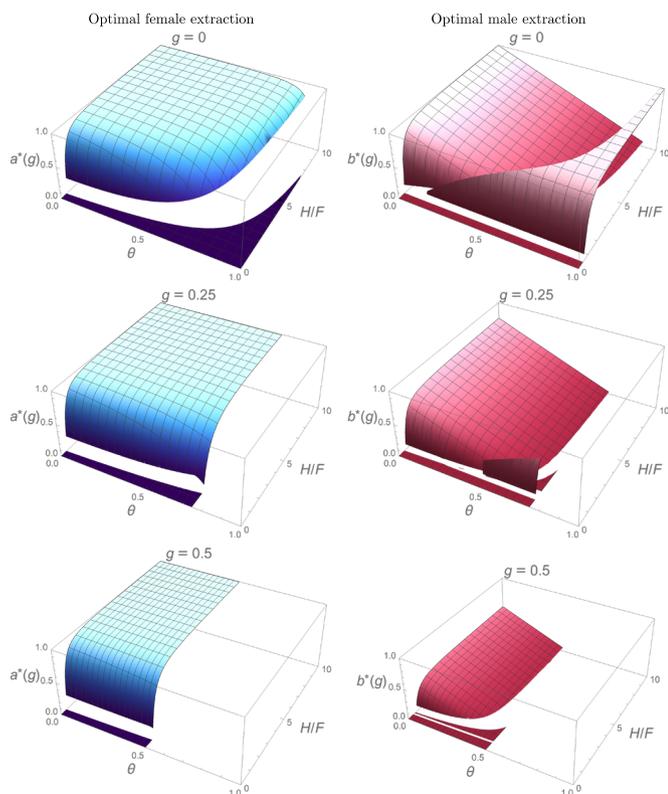


Fig. 2. Optimal strategies of extractive foraging by sex. The *Left* (respectively *Right*) column of figures shows, for three different values of mate guarding, g (from *Top* to *Bottom*, $g = 0$, $g = 0.25$, and $g = 0.5$), the optimal amount of time that females $a^*(g)$ respectively males ($b^*(g)$) 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

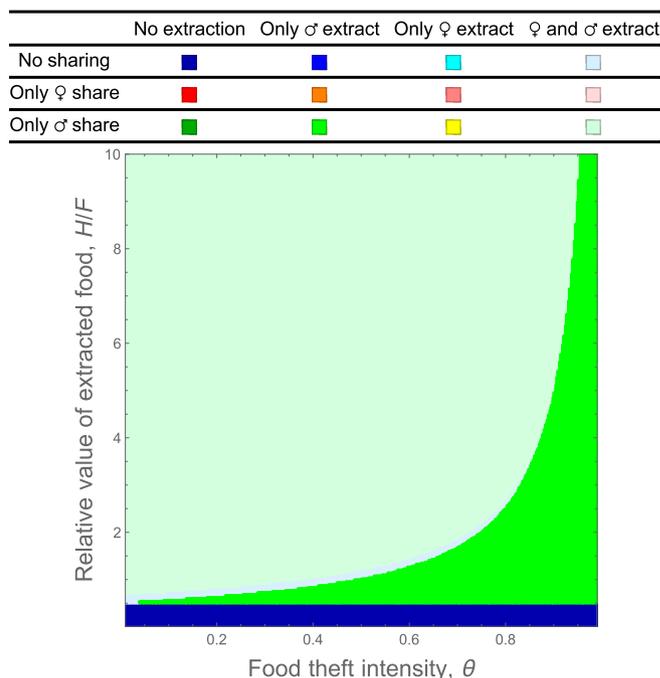


Fig. 3. Sex differences in food production and sharing in the promiscuous mating system. The plotted regions correspond to the combinations of three possible types of evolutionarily stable sharing pairs, (s^*, t^*) , and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table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

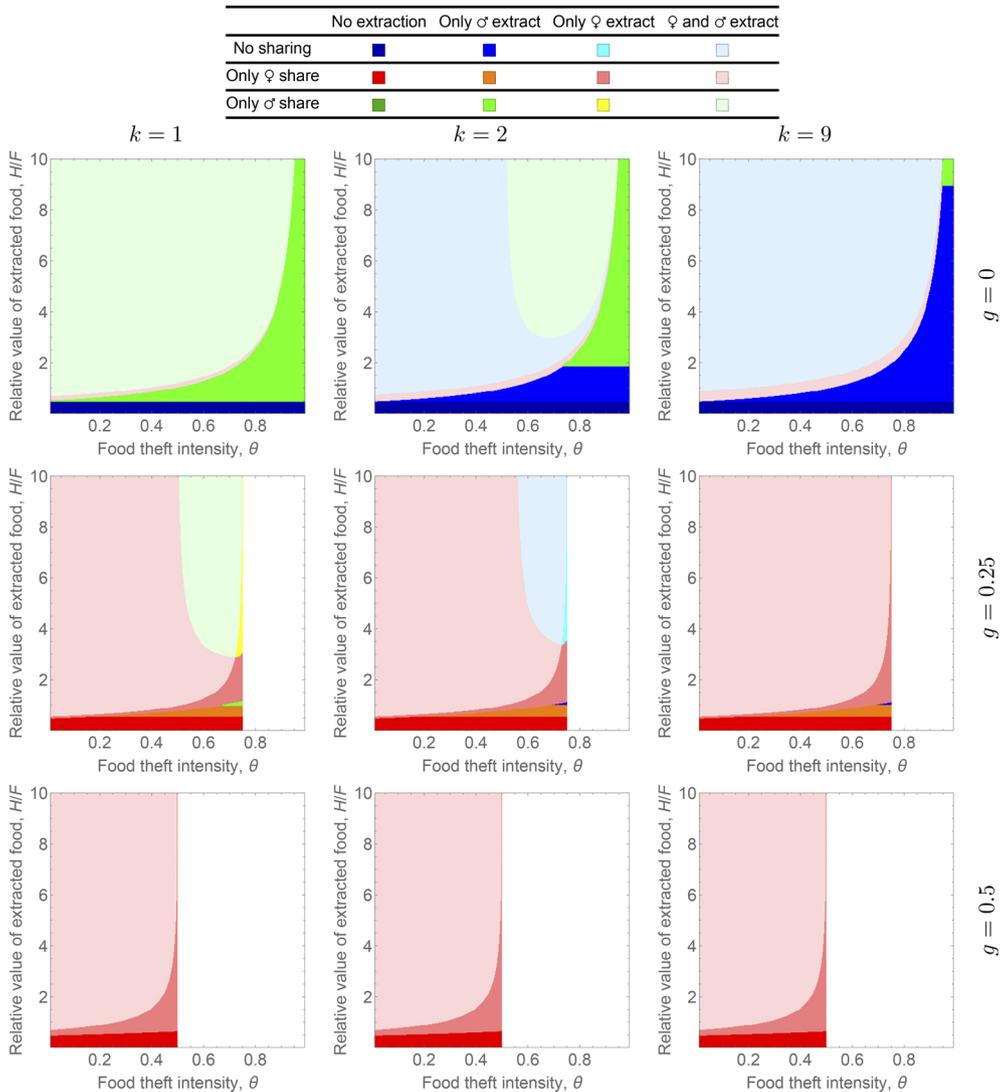


Fig. 4. Sex differences in food production and sharing in monogamous and polygynous mating systems. The plotted regions correspond to the combinations of the three possible types of evolutionarily stable sharing pairs, (s^* , t^*), and the four possible types of optimal foraging strategies ($a^*(g)$, $b^*(g)$). 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

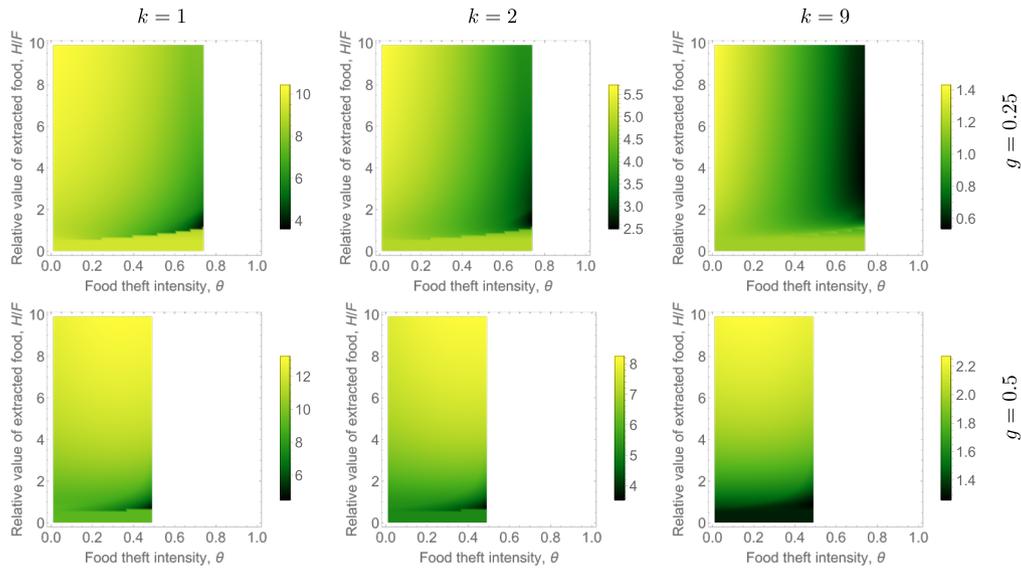


Fig. 5. Comparison of reproductive success between promiscuous vs. monogamous (*Leftmost* column) and polygynous mating systems (*Middle and Rightmost* columns). Shading represents the ratio of the reproductive success per unit of adult time spent foraging evaluated at the evolutionarily stable state in either monogamous or polygynous systems (numerator) over the fitness per unit of adult time spent foraging in the promiscuous system (denominator), i.e., $\frac{\hat{w}_P(s^*, s^*; t^*) / (2 - \delta\theta - g)}{\hat{w}_P(s_P^*, s_P^*; t_P^*) / (1 + N(1 - \delta\theta))}$, 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. 1C); 2) extractive foragers faced a risk of theft (Fig. 1J); 3) sexual pair-bonds existed (Fig. 1G); 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. 1H). 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 kcal, 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 ($\hat{Y}(z, \hat{s}; s)$). 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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1

2 **Supplementary Information for**

3 **The evolution of early hominin food production and sharing**

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7 **This PDF file includes:**

- 8 Supplementary text
- 9 Figs. S1 to S12 (not allowed for Brief Reports)
- 10 SI References

11 Supporting Information Text

12 In this document, we describe the model and prove the general results that are used in the main text. A reader who is only
13 interested in the model can read exclusively this Supplementary Information, which is self-contained in this regard (hence the
14 apparent redundancies between the main text and the present document).

15 A Mathematica notebook containing all the code necessary to produce the figures can be accessed at the follow-
16 ing address: <https://www.wolframcloud.com/obj/slimane.dridi0/Published/The%20evolution%20of%20early%20hominin%20food%20production%20and%20sharing.nb>
17

18 1. Model

19 Consider a population in which males and females in each generation interact in groups of equal size and with balanced sex
20 ratios. We model the evolution of four traits: *foraging behavior* and *food sharing* in both the male and the female side of the
21 population. We compare three different mating systems: promiscuity (where there is no pair-bonding), polygyny (some males
22 have several pair-bonded mates while others have none), and monogamy (each male has one pair-bonded mate). Pair-bonded
23 males and females mate, but extra-pair matings may also occur.

24 We assume that the female (and respectively male) food sharing trait is transmitted vertically from mother to daughters
25 (and respectively from fathers to sons). This can be interpreted either as biological transmission (under a diploid autosomal
26 additive genetic system with sex-specific phenotypic expression), or as sex-specific cultural transmission. Foraging on the other
27 hand is considered to be learned during an individual's lifespan, and we will assume that each individual reaches the optimal
28 foraging strategy quickly enough for the learning period to be ignored. We will see below that we could also interpret this
29 optimization process as frequency-independent cultural evolution of the trait.

30 Formally, consider a population subdivided into groups, all consisting of the same number of adult males and adult females,
31 denoted N . Pair-bonds may exist between males and females within each group. We assume that a limited number of males
32 are pair-bonded. Conditional on there being some pair-bonded males at all, each such male is pair-bonded with k females,
33 while the remaining males ($N - N/k$) are mateless (note that all females are distributed equally across the pair-bonded males).
34 For convenience, we always choose N and k such that N is divisible by k . In this way all N females are pair-bonded, i.e., there
35 are no mateless females. Under these assumptions the parameter k fully defines the mating system, which can be monogamous
36 ($k = 1$), polygynous ($1 < k < N$), or promiscuous ($k = 0$) (see Fig. S1). We rule out polyandry by assumption, since this mating
37 system is rarely documented in great apes and likely did not characterize mating systems of early hominins. Importantly, N
38 and k are exogenously given parameters, i.e., we do not model the evolution of group size and mating systems. Moreover, for
39 simplicity we ignore reproductive skew by assuming that all pair-bonded males have the same number of mates k .

40 *Foraging behavior* is modeled as the allocation of time between collecting easily accessible foods of lower nutritional value
41 (e.g., leaves and fruits) and extracting more difficult to acquire foods of higher nutritional value (e.g., nuts and tubers). Letting
42 each female's foraging time budget be 1, we denote by $a_i \in [0, 1]$ the time female i spends extracting foods that are difficult to
43 access; henceforth, this will simply be referred to as *extracting*. The remainder of the foraging time, $1 - a_i$, represents the time
44 spent collecting easily accessible foods. Males allocate their time budget, which is also normalized to 1, between guarding their
45 pair-bonded mates (in proportion g), and extracting and collecting foods; moreover, if females extract food, males can spend a
46 share θ of their time budget trying to steal extracted food from females. We will denote by b_j the share of time that male j
47 spends on extracting foods. The time spent on mate-guarding, g , and the time spent on stealing extracted food from females,
48 θ , are both taken to be exogenously given parameters.

49 Turning to *food sharing*, let $s_i \in [0, 1]$ denote the share of her acquired food that female i gives to some male(s), and
50 $t_j \in [0, 1]$ denote the share of his acquired food that male j gives to some female(s) (more on this below).

51 In Sections 2 and 3 we derive general results on the foraging and sharing strategies. In Section 4 we provide characterization
52 results as well as graphical representations of these (readers who are primarily interested in understanding how foraging and
53 sharing strategies depend on the parameter values can skip Sections 2 and 3).

54 2. Foraging

55 In this section we analyze the foraging behaviors of a focal female and a focal male.

56 Let $F > 0$ denote the expected nutritional value of collected foods and H the expected nutritional value of extracted foods
57 (the expected values of H and F capture the possibility that the search for food may be unsuccessful; however, we disregard
58 the effects of this risk). We posit that a female i who uses foraging behavior a_i and whose pair-bonded mate j (if she has one)
59 spends time g on mate-guarding, acquires the following total energy:

$$60 \quad x_i = x(a_i, g) = (1 - a_i)^{1/2} \cdot F + a_i \cdot [1 - (1 - g)\theta] \cdot H. \quad [1]$$

61 The first term in Eq. (1) is the total energy of collected foods acquired, given that the female spends time $1 - a_i$ on this
62 activity; we take the square root of $1 - a_i$ to capture the fact that there are decreasing marginal returns to time spent on
63 this activity (e.g. the more time the female spends consuming leaves in a given location, the farther she will have to travel to
64 collect even more leaves). The second term is the total expected energy of extracted foods acquired. She spends the share a_i of
65 her time on this activity. The parameter $\theta \in [0, 1]$ is the share of extracted foods that she acquires that is stolen by males other
66 than her pair-bonded mate; this *food theft intensity* is a non-evolving parameter. The food theft risk is, however, reduced by
67 the indirect protection provided by her pair-bonded mate's guarding, captured by the term $(1 - g)$ that multiplies θ ; the food

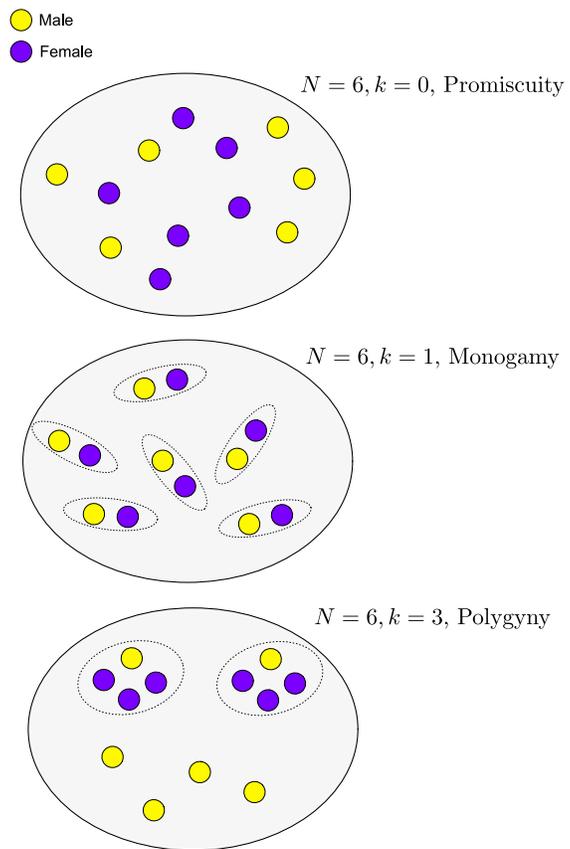


Fig. S1. The different types of mating systems captured by our model.

68 theft risk is fully eliminated when the male uses the maximal amount of mate-guarding $g = 1$. By being close to the female
69 while she forages, a mate-guarding male protects her from food theft by other males. Note that the returns to extracting are
70 constant instead of decreasing. This reflects the idea that once an individual starts extractive foraging (e.g. digging for tubers),
71 either there are food items to be found or not; in other words, the probability of finding specific extracted food items does not
72 depend on the amount of time spent in extractive foraging, but rather on whether the individual started extractive foraging in
73 the right place or not.

74 For any given $\theta \in [0, 1]$ and $g \in [0, 1]$, there is a unique value of $a_i \in [0, 1]$ that maximizes $x(a_i, g)$. Specifically, letting $a^*(g)$
75 denote the value of a_i that maximizes $x(a_i, g)$, we have:

$$76 \quad a^*(g) = \max \left\{ 0, 1 - \left(\frac{F}{2[1 - (1 - g)\theta]H} \right)^2 \right\}. \quad [2]$$

77 For a female to spend time extracting foods, i.e., for $a^*(g)$ to be positive, the marginal return from doing so—i.e., $[1 - (1 - g)\theta]H$ —
78 must be large compared to the nutritional value of collected foods, F .

79 Turning to a focal male j , let $\delta_a \in \{0, 1\}$ be a dummy variable that equals one if there is some extracted food that he can
80 steal from some female(s) in the group, and zero otherwise. Then the amount of time available for him to forage is $1 - \delta_a \cdot \theta - g$.
81 In other words, food theft occurs only if there is extracted food to be stolen from females, in which case he can spend less time
82 foraging. If the focal male spends his time in extractive foraging $b_j \in [0, 1 - \theta - g]$ then he acquires the following total energy:

$$83 \quad y_j = y(b_j, g) = (1 - \delta_a \cdot \theta - g - b_j)^{1/2} \cdot F + b_j \cdot H. \quad [3]$$

84 For any given value $g \in [0, 1 - \delta_a \cdot \theta]$, there is a unique value of $b^*(g) \in [0, 1 - \delta_a \cdot \theta - g]$ that maximizes $y(b_j, g)$:

$$85 \quad b^*(g) = \max \left\{ 0, 1 - \delta_a \cdot \theta - g - \left(\frac{F}{2H} \right)^2 \right\}. \quad [4]$$

86 We state the following claim (proving this claim here in general would require a significant amount of cumbersome notation,
87 but will be easily verified below for each mating system separately):

88 **Claim 1** *In any mating system and for any amounts of food sharing s and t and mate guarding g , each female i chooses*
89 *$a_i = a^*(g)$ and any male j chooses $b_j = b^*(g)$.*

90 As mentioned above, the foraging strategies that maximize the expected energy acquired are frequency-independent. Hence,
91 they can be interpreted as the result of either individual optimization or cultural inheritance.

92 For further use below, let $x^*(g)$ and $y^*(g)$ denote the amounts of energy acquired by any given female and any given male,
93 respectively, who are using the respective optimal foraging strategies $a^*(g)$ and $b^*(g)$, in a population where all males use the
94 same mate-guarding strategy $g \in [0, 1]$:

$$95 \quad x^*(g) \equiv x(a^*(g), g) = [1 - a^*(g)]^{1/2} \cdot F + a^*(g) \cdot [1 - (1 - g)\theta]H \quad [5]$$

$$96 \quad y^*(g) \equiv y(b^*(g), g) = [1 - \delta_a \cdot \theta - g - b^*(g)]^{1/2} \cdot F + b^*(g) \cdot H. \quad [6]$$

98 3. Food sharing

99 Consider a population where all males mate-guard and steal food according to some $(g, \theta) \in [0, 1]^2$, all males use the same
100 foraging strategy $b^*(g)$, and all females use the same foraging strategy $a^*(g)$ (see Eq. (5) and Eq. (6)). A female i may give
101 some of her acquired food to some male(s), and a male j may give some of his acquired food to some female(s). In this section
102 we determine the equilibrium values of such transfers in each mating system.

103 As mentioned above, our model encompasses both a biological and a cultural mode of transmission of the sharing traits.
104 First, our model could capture genetic evolution in a diploid population where the male and female traits are coded by alleles
105 at unlinked loci and the female sharing trait s is only expressed in females, while the male sharing trait t is only expressed in
106 males. Since the traits are coded by unlinked loci and are respectively only expressed in one sex their evolution is effectively
107 independent (like in, e.g., (1)). The model description below defines reproductive success as the biological one. Second, and as
108 will be shown below, our assumptions imply that the transmission can also be interpreted as one of the following two cultural
109 learning processes: (1) adult individuals that have more biological offspring are more likely to be copied by juveniles in the
110 group, and the copying is sex-specific; (2) the sharing traits are culturally transmitted from parent to same-sex offspring
111 (mother to daughter, father to son).

Whether transmission is biological or cultural, we assume that mutations occur so rarely that when a mutant appears, it
either gets lost or fixates in the population before the next mutation appears; in the latter case, the mutant strategy then
becomes the resident one. Under cultural evolution new traits do not appear by mutation but by innovation. For simplicity, we
still call the innovator a mutant in what follows. We will assume that a mutant's trait is a small deviation from the resident's

trait (i.e., weak mutation in adaptive dynamics). In order to determine whether a female mutant with trait \hat{s} will invade a population where residents adopt strategy s , we will analyze the fitness (or selection) gradient, defined as

$$W(s, t) = \left. \frac{\partial \hat{w}(\hat{s}, s; t)}{\partial \hat{s}} \right|_{\hat{s}=s}, \quad [7]$$

112 where $\hat{w}(\hat{s}, s; t)$ denotes the fitness of a rare mutant (also called invasion fitness) with trait \hat{s} in a population where female
 113 residents have trait s and the male population is monomorphic for trait t . The invasion fitness for females is evaluated for a
 114 monomorphic male population because the assumption of rare mutations implies that it is very unlikely that a mutant appears
 115 simultaneously in both the female and the male populations. If sharing is a cultural trait—which can thus be transmitted to
 116 “cultural offspring” who may differ from biological offspring—in our analysis we will take the fitness function \hat{w} to coincide with
 117 biological reproductive success. We do this for two reasons. First, to the extent that biological offspring tend to remain in the
 118 proximity of their mother, it is natural to assume a high probability that they would copy their mother’s trait; for simplicity
 119 we take this probability to equal 1. Second, we argue that it is reasonable to use biological reproductive success as a proxy for
 120 social status, so that if the propensity to be used as a cultural role model is correlated with social status, it is also a proxy for
 121 cultural fitness.

With this, we can turn to the male population where the fitness gradient is

$$V(s, t) = \left. \frac{\partial \hat{v}(\hat{t}, t; s)}{\partial \hat{t}} \right|_{\hat{t}=t}. \quad [8]$$

122 The fitness gradient is the derivative of $\hat{v}(\hat{t}, t; s)$, a rare mutant’s fitness evaluated at the resident trait value t in a population
 123 where the female population is monomorphic for trait s . As we do for females, for males we will take the fitness function \hat{v} to
 124 coincide with biological reproductive success. The exact expressions for the fitness functions \hat{w} and \hat{v} will be defined precisely
 125 below for each of the three mating systems that we examine.

Given these definitions and assumptions, on a relatively long evolutionary timescale, the population appears to be monomorphic at almost all time points so that the time evolution of traits s and t can be approximated by the canonical system of equations of adaptive dynamics

$$\begin{aligned} \dot{s} &= \mu_s W(s, t) \\ \dot{t} &= \mu_t V(s, t) \end{aligned} \quad [9]$$

126 where μ_s and μ_t control the speed of evolution (due in part to the innovation rate), and we used \dot{s} and \dot{t} to denote the time
 127 derivative of s and t , respectively. A rest point (s^*, t^*) of eq. 9 corresponds to a candidate *Evolutionarily Stable* (ES) pair
 128 of sharing strategies. A rest point that lies in the interior of the considered set, i.e., a rest point such that $(s^*, t^*) \in (0, 1)^2$,
 129 satisfies the system of first-order conditions

$$\begin{cases} W(s^*, t^*) = 0 \\ V(s^*, t^*) = 0. \end{cases} \quad [10]$$

A sufficient condition for such a singular state (s^*, t^*) to be a *Evolutionarily Stable Strategy Profile* (ESSP) is that, additionally, it satisfies the two second-order conditions, which state that both invasion fitness functions are strictly concave in the mutant strategy at hand:

$$\frac{\partial^2 \hat{w}(\hat{s}, s^*; t^*)}{\partial \hat{s}^2} < 0 \quad \text{for all } \hat{s} \in [0, 1] \quad [11]$$

$$\frac{\partial^2 \hat{v}(\hat{t}, s^*; t^*)}{\partial \hat{t}^2} < 0 \quad \text{for all } \hat{t} \in [0, 1]. \quad [12]$$

131 Such strict concavity indeed ensures that $\hat{s} = s^*$ is the unique and global maximum of the invasion fitness $\hat{w}(\hat{s}, s^*; t^*)$ and
 132 $\hat{t} = t^*$ the unique and global maximum of the invasion fitness $\hat{v}(\hat{t}, s^*; t^*)$. Turning finally to any (s^*, t^*) such that both $\hat{s} = s^*$
 133 is a local maximum of $\hat{w}(\hat{s}, s^*; t^*)$ and $\hat{t} = t^*$ is a local maximum of $\hat{v}(\hat{t}, s^*; t^*)$, but which does not lie in the interior of $[0, 1]^2$,
 134 we note that these two second-order conditions are also sufficient for (s^*, t^*) to be an ESSP.

135 **A. Promiscuous mating system.** In a promiscuous mating system there are no pair-bonds between males and females, and
 136 there is no mate-guarding ($g = 0$) (a male may guard a female that he mates with but only during oestrus, to seek to ensure
 137 paternity; however, he would not guard her once her offspring are born, and this is the mate-guarding that matters in our
 138 model). Females may still share some food with the males in her group, and *vice versa*. We posit that if a female shares, she
 139 gives the same amount to all the N males in her group. All the males in any given group thus obtain the same energy via the
 140 transfers from the females. Likewise, we posit that if a male shares, he gives the same amount to all the N females in his group,
 141 so that all the females in any given group thus obtain the same energy via the transfers from the males. Let $\mathbf{a} = (a_1, a_2, \dots, a_N)$
 142 denote the vector of the foraging strategies and $\mathbf{s} = (s_1, s_2, \dots, s_N)$ the vector of the sharing strategies used by the females in

143 the focal group. Likewise, let $\mathbf{b} = (b_1, b_2, \dots, b_N)$ be the vector of the foraging strategies and $\mathbf{t} = (t_1, t_2, \dots, t_N)$ the vector of the
 144 sharing strategies used by the males in the focal group. Then the total energy that female i has at her disposal equals

$$145 \quad X(a_i, s_i, \mathbf{b}, \mathbf{t}) = (1 - s_i) \cdot x(a_i, 0) + \sum_{j=1}^N \left[\frac{t_j}{N} \cdot y(b_j, 0) \right], \quad [13]$$

146 while the total energy that male j has at his disposal equals

$$147 \quad Y(b_j, t_j, \mathbf{a}, \mathbf{s}) = (1 - t_j) \cdot y(b_j, 0) + \sum_{i=1}^N \left[\frac{s_i}{N} \cdot x(a_i, 0) \right] + \frac{\theta}{N} \sum_{i=1}^N a_i H, \quad [14]$$

148 where the last term is the amount of extracted food that the male steals from females, and we assume that each male obtains a
 149 share $1/N$ of the aggregate amount of food stolen from the females.

150 In order to find an expression for invasion fitness, it is useful to rewrite Eq. (13) in a population where there is one focal
 151 female with trait \hat{s} , one focal male trait \hat{t} , while all other $N - 1$ males share t . This leads to:

$$152 \quad \hat{X}(\hat{s}, \hat{t}; t) = (1 - \hat{s}) \cdot x(a^*, 0) + \left(\frac{\hat{t}}{N} + \frac{N-1}{N} t \right) \cdot y(b^*, 0), \quad [15]$$

153 where we also assume that all females in the population employ the optimal foraging strategy a^* and all males employ b^* .
 154 Similarly, we rewrite Eq. (14) for a focal male who shares \hat{t} in a group where a focal female shares \hat{s} , while all other $N - 1$
 155 females share s , and thus obtain:

$$156 \quad \hat{Y}(\hat{t}, \hat{s}; s) = (1 - \hat{t}) \cdot y(b^*, 0) + \left(\frac{\hat{s}}{N} + \frac{N-1}{N} s \right) \cdot x(a^*, 0) + \theta a^* H. \quad [16]$$

157 Turning now to reproductive success, as explained above, whether the sharing traits are transmitted biologically or culturally,
 158 we take an individual's reproductive success to be the expected number of his/her biological offspring that survive to sexual
 159 maturity. Starting with female reproductive success, we posit that it is proportional to the total nutritional value that she
 160 consumes. Furthermore, we assume that a female benefits from the males in her group because they reduce the risk that her
 161 offspring are eaten by predators. In the promiscuous system, a female has no pair-bonded mate, and we assume that her
 162 reproductive success increases with the nutrition of males in her group as follows:

$$163 \quad w((a_i, \mathbf{a}_{-i}), (s_i, \mathbf{s}_{-i}), \mathbf{b}, \mathbf{t}) = X(a_i, s_i, \mathbf{b}, \mathbf{t}) \cdot p \cdot \sum_{j=1}^N Y(b_j, t_j, (a_i, \mathbf{a}_{-i}), (s_i, \mathbf{s}_{-i})), \quad [17]$$

164 where $p \in [\frac{1}{N}, 1]$ is a parameter that measures how much protection she can hope to get from the males against predators. For
 165 example, $p = 1/N$ means that she may expect one male to come and protect her, should her offspring be attacked by predators;
 166 at the other extreme, if $p = 1$, she benefits from the protection of all males. In this expression the vectors \mathbf{a} and \mathbf{s} are written
 167 (a_i, \mathbf{a}_{-i}) and (s_i, \mathbf{s}_{-i}) , respectively, to show clearly how the reproductive success of the focal female i depends on the foraging
 168 and sharing strategies of the other females in her group. From Eq. (17) and using Eq. (15)–Eq. (16), invasion fitness of a female
 169 who shares \hat{s} in a population where resident females share s and resident males share t takes the form

$$170 \quad \hat{w}(\hat{s}, s; t) = \hat{X}(\hat{s}, \hat{t}; t) \cdot p \cdot N \cdot \hat{Y}(\hat{t}, \hat{s}; s), \quad [18]$$

171 Turning now to a focal male j , his reproductive success depends on how many females he can mate with. Assuming that all
 172 males have an equal chance of mating, we obtain:

$$173 \quad v((b_j, \mathbf{b}_{-j}), (t_j, \mathbf{t}_{-j}), \mathbf{a}, \mathbf{s}) = \frac{1}{N} \sum_{i=1}^N w((a_i, \mathbf{a}_{-i}), (s_i, \mathbf{s}_{-i}), (b_j, \mathbf{b}_{-j}), (t_j, \mathbf{t}_{-j})) \quad [19]$$

$$174 \quad = \frac{1}{N} \sum_{i=1}^N \left[X(a_i, s_i, (b_j, \mathbf{b}_{-j}), (t_j, \mathbf{t}_{-j})) \cdot p \cdot \sum_{\ell=1}^N Y(b_\ell, t_\ell, (a_i, \mathbf{a}_{-i}), (s_i, \mathbf{s}_{-i})) \right].$$

175 In this expression the vectors \mathbf{b} and \mathbf{t} are written (b_j, \mathbf{b}_{-j}) and (t_j, \mathbf{t}_{-j}) , respectively, to show clearly how the reproductive
 176 success of the focal male j depends on the foraging and sharing strategies of the other males in his group. This allows us to
 177 write the invasion fitness of a focal mutant male who shares \hat{t} in a population where resident females share s and resident males
 178 share t as

$$179 \quad \hat{v}(\hat{t}, t; s) = \hat{X}(\hat{s}, \hat{t}; t) \cdot p \cdot \left[\hat{Y}(\hat{t}, \hat{s}; s) + (N - 1) \hat{Y}(t, s; s) \right]. \quad [20]$$

180 Before analyzing the evolution of sharing, we prove that Claim 1 is valid.

181 **Proof. [Proof of Claim 1.]** Starting with female foraging behavior, suppose—to the contrary of Claim 1—that some female
 182 i uses a foraging strategy $\hat{a} \neq a^*(0)$. For any given sharing strategy s_i , any given vector of strategies used by the other females
 183 in her group, $(\mathbf{a}_{-i}, \mathbf{s}_{-i})$, and any given vector of strategies used by the males in her group, (\mathbf{b}, \mathbf{t}) , she would then fail to

184 maximize her reproductive success (see Eq. (17)), since both $X(a_i, s_i, \mathbf{b}, \mathbf{t})$ and the sum in this expression are non-decreasing in
 185 $x(a_i, 0)$, and at least one of them is strictly increasing. A contradiction is reached. Turning now to male foraging behavior,
 186 suppose—to the contrary of Claim 1—that some male j uses a foraging strategy $\hat{b} \neq b^*(0)$. For any given sharing strategy t_j ,
 187 any given vector of strategies used by the other males in his group, $(\mathbf{b}_{-j}, \mathbf{t}_{-j})$, and any given vector of strategies used by the
 188 females in his group, (\mathbf{a}, \mathbf{s}) , he would then fail to maximize his reproductive success (see Eq. (19)), since both $X(a_i, s_i, \mathbf{b}, \mathbf{t})$
 189 and $Y(b_\ell, t_\ell, (a_i, \mathbf{a}_{-i}), (s_i, \mathbf{s}_{-i}))$ for $\ell = j$ are non-decreasing in $y(b_j, 0)$, and at least one of them is strictly increasing. A
 190 contradiction is reached.

191 To obtain the expressions for $W(s, t)$ and $V(s, t)$ that will be used to determine the candidates for stable female and male
 192 sharing strategies (see equations (7) and (8)), we first write the full expressions for the partial derivative of the focal female's
 193 reproductive success with respect to her sharing strategy, and likewise for the focal male (to keep the notation as simple as
 194 possible, we write $\mathbf{a}^*(\mathbf{0})$ for the N -dimensional vector with all components equal to $a^*(0)$, and $\mathbf{b}^*(\mathbf{0})$ for the N -dimensional
 195 vector with all components equal to $b^*(0)$):

$$196 \quad \frac{\partial w(\mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}), \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i} = \frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i} \cdot p \cdot \sum_{j=1}^N Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i})) \quad [21]$$

$$197 \quad + X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t}) \cdot p \cdot \sum_{j=1}^N \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}))}{\partial s_i}$$

$$198 \quad \frac{\partial v(\mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j} = \frac{p}{N} \sum_{i=1}^N \left[\frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}))}{\partial t_j} \cdot \sum_{\ell=1}^N Y(b_\ell, t_\ell, \mathbf{a}^*(\mathbf{0}), \mathbf{s}) \right] \quad [22]$$

$$199 \quad + \frac{p}{N} \sum_{i=1}^N \left[X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j})) \cdot \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j} \right].$$

201 Writing $\mathbf{s}^{(N)}$ (respectively $\mathbf{t}^{(N)}$) for the N -dimensional vector whose components all equal s (respectively t), and recalling the
 202 notation for $x^*(0)$ and $y^*(0)$ (see Eq. (5) and Eq. (6)) from these expressions we obtain (upon simplification):

$$203 \quad W(s, t) = \frac{\partial w(\mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}), \mathbf{b}^*(\mathbf{0}), \mathbf{t}^{(N)})}{\partial s_i} \Big|_{(s_i, \mathbf{s}_{-i}) = \mathbf{s}^{(N)}} \quad [23]$$

$$204 \quad = p \cdot x^*(0) \cdot [X(a^*, s, \mathbf{b}^*, \mathbf{t}^{(N)}) - N \cdot Y(b^*, t, \mathbf{a}^*, \mathbf{s}^{(N)})]$$

$$205 \quad V(s, t) = \frac{\partial v(\mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{0}), \mathbf{s}^{(N)})}{\partial t_j} \Big|_{(t_j, \mathbf{t}_{-j}) = \mathbf{t}^{(N)}} \quad [24]$$

$$206 \quad = p \cdot y^*(0) \cdot [Y(b^*, t, \mathbf{a}^*, \mathbf{s}^{(N)}) - X(a^*, s, \mathbf{b}^*, \mathbf{t}^{(N)})].$$

208 One might notice a difference between the definitions of $W(s, t)$ and $V(s, t)$ in Eq. (7)–Eq. (8) and their respective definitions
 209 here in Eq. (23)–Eq. (24), which stems only from two different approaches, but lead to the same result. In Eq. (23)–Eq. (24)
 210 we track all individuals in the group, an approach more widespread in game theory, while in Eq. (7)–Eq. (8) we focus on a
 211 mutant in a group where all other individuals are residents, an approach more known to students of adaptive dynamics. In
 212 order to keep track of these two different approaches, we have used hat notation for all functions that take the standpoint of a
 213 focal mutant in a group of residents. Next we show that a female's reproductive success is strictly concave in her own sharing
 214 strategy, and that a male's reproductive success is strictly concave in his own sharing strategy. Recall from above (see Eq. (10)
 215 and Eq. (12)) that such strict concavity is sufficient for any candidate ES pair of sharing strategies to indeed be ES.

216 **Lemma 1** For any $t \in [0, 1]$, $w(\mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}), \mathbf{b}^*(\mathbf{0}), \mathbf{t}^{(N)})$ is strictly concave in s_i . For any $s \in [0, 1]$, $v(\mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{0}), \mathbf{s}^{(N)})$
 217 is strictly concave in t_j .

218 **Proof.** We prove the lemma by proving that the relevant second-order partial derivatives are strictly negative. From Eq. (21)
 219 we obtain:

$$220 \quad \frac{\partial^2 w(\mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}), \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i^2} = \frac{\partial^2 X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i^2} \cdot p \cdot \sum_{j=1}^N Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i})) \quad [25]$$

$$221 \quad + \frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i} \cdot p \cdot \sum_{j=1}^N \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}))}{\partial s_i}$$

$$222 \quad + \frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i} \cdot p \cdot \sum_{j=1}^N \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}))}{\partial s_i}$$

$$223 \quad + X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t}) \cdot p \cdot \sum_{j=1}^N \frac{\partial^2 Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}))}{\partial s_i^2},$$

224 which simplifies to the following expression due to the linearity of $X(\cdot)$ and $Y(\cdot)$ in s_i :

$$225 \quad \frac{\partial^2 w(\mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}), \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i^2} = 2p \cdot \frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), \mathbf{t})}{\partial s_i} \sum_{j=1}^N \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), (s_i, \mathbf{s}_{-i}))}{\partial s_i}. \quad [26]$$

226 Since $X(\cdot)$ is strictly decreasing in s_i while $Y(\cdot)$ (for any $j = 1, \dots, N$) is strictly increasing in s_i , this expression is strictly
227 negative.

228 From Eq. (22) we obtain:

$$229 \quad \frac{\partial^2 v(\mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j^2} = \frac{p}{N} \sum_{i=1}^N \left[\frac{\partial^2 X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}))}{\partial t_j^2} \cdot \frac{\sum_{\ell=1}^N Y(b_\ell, t_\ell, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{N} \right] \quad [27]$$

$$230 \quad + \frac{p}{N} \sum_{i=1}^N \left[\frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}))}{\partial t_j} \cdot \frac{1}{N} \frac{\partial Y(b_t, t_j, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j} \right]$$

$$231 \quad + \frac{p}{N} \sum_{i=1}^N \left[\frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}))}{\partial t_j} \cdot \frac{1}{N} \frac{\partial Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j} \right]$$

$$232 \quad + \frac{p}{N} \sum_{i=1}^N \left[X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j})) \cdot \frac{1}{N} \frac{\partial^2 Y(b^*(0), t_j, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j^2} \right].$$

233 Due to the linearity of $X(\cdot)$ and $Y(\cdot)$ in t_j , this simplifies to the following expression:

$$234 \quad \frac{\partial^2 v(\mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j^2} = \frac{2p}{N} \sum_{i=1}^N \left[\frac{\partial X(a^*(0), s_i, \mathbf{b}^*(\mathbf{0}), (t_j, \mathbf{t}_{-j}))}{\partial t_j} \cdot \frac{1}{N} \frac{\partial Y(b_t, t_j, \mathbf{a}^*(\mathbf{0}), \mathbf{s})}{\partial t_j} \right], \quad [28]$$

235 which is strictly negative since $X(\cdot)$ is strictly increasing in t_j (for any $i = 1, \dots, N$) while $Y(\cdot)$ is strictly decreasing in t_j .

236 This lemma implies that for any parameter values and for any $t \in [0, 1]$, there exists at most one value of s such that
237 $W(s, t) = 0$. Solving $W(s, t) = 0$ for s yields the solution

$$238 \quad \sigma(t) = \frac{x^*(0) + Nty^*(0) - N[(1-t)y^*(0) + \theta a^*(0)H]}{x^*(0)(N+1)}. \quad [29]$$

239 Likewise, solving $V(s, t) = 0$ for t yields the solution

$$240 \quad \tau(s) = \frac{(2s-1)x^*(0) + y^*(0) + \theta a^*(0)H}{2y^*(0)}. \quad [30]$$

241 Henceforth we write (s^*, t^*) to denote a pair of sharing strategies (s, t) that is evolutionarily stable. The following proposition
242 establishes that there exists no (s^*, t^*) such that both males and females share food.

243 **Proposition 1** *Any (s^*, t^*) is such that either $s^* = 0$, or $t^* = 0$, or $s^* = t^* = 0$.*

244 **Proof.** First, we show that $s^* > 0$ implies $t^* = 0$. If $s^* > 0$, then either (i) $s^* < 1$ and $W(s^*, t^*) = 0$, or (ii) $s^* = 1$
245 and $W(1, t^*) \geq 0$. In both cases, $W(s^*, t^*) \geq 0$. From Eq. (23), and since $x^*(0) > 0$, the inequality $W(s^*, t^*) \geq 0$ implies
246 $X(a^*, s^*, \mathbf{b}^*, \mathbf{t}^*) \geq N \cdot Y(b^*, t^*, \mathbf{a}^*, \mathbf{s}^*)$. Hence, for any $N \geq 2$, $Y(b^*, t^*, \mathbf{a}^*, \mathbf{s}^*) - X(a^*, s^*, \mathbf{b}^*, \mathbf{t}^*) < 0$; but since $y^*(0) > 0$, this
247 implies $V(s^*, t^*) < 0$ (see Eq. (24)). By strict concavity of v (see Lemma 1), and given that t^* must lie in the interval $[0, 1]$, it
248 follows that $t^* = 0$.

249 Second, we show that $t^* > 0$ implies $s^* = 0$. If $t^* > 0$, then either (i) $t^* < 1$ and $V(s^*, t^*) = 0$, or (ii) $t^* = 1$ and
250 $V(s^*, 1) \geq 0$. In both cases, $V(s^*, t^*) \geq 0$. From Eq. (24), and since $y^*(0) > 0$, the inequality $V(s^*, t^*) \geq 0$ implies
251 $Y(b^*, t^*, \mathbf{a}^*, \mathbf{s}^*) \geq X(a^*, s^*, \mathbf{b}^*, \mathbf{t}^*)$. Hence, for any $N \geq 2$, $X(a^*, s^*, \mathbf{b}^*, \mathbf{t}^*) - N \cdot Y(b^*, t^*, \mathbf{a}^*, \mathbf{s}^*) < 0$; since $x^*(0) > 0$, this
252 implies $W(s^*, t^*) < 0$ (see Eq. (23)). By strict concavity of w (see Lemma 1), and given that s^* must lie in the interval $[0, 1]$, it
253 follows that $s^* = 0$.

254 Next we establish existence and uniqueness of ES pair of sharing strategies.

255 **Proposition 2** *For any parameter constellation there exists a unique ES pair of sharing strategies (s^*, t^*) .*

256 **Proof.** First, strict concavity of w and of v (see Lemma 1) implies that:

- 257 1. for any parameter values such that $t^* = 0$, there exists a unique s^* , which is either strictly positive or equal to zero;
- 258 2. for any parameter values such that $s^* = 0$, there exists a unique t^* , which is either strictly positive or equal to zero.

259 Second, if parameter values are such that $(s^*, 0)$ is ES for some $s^* \in (0, 1]$, then there exists no $t^* \in (0, 1]$ such that $(0, t^*)$ is
 260 ES. To see this, suppose that $(s^*, 0)$ is ES for some $s^* \in (0, 1]$. Then, $\sigma(0) > 0$ (see Eq. (29)) and $s^* = \min\{\sigma(0), 1\}$. Now, note
 261 that $\sigma(t)$ is increasing in t . Hence, $\sigma(0) > 0$ implies $\sigma(t) > 0$ for any $t > 0$, i.e., $(0, t)$ with $t > 0$ cannot be an evolutionarily
 262 stable pair of sharing strategies.

263 Likewise, if parameter values are such that $(0, t^*)$ is ES for some $t^* \in (0, 1]$, then there exists no $s^* \in (0, 1]$ such that $(s^*, 0)$ is
 264 ES. To see this, suppose that $(0, t^*)$ is ES for some $t^* \in (0, 1]$. Then, $\tau(0) > 0$ (see Eq. (30)) and $t^* = \min\{\tau(0), 1\}$. Now, note
 265 that $\tau(s)$ is increasing in s . Hence, $\tau(0) > 0$ implies $\tau(s) > 0$ for any $s > 0$, i.e., $(s, 0)$ with $s > 0$ cannot be an evolutionarily
 266 stable pair of sharing strategies.

267 **B. Monogamous and polygynous mating systems.** We now consider a polygynous mating system where some males (exactly
 268 N/k of them) reproduce exclusively with a fixed number of k females each, while the remaining males are mateless (monogamy
 269 will be the special case where $k = 1$). We assume that each female shares food only with her pair-bonded mate (if she shares
 270 at all), and that she gets protection only from him. We also assume that all males can steal from any of the females he is
 271 not pair-bonded with. Let us use an index ij to denote a female i who belongs to the unit U_j consisting of male j and all
 272 the females he is pair-bonded with. Let $\mathbf{s}_j = (s_{1j}, s_{2j}, \dots, s_{Nj})$ denote the vector of the sharing strategies used by the females
 273 in the unit of the focal male j . Then the total amount of energy that a focal female ij has at her disposal, given that her
 274 pair-bonded male uses the amount g of mate-guarding, equals

$$275 \quad X(a_{ij}, s_{ij}, b_j, t_j) = (1 - s_{ij}) \cdot x(a_{ij}, g) + t_j \cdot \frac{y(b_j, g)}{k}, \quad [31]$$

276 while the total amount of energy that the focal male j has at his disposal equals

$$277 \quad Y(b_j, t_j, \mathbf{a}, \mathbf{s}_j) = (1 - t_j) \cdot y(b_j, g) + \sum_{i=1}^k [s_{ij} \cdot x(a_{ij}, g)] + \frac{\theta(1-g)}{N-1} \sum_{d \neq j} \left(\sum_{\ell=1}^k a_{\ell d} H \right). \quad [32]$$

278 The last term reflects the assumption that each male garners a fraction $1/(N-1)$ of any food stolen from each female who
 279 does not belong to his unit (each such female indeed gets food stolen by all the $N-1$ males other than her pair-bonded mate).

280 Just as in the promiscuous system, we rewrite Eq. (31) and Eq. (32) to find an expression for invasion fitness focusing on a
 281 focal mutant in a monomorphic population of residents. The total energy that a focal female who shares \hat{s} has at her disposal,
 282 given that her pair-bonded male spends time g mate-guarding and shares \hat{t} , equals

$$283 \quad \hat{X}(\hat{s}, \hat{t}) = (1 - \hat{s}) \cdot x(a^*, g) + \hat{t} \cdot \frac{y(b^*, g)}{k}. \quad [33]$$

284 Similarly, rewriting Eq. (32) for a focal male who shares \hat{t} has at his disposal, given that a focal female in his unit shares \hat{s}
 285 while his other pair-bonded females share s , gives

$$286 \quad \hat{Y}(\hat{t}, \hat{s}, s) = (1 - \hat{t}) \cdot y(b^*, g) + [(k-1)s + \hat{s}] \cdot x(a^*, g) + \frac{N-k}{N-1} \theta(1-g) a^* H. \quad [34]$$

287 Writing \mathbf{a}_{-ij} (respectively \mathbf{s}_{-ij}) for the vector of foraging (respectively sharing) strategies used by the other $k-1$ females
 288 in her unit, and \mathbf{a}_{-j} for the vector of foraging strategies used by the $N-k$ females outside her unit (i.e., the unit of male j),
 289 the reproductive success of the focal female ij thus equals

$$290 \quad w((a_{ij}, \mathbf{a}_{-ij}, \mathbf{a}_{-j}), (s_{ij}, \mathbf{s}_{-ij}), b_j, t_j) = X(a_{ij}, s_{ij}, b_j, t_j) \cdot q \cdot Y(b_j, t_j, (a_{ij}, \mathbf{a}_{-ij}, \mathbf{a}_{-j}), (s_{ij}, \mathbf{s}_{-ij})). \quad [35]$$

291 The parameter $q \in [\frac{1}{k}, 1]$ measures how much protection she can hope to get from her pair-bonded male against predators. For
 292 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
 293 unit is attacked by predators; at the other extreme, if $q = 1$, the male can protect them all. Since q is a positive constant, we
 294 can without loss of generality drop it to determine the stable sharing strategies. Using Eq. (33)–Eq. (34) and starting from
 295 Eq. (35), we can write the invasion fitness of a mutant female who shares \hat{s} in a group where all other females use the resident
 296 sharing strategy s and all males (including her pair-bonded male) share t , as

$$297 \quad \hat{w}(\hat{s}, s, t) = \hat{X}(\hat{s}, t) \cdot q \cdot \hat{Y}(t, \hat{s}, s). \quad [36]$$

298 Turning now to a focal male j , his reproductive success depends on how many females he can mate with, and it is also
 299 proportional to the total nutritional value that he consumes. While each pair-bonded male mates preferentially with his
 300 pair-bonded mates, that he guards with intensity $g \in [0, 1]$, he also resorts to extra-pair copulations. Letting $\phi \in [0, 1]$
 301 denote the share of her copulatory acts that any female concedes to males other than her pair-bonded male if unguarded, and
 302 $\mathbf{g} = (g_1, g_2, \dots, g_N)$ the vector of mate-guarding investments of males in the focal group, we posit that the reproductive success
 303 of the focal pair-bonded male j equals

$$304 \quad v((b_j, \mathbf{b}_{-j}), (t_j, \mathbf{t}_{-j}), \mathbf{a}, \mathbf{s}, \mathbf{g}) = [1 - \phi(1-g)] \cdot \sum_{i=1}^k w((a_{ij}, \mathbf{a}_{-ij}, \mathbf{a}_{-j}), (s_{ij}, \mathbf{s}_{-ij}), b_j, t_j) \quad [37]$$

$$305 \quad + \frac{1}{N-1} \sum_{d \neq j} \sum_{\ell=1}^k (1-g)\phi \cdot w((a_{\ell d}, \mathbf{a}_{-\ell d}, \mathbf{a}_{-d}), (s_{\ell d}, \mathbf{s}_{-\ell d}), b_d, t_d).$$

306 In the first term, the expression inside the square brackets is the expected proportion of offspring born to females in his unit for
 307 which he is the biological father. The second term represents the expected number of paternities that he can steal from females
 308 outside his own unit: of all the extra-pair copulations by females outside his unit that are not protected by these females'
 309 pair-bonded males, the focal male gets a share $1/(N-1)$. We indeed assume that for any given female, each male besides her
 310 pair-bonded male gets an equal share of her extra-pair copulations.

311 From Eq. (37) and using Eq. (31)–Eq. (36), we can write the invasion fitness of a mutant male who shares \hat{t} in a group
 312 where all other males use the resident sharing strategy t and all females share s as

$$313 \quad \hat{v}(\hat{t}, t, s) = [1 - \phi(1 - g)]kq\hat{X}(s, \hat{t})\hat{Y}(\hat{t}, s, s) + \phi(1 - g)\frac{N/k - 1}{N - 1}kq\hat{X}(s, t)\hat{Y}(t, s, s). \quad [38]$$

314 The first term is the number of offspring of the focal male's pair-bonded mates for which he is the biological father. The second
 315 term is the share of the offspring of all the other females for which he is the biological father, where $N/k - 1$ is the number of
 316 units with k females besides that of the focal male, and the denominator $N - 1$ is the total number of males (including the
 317 focal male) who compete for the extra-pair matings conceded by the females in these units.

318 **Remark 1** *As is clear from equation Eq. (38), our model encompasses male-male competition for extra-pair matings conceded*
 319 *by females. However, as can be seen in equation Eq. (38), the second term actually does not depend on the focal male's sharing*
 320 *strategy, and it is the sign of the derivative of the first term with respect to \hat{t} that will matter for whether a higher or a lower*
 321 *sharing is selected for. The constant term in square brackets being strictly positive, its value is inconsequential for the sign of*
 322 *the said derivative. In sum, in our model the male-male competition for extra-pair matings has no impact on the selection of*
 323 *the male sharing trait. This “separability” stems from our assumption that a male shares only with the females with whom he*
 324 *is pair-bonded (which in turn implies that females concede extra-pair matings randomly across males – without regard to the*
 325 *males' sharing strategies). This modeling choice was made because our goal is to understand forces other than sexual selection*
 326 *as a driver of the traits under scrutiny. We leave it to future research to examine the robustness of our results to the inclusion*
 327 *of such sexual selection forces.*

328 Before analyzing the evolution of sharing, we prove that Claim 1 is valid.

329 **Proof. [Proof of Claim 1.]** Starting with female foraging behavior, suppose—to the contrary of Claim 1—that some female
 330 ij uses a foraging strategy $\hat{a} \neq a^*(0)$. For any given sharing strategy s_i , any given vector of strategies used by the other
 331 females in her group, $(\mathbf{a}_{-i}, \mathbf{s}_{-i})$, and any given vector of strategies used by the males in her group, (\mathbf{b}, \mathbf{t}) , she would then fail to
 332 maximize her reproductive success (see Eq. (35)), since both $X(\cdot)$ and $Y(\cdot)$ in this expression are non-decreasing in $x(a_{ij}, 0)$,
 333 and at least one of them is strictly increasing. A contradiction is reached. Turning now to male foraging behavior, suppose—to
 334 the contrary of Claim 1—that some male j uses a foraging strategy $\hat{b} \neq b^*(0)$. For any given sharing strategy t_j , any given
 335 vector of strategies used by the other males in his group, $(\mathbf{b}_{-j}, \mathbf{t}_{-j})$, and any given vector of strategies used by the females in his
 336 group, (\mathbf{a}, \mathbf{s}) , he would then fail to maximize his reproductive success (see Eq. (37)). To see this, note first that his reproductive
 337 success is strictly increasing in the reproductive success of each female in his unit (i.e., in $w((a_{ij}, \mathbf{a}_{-ij}, \mathbf{a}_{-j}), (s_{ij}, \mathbf{s}_{-ij}), b_j, t_j)$
 338 for all $i = 1, \dots, k$), and that this in turn is strictly increasing in b_j (since both $X(\cdot)$ and $Y(\cdot)$ in Eq. (35) are non-decreasing in
 339 b_j and at least one is strictly increasing). A contradiction is reached.

340 To obtain the expressions for $W(s, t)$ and $V(s, t)$ that will be used to determine the candidates for stable female and male
 341 sharing strategies (see equations (7) and (8)), we first write the full expressions for the partial derivative of the focal female's
 342 reproductive success with respect to her sharing strategy, and likewise for the focal male, in a population where all males apply
 343 mate-guarding amount g (we write $\mathbf{a}^*(g)$ for the N -dimensional vector with all components equal to $a^*(g)$, and $\mathbf{b}^*(g)$ for the
 344 N -dimensional vector with all components equal to $b^*(g)$):

$$345 \quad \frac{\partial w(\mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t_j)}{\partial s_{ij}} = \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot Y(b^*(g), t_j, \mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij})) \quad [39]$$

$$346 \quad + X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij}))}{\partial s_{ij}}$$

$$347 \quad \frac{\partial v(\mathbf{b}^*(g), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(g), \mathbf{s}, g)}{\partial t_j} = [1 - \phi(1 - g)] \cdot \sum_{i=1}^k \frac{\partial w(\mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t_j)}{\partial t_j} \quad [40]$$

$$348 \quad = [1 - \phi(1 - g)] \cdot \sum_{i=1}^k \cdot \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot Y(b^*(g), t_j, \mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij})) \right]$$

$$349 \quad + [1 - \phi(1 - g)] \cdot \sum_{i=1}^k \cdot \left[X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij}))}{\partial t_j} \right].$$

351 Writing $\mathbf{s}^{(k)}$ for the k -dimensional vector whose components all equal s , we obtain the following expressions for $W(s, t)$ and
 352 $V(s, t)$:

$$353 \quad W(s, t) = \frac{\partial w(\mathbf{a}^*(g), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t)}{\partial s_{ij}} \Big|_{(s_{ij}, \mathbf{s}_{-ij}) = \mathbf{s}^{(k)}} \quad [41]$$

$$354 \quad = x^*(g) [X(a^*(g), s, b^*(g), t) - Y(b^*(g), t, \mathbf{a}^*(g), \mathbf{s}^{(k)})]$$

$$\begin{aligned}
V(s, t) &= \frac{\partial v(\mathbf{b}^*(\mathbf{g}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{g}), \mathbf{s}^{(N)}, \mathbf{g})}{\partial t_j} \Big|_{(t_j, \mathbf{t}_{-j})=\mathbf{t}^{(N)}} \\
&= [1 - \phi(1 - g)] y(b^*(g)) \left[Y(b^*(g), t, \mathbf{a}^*(\mathbf{g}), \mathbf{s}^{(k)}) - k \cdot X(a^*(g), s, b^*(g), t) \right].
\end{aligned} \tag{42}$$

Like in the promiscuous system, we prove strict concavity of reproductive success in own sharing, for both males and females.

Lemma 2 For any $t \in [0, 1]$, $w(\mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t)$ is strictly concave in s_{ij} . For any $s \in [0, 1]$, $v(\mathbf{b}^*(\mathbf{g}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{g}), \mathbf{s}^{(N)}, \mathbf{g})$ is strictly concave in t_j .

Proof. We prove the lemma by proving that the relevant second-order partial derivatives are strictly negative. From Eq. (39) we obtain:

$$\begin{aligned}
\frac{\partial^2 w(\mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t_j)}{\partial s_{ij}^2} &= \frac{\partial^2 X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}^2} \cdot Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij})) \\
&+ \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial s_{ij}} \\
&+ \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial s_{ij}} \\
&+ X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial^2 Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial s_{ij}^2}.
\end{aligned} \tag{43}$$

This simplifies to the following expression due to the linearity of $X(\cdot)$ and $Y(\cdot)$ in s_{ij} :

$$\frac{\partial^2 w(\mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}), b^*(g), t_j)}{\partial s_{ij}^2} = 2 \cdot \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial s_{ij}}. \tag{44}$$

Since $X(\cdot)$ is strictly decreasing while $Y(\cdot)$ is strictly increasing in s_{ij} , this expression is strictly negative.

From Eq. (40) we obtain that $\frac{\partial^2 v(\mathbf{b}^*(\mathbf{g}), (t_j, \mathbf{t}_{-j}), \mathbf{a}^*(\mathbf{g}), \mathbf{s}, \mathbf{g})}{\partial t_j^2}$ has the same sign as (since $[1 - \phi(1 - g)] > 0$):

$$\begin{aligned}
&\sum_{i=1}^k \left[\frac{\partial^2 X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j^2} \cdot Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij})) \right] \\
&+ \sum_{i=1}^k \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial t_j} \right] \\
&+ \sum_{i=1}^k \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial t_j} \right] \\
&+ \sum_{i=1}^k \left[X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial^2 Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial t_j^2} \right].
\end{aligned} \tag{45}$$

Due to the linearity of $X(\cdot)$ and $Y(\cdot)$ in t_j , this simplifies to the following expression:

$$2 \cdot \sum_{i=1}^k \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \mathbf{a}^*(\mathbf{g}), (s_{ij}, \mathbf{s}_{-ij}))}{\partial t_j} \right] \tag{46}$$

which is strictly negative since $X(\cdot)$ is strictly increasing in t_j (for any $i = 1, \dots, N$) while $Y(\cdot)$ is strictly decreasing in t_j .

This lemma implies that for any parameter values and for any $t \in [0, 1]$, there exists at most one value of s such that $W(s, t) = 0$. Solving $W(s, t) = 0$ for s yields the solution

$$\sigma(t) = \frac{x^*(g) - y^*(g) + \frac{ty^*(g)(1+k)}{k} - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{(1+k)x^*(g)}. \tag{47}$$

Likewise, solving $V(s, t) = 0$ for t yields the solution

$$\tau(s) = \frac{y^*(g) + (2s-1)ky^*(g) + \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{2y^*(g)}. \tag{48}$$

Again, let (s^*, t^*) denote a pair of sharing strategies (s, t) that is evolutionarily stable. It appears that it is useful to treat monogamy and strict polygyny ($k \geq 2$) separately, and we first examine the latter mating system.

384 **B.1. Strict polygyny.** The following proposition establishes that under strict polygyny there exists no ES such that both males
385 and females share food.

386 **Proposition 3** For any $k \geq 2$, any (s^*, t^*) is such that either $s^* = 0$, or $t^* = 0$, or $s^* = t^* = 0$.

387 **Proof.** First, we show that $s^* > 0$ implies $t^* = 0$. If $s^* > 0$, then either (i) $s^* < 1$ and $W(s^*, t^*) = 0$, or (ii) $s^* = 1$ and
388 $W(1, t^*) \geq 0$. In both cases, $W(s^*, t^*) \geq 0$. From the expression in Eq. (41), and since $x^*(0) > 0$, the inequality $W(s^*, t^*) \geq 0$
389 implies $X(a^*, s^*, \mathbf{b}^*, t^*) \geq Y(b^*, t^*, \mathbf{a}^*, s^*)$. Hence, for any $k \geq 2$, $Y(b^*, t^*, \mathbf{a}^*, s^*) - k \cdot X(a^*, s^*, \mathbf{b}^*, t^*) < 0$; but since $y^*(0) > 0$,
390 this implies $V(s^*, t^*) < 0$ (see Eq. (42)). By strict concavity of v (see Lemma 2), and given that t^* must lie in the interval
391 $\in [0, 1]$, it follows that $t^* = 0$.

392 Second, we show that $t^* > 0$ implies $s^* = 0$. If $t^* > 0$, then either (i) $t^* < 1$ and $V(s^*, t^*) = 0$, or (ii) $t^* = 1$ and
393 $V(s^*, 1) \geq 0$. In both cases, $V(s^*, t^*) \geq 0$. From the expression in Eq. (42), and since $y^*(0) > 0$, the inequality $V(s^*, t^*) \geq 0$
394 implies $Y(b^*, t^*, \mathbf{a}^*, s^*) \geq k \cdot X(a^*, s^*, \mathbf{b}^*, t^*)$. Hence, for any $k \geq 2$, $X(a^*, s^*, \mathbf{b}^*, t^*) - Y(b^*, t^*, \mathbf{a}^*, s^*) < 0$; since $x^*(0) > 0$,
395 this implies $W(s^*, t^*) < 0$ (see Eq. (41)). By strict concavity of w (see Lemma 2), and given that s^* must lie in the interval
396 $\in [0, 1]$, it follows that $s^* = 0$.

397 Next we establish existence and uniqueness of ES under strict polygyny.

398 **Proposition 4** For any $k \geq 2$ and for any parameter constellation, there exists a unique ES (s^*, t^*) .

399 **Proof.** First, strict concavity of w and of v (see Lemma 2) implies that:

- 400 1. for any parameter values such that $t^* = 0$, there exists a unique s^* , which is either strictly positive or equal to zero;
401 2. for any parameter values such that $s^* = 0$, there exists a unique t^* , which is either strictly positive or equal to zero.

402 Second, if parameter values are such that $(s^*, 0)$ is ES for some $s^* \in (0, 1]$, then there exists no $t^* \in (0, 1]$ such that $(0, t^*)$ is
403 ES. To see this, suppose that $(s^*, 0)$ is ES for some $s^* \in (0, 1]$. Then, $\sigma(0) > 0$ (see Eq. (47)) and $s^* = \min\{\sigma(0), 1\}$. Now,
404 note that $\sigma(t)$ is increasing in t . Hence, $\sigma(0) > 0$ implies $\sigma(t) > 0$ for any $t > 0$, i.e., $(0, t)$ with $t > 0$ cannot be a evolutionarily
405 stable pair of sharing strategies.

406 Likewise, if parameter values are such that $(0, t^*)$ is ES for some $t^* \in (0, 1]$, then there exists no $s^* \in (0, 1]$ such that $(s^*, 0)$ is
407 ES. To see this, suppose that $(0, t^*)$ is ES for some $t^* \in (0, 1]$. Then, $\tau(0) > 0$ (see Eq. (48)) and $t^* = \min\{\tau(0), 1\}$. Now, note
408 that $\tau(s)$ is increasing in s . Hence, $\tau(0) > 0$ implies $\tau(s) > 0$ for any $s > 0$, i.e., $(s, 0)$ with $s > 0$ cannot be an evolutionarily
409 stable pair of sharing strategies.

410 In sum, under strict polygyny ($k \geq 2$) the unique ES pair of sharing strategies is either such that $t^* = 0$ and $s^* = \min\{1, \sigma(0)\}$,
411 where

$$412 \sigma(0) = \frac{x^*(g) - y^*(g) - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{(1+k)x^*(g)}, \quad [49]$$

413 or such that $s^* = 0$ and $t^* = \min\{1, \tau(0)\}$, where

$$414 \tau(0) = \frac{y^*(g) - kx^*(g) + \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{2y^*(g)}, \quad [50]$$

415 or $(s^*, t^*) = (0, 0)$.

416 Finally, we turn to the monogamous system.

417 **B.2. Monogamy.** We obtain the following result:

418 **Proposition 5** In the monogamous system, there are two cases:

- 419 1. if $x^*(g) + y^*(g) \geq \theta(1-g)a^*(g)H$, there exists at least one ES pair of sharing strategies $(s^*, t^*) \in [0, 1]^2$; moreover, any
420 ES (s^*, t^*) is then such that $X(a^*(g), s^*, b^*(g), t^*) = Y(b^*(g), t^*, \mathbf{a}^*(g), s^*)$;
421 2. if $\theta(1-g)a^*(g)H > x^*(g) + y^*(g)$, the unique ES pair of sharing strategies is $(s^*, t^*) = (0, 1)$, and $Y(b^*(g), t^*, \mathbf{a}^*(g), s^*) >$
422 $X(a^*(g), s^*, b^*(g), t^*)$.

423 **Proof.** Plugging $k = 1$ into Eq. (41) and Eq. (42), we see that either both $W(s, t) = V(s, t) = 0$, or $W(s, t)$ and $V(s, t)$ have
424 opposite signs. Clearly, if $W(s, t) > 0 > V(s, t)$, it must be that $s = 1$ and $t = 0$: indeed, by strict concavity of the invasion
425 fitness function w , maximization of w is compatible with a strictly positive selection gradient if and only if s is at its maximum
426 value, 1; likewise, by strict concavity of the invasion fitness function v , maximization of v is compatible with a strictly negative
427 selection gradient if and only if t is at its minimum value, 0. Based on similar reasoning, if $V(s, t) > 0 > W(s, t)$, it must
428 be that $t = 1$ and $s = 0$. To examine whether such corner solutions are relevant for any parameter constellations, we now
429 determine whether there are parameter values for which there exists no $(s, t) \in [0, 1]^2$ such that $W(s, t) = V(s, t) = 0$, i.e., such
430 that (see Eq. (41) and Eq. (42)):

$$431 X(a^*(g), s, b^*(g), t) = Y(b^*(g), t, \mathbf{a}^*(g), s). \quad [51]$$

432 Using Eq. (31) and Eq. (32), this equality becomes

$$433 (1-s)x^*(g) + ty^*(g) = (1-t)y^*(g) + sx^*(g) + \theta(1-g)a^*(g)H. \quad [52]$$

434 To begin, note that the left-hand side (LHS) is decreasing in s and increasing in t , while the opposite is true for the right-hand
435 side (RHS). Specifically, for any given values of $x^*(g)$, $y^*(g)$, and $\theta a^*(g)H$:

- the LHS is minimized and equal to 0 for $s = 1 - t = 1$, while it is maximized and equal to $x^*(g) + y^*(g)$ for $s = 1 - t = 0$;
- the RHS is maximized and equal to $y^*(g) + x^*(g) + \theta(1 - g)a^*(g)H$ for $s = 1 - t = 1$, while it is minimized and equal to $\theta(1 - g)a^*(g)H$ for $s = 1 - t = 0$.

These observations imply that as long as $x^*(g) + y^*(g) \geq \theta(1 - g)a^*(g)H$, there exists at least one pair of sharing strategies $(s, t) \in [0, 1]^2$ that satisfies Eq. (52). Any such pair is ES, since s then maximizes the invasion fitness w , given t , and t maximizes the invasion fitness v , given s . By contrast, consider the case $\theta(1 - g)a^*(g)H > x^*(g) + y^*(g)$. Then the LHS of Eq. (52) is strictly smaller than the RHS for any $(s, t) \in [0, 1]^2$. In other words, $Y(b^*(g), t, a^*(g), s) < X(a^*(g), s, b^*(g), t)$, and the observation above implies that the unique ES is $(s, t) = (0, 1)$.

The result is intuitive. In a bonded pair the female's reproductive success is maximized if her energy intake is the same as that of the male. In the monogamous system the interest of the male is aligned with that of the female, since the part of his reproductive success that he achieves within the bonded pair is equal to her reproductive success. Hence, whenever the amounts of food that they have at their disposal allow for it, sharing will be such that the female's energy intake equals that of the male, i.e., $X(a^*(g), s^*, b^*(g), t^*) = Y(b^*(g), t^*, a^*(g), s^*)$. Such equalization is impossible to achieve, however, if the food that the male steals from other females exceeds the amount of food that the female gets when she shares nothing and the male shares all of his collected and extracted food with her ($\theta(1 - g)a^*(g)H > x^*(g) + y^*(g)$). In that case, $Y(b^*(g), t^*, a^*(g), s^*) > X(a^*(g), s^*, b^*(g), t^*)$.

4. Characterization of optimal foraging and ES sharing strategies

In the preceding sections we proved the existence and (sometimes) uniqueness of optimal foraging strategies and evolutionarily stable sharing strategies. In this section we derive characterization results, the aim being to understand how these strategies depend on the parameter values. In particular we seek to precisely identify parameter constellations for which sharing emerges.

Prior to examining in detail each mating system, we state the detailed expressions for the optimal foraging strategies, and the associated expressions for $x^*(g)$ and $y^*(g)$. Since

$$a^*(g) = \max \left\{ 0, 1 - \left(\frac{F}{2(1 - \theta + \theta g)H} \right)^2 \right\} \quad [53]$$

and

$$b^*(g) = \max \left\{ 0, 1 - \delta_a \cdot \theta - g - \left(\frac{F}{2H} \right)^2 \right\}, \quad [54]$$

we obtain

$$x^*(g) = \begin{cases} F & \text{if } a^*(g) = 0 \\ \frac{F^2}{4(1 - \theta + \theta g)H} + (1 - \theta + \theta g)H & \text{otherwise} \end{cases} \quad [55]$$

and

$$y^*(g) = \begin{cases} (1 - \delta_a \cdot \theta - g)^{1/2} \cdot F & \text{if } b^*(g) = 0 \\ \frac{F^2}{4H} + (1 - \delta_a \cdot \theta - g)H & \text{otherwise.} \end{cases} \quad [56]$$

In Fig. S2 we show the regions of parameter space where extractive foraging is optimal for females and/or males. Below we derive more precise results about these regions.

A. Foraging and sharing in the promiscuous system ($g = 0$). To begin, we obtain the following characterization of the optimal foraging strategies:

Proposition 6 *In the promiscuous mating system the optimal foraging strategies are as follows:*

(Case A) $a^*(0) = b^*(0) = 0$ iff $F/H \geq 2$;

(Case B) $a^*(0) = 0$ and $b^*(0) > 0$ iff $2 > F/H \geq 2(1 - \theta)$;

(Case C) $a^*(0) > 0$ and $b^*(0) > 0$ iff $2(1 - \theta) > F/H$.

Proof. The results follow from the fact that $a^*(0) = 0$ iff $F/H \geq 2(1 - \theta)$ and $b^*(0) = 0$ iff $F/H \geq 2(1 - \delta_a \cdot \theta)^{1/2}$, and from noting, moreover, that $(1 - \theta)^{1/2} > 1 - \theta$.

Proposition 6 provides us with two main messages:

1. As expected, extractive foraging occurs when the value of collected foods is small relative to that of extracted foods (F/H small enough).
2. When there is no mate-guarding ($g = 0$), it is never optimal for females to extract if males don't extract. This is because the threat of food theft to which females are exposed makes time invested in extraction less beneficial for females than for males (consistent with this, note that Case B vanishes if $\theta = 0$). Thus:

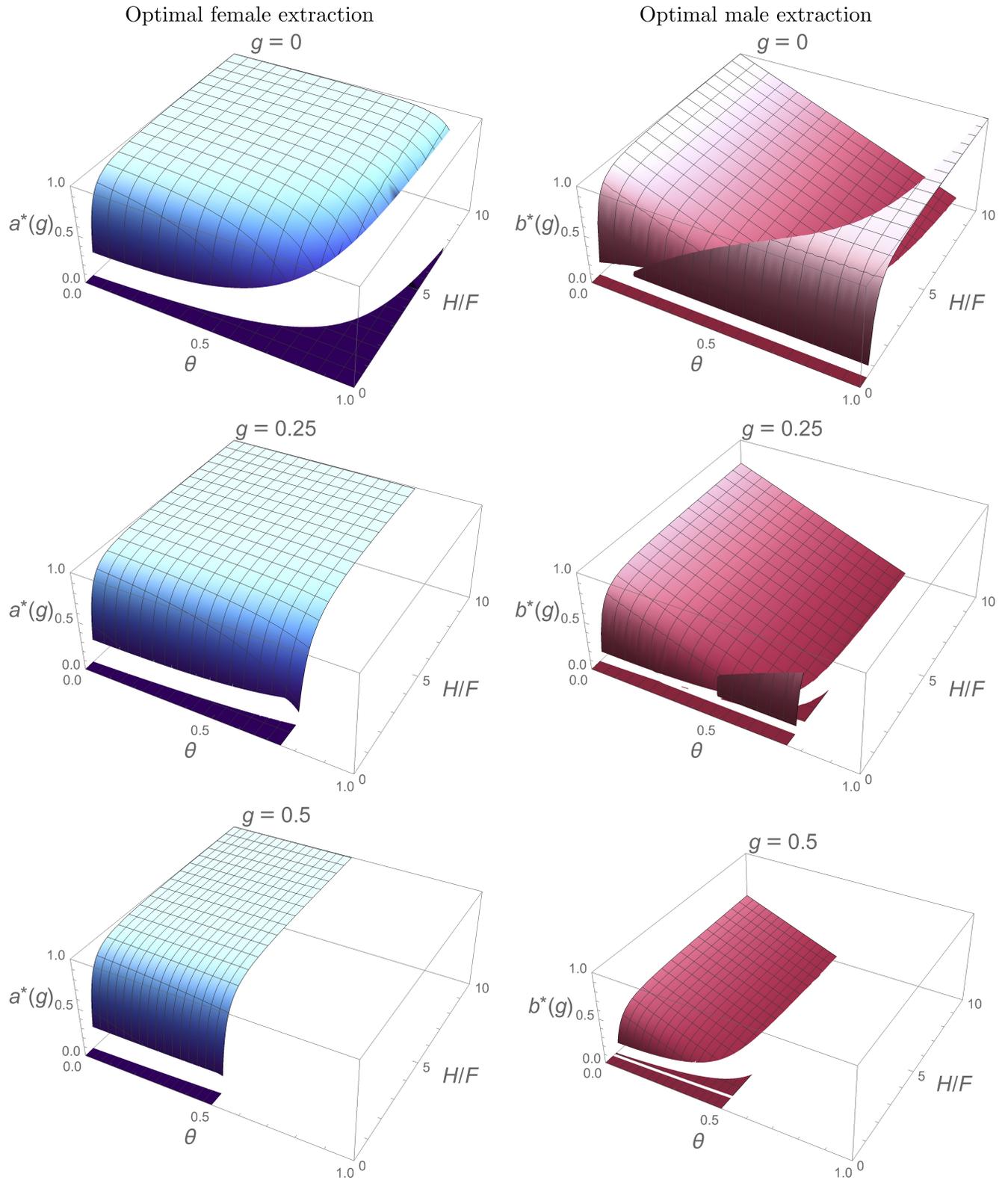


Fig. S2. The left (respectively right) column of figures shows, for three different values of g (from top to bottom, $g = 0$, $g = 0.25$, and $g = 0.5$) the amount of time that females ($a^*(g)$) (respectively males ($b^*(g)$)) spend extractive foraging, as a function of θ and H/F . Parameter regions shown in white are irrelevant, due to the time budget constraint $\theta + g + b^*(g) \leq 1$.

- For any given value of food theft intensity θ , as the value of collected foods relative to that of extracted foods F/H becomes large enough, females stop extracting while a further increase is required to make males stop extracting.
- For any given value of collective foods relative to that of extracted foods F/H , as food theft intensity (θ) becomes large enough, females stop extracting while males—who do not face any threat of getting their food stolen—still find it worthwhile to extract.

The optimal foraging strategies in the promiscuous system (where $g = 0$) are shown in the two top panels of Fig. S2. We note that when only males engage in extraction ($b^*(0) > a^*(0) = 0$), they have more food than females: indeed, for such parameter values females would also have chosen to extract had the food theft threat been absent.

Turning now to sharing strategies, Proposition 1 shows that, for any given parameter values, there are at most three mutually exclusive parameter regions: one in which neither males nor females share, one in which only males share, and one in which only females share. As we will now show, however, it turns out that only the first two are relevant. Some preliminary remarks about the three possible outcomes (see Proposition 1) are in order before we state and prove the exact result.

First, if males do not share ($t^* = 0$), we obtain the following expression from eq. 29:

$$\sigma(0) = \frac{x^*(0) - N[y^*(0) + \theta a^*(0)H]}{x^*(0)(N+1)}. \quad [57]$$

Hence, a necessary and sufficient condition for $s^* > 0$ is

$$\frac{x^*(0)}{y^*(0) + \theta a^*(0)H} > N. \quad [58]$$

Because the fitness of a female w is always increasing in other females' sharing strategies, one can interpret female sharing as a contribution to a public good. Inequality Eq. (58) gives the condition such that the fitness of a female is increasing in her own sharing strategy, evaluated at $s = 0$. The left-hand side of Eq. (58) can thus be interpreted as the synergy factor of this public goods game. The condition in Eq. (58) then simply restates the well-known condition that for cooperation to be an equilibrium of a public goods game, the synergy factor should exceed the number of players.

Second, if females do not share ($s^* = 0$), we obtain the following expression from Eq. (30):

$$\tau(0) = \frac{y^*(0) - x^*(0) + \theta a^*(0)H}{2y^*(0)}. \quad [59]$$

Hence, $t^* > 0$ iff

$$y^*(0) > x^*(0) - \theta a^*(0)H, \quad [60]$$

and $t^* < 1$ iff

$$x^*(0) + y^*(0) > \theta a^*(0)H. \quad [61]$$

Note that the latter inequality holds for all parameter values such that $a^*(0) = 0$.

Finally, Propositions 1 and 2 together imply that $(s^*, t^*) = (0, 0)$ iff neither Eq. (58) nor Eq. (60) holds. We use these conditions to prove the following results:

Proposition 7 *In the promiscuous system:*

- whether or not they engage in food extraction, females do not share food with males;*
- males share food with females if they extract food while females don't, or if both males and females extract food and $\frac{F(\sqrt{F^2+16H^2+F})}{8H^2} < 1 - \theta$; otherwise they do not share.*

Proof. The proof is based on the necessary and sufficient conditions derived above for $s^* > 0$ (see Eq. (58)), for $t^* > 0$ (see Eq. (60)), and for $t^* < 1$ (see Eq. (61)). Specifically, we examine these inequalities in Cases A-C of Proposition 6.

In **Case A**, $x^*(0) = F$ and $y^*(0) = F$. Using this in Eq. (58) and Eq. (60), we obtain:

- $s^* > 0 \iff F > NF$, which is false;
- $t^* > 0 \iff F < F$, which is false.

In **Case B**, $x^*(0) = F$ and $y^*(0) = \frac{F^2}{4H} + H$. Using this in Eq. (58) and Eq. (60), we obtain:

- $s^* > 0 \iff F > N \left(\frac{F^2}{4H} + H \right) \iff N < \frac{4HF}{F^2+4H^2}$; recalling that $N \geq 2$, a necessary condition for $N < \frac{4HF}{F^2+4H^2}$ for some N is that $\frac{4HF}{F^2+4H^2} > 2$, or $2H(F-2H) > F^2$, an inequality which holds only if $F > 2H$; however, this is false in Case B (which requires $2 > F/H$, see Proposition 6);
- $t^* > 0 \iff y^*(0) > x^*(0)$, which is true, since if it were not true it would have been optimal for the male to refrain from extracting (indeed, given that $g = 0$ and $\delta_a = 0$, $x^*(0) = F$ is the amount of food that the male would collect if he did not extract).

527 In **Case C**, $x^*(0) = \frac{F^2}{4(1-\theta)H} + (1-\theta)H$ and $y^*(0) = \frac{F^2}{4H} + (1-\theta)H$. Using this in Eq. (58) and Eq. (60), we obtain:

528 • a necessary condition for $s^* > 0$ is that $x^*(0) > y^*(0)$, or $\frac{F^2}{4(1-\theta)H} + (1-\theta)H > N \left[\frac{F^2}{4H} + (1-\theta)H \right]$; rewriting this
 529 inequality as $[1 - N(1-\theta)]F^2 > 4(N-1)(1-\theta)^2H^2$, we see that it is violated for any $N \geq \frac{1}{1-\theta}$; for $N < \frac{1}{1-\theta}$, the
 530 inequality can be rewritten as $\frac{F}{H} > 2(1-\theta) \left[\frac{N-1}{1-N(1-\theta)} \right]^{1/2}$; recalling that Case C applies only if $\frac{F}{H} < 2(1-\theta)$, a necessary
 531 condition for $\frac{F}{H} > 2(1-\theta) \left[\frac{N-1}{1-N(1-\theta)} \right]^{1/2}$ is that $\frac{N-1}{1-N(1-\theta)} < 1$, which is equivalent to $N < \frac{2}{2-\theta}$, which is false for any
 532 $N \geq 2$;

533 • $t^* > 0 \iff \frac{F^2}{4H} + (1-\theta)H + \left[1 - \left(\frac{F}{2(1-\theta+\theta_g)H} \right)^2 \right] \theta H > \frac{F^2}{4(1-\theta)H} + (1-\theta)H$, which is true if $\frac{F(\sqrt{F^2+16H^2+F})}{8H^2} < 1-\theta$.

534 Proposition 7 shows that in a promiscuous system:

- 535 1. Female sharing does not arise for any parameter constellations. This is because when males do not spend any time on
 536 mate-guarding, they always have at least as much food as females do: when both females and males extract, males have
 537 more food because they steal food from females, and when only males extract they have more food than females (as
 538 explained above). The synergy factor in the public goods game between the females (see inequality Eq. (58) and the
 539 comment below it) is therefore always smaller than 1 and thus fails to trigger any sharing by females.
- 540 2. If both males and females extract, males share only if θ is small enough.
- 541 3. If females do not extract, then food theft does not impact the ES sharing of males.

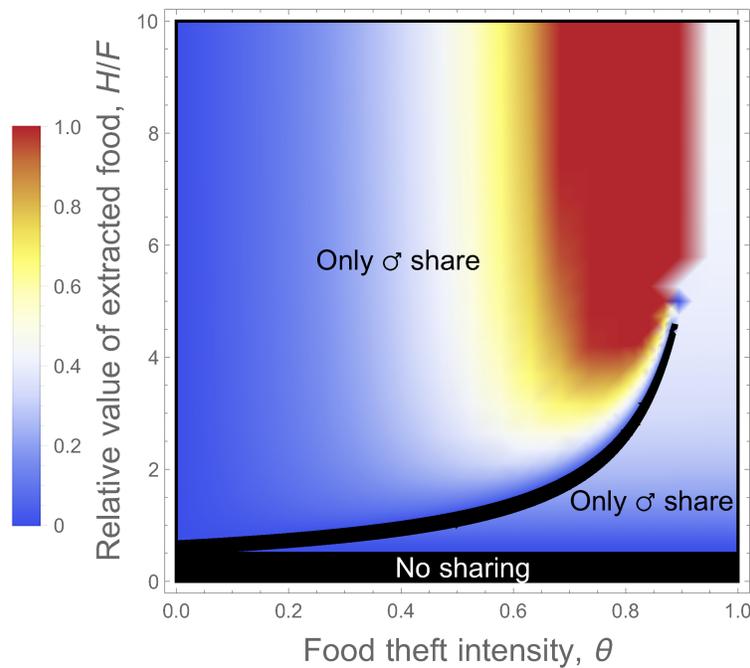


Fig. S3. Regions of parameter space in the promiscuous mating system corresponding to the two possible types of ES sharing pairs, (s^*, t^*) , described in Prop. 7. In regions labelled "Only males (σ) share", we have $s^* > 0$ and $t^* = 0$, while in regions labelled "No sharing" we have $s^* = 0$ and $t^* = 0$. The shading indicates the exact value of t^* , when it is not 0 ($s^* > 0$ is never ES as shown in Prop. 7).

542 Proposition 7 is displayed in Fig. S9. Moving leftward in the figure, the first black region corresponds to parameter values
 543 such that neither males nor females extract, and hence do not share. In the first blue region, only males extract. In the second
 544 black region, both males and females extract, and males steal extracted food from females; however, because males now spend
 545 time on food theft, their own food production is below that of females, and because the food theft yields only a small return
 546 (since females do not spend much time on extraction), males end up having a total amount of food that is still smaller than
 547 that of females, and hence they do not share food with them. Finally, in the leftmost region, males do share, and they share
 548 more the more they steal from females.

549 **B. Foraging in the polygynous and the monogamous systems.** Recall that $a^*(g) = 0$ iff $F/H \geq 2(1 - \theta + \theta g)$ and $b^*(0) = 0$
550 iff $F/H \geq 2(1 - \delta_a \cdot \theta - g)^{1/2}$. Hence, we obtain the following characterization of the foraging strategies (the proposition is
551 illustrated in Figures S4-S6, which will also be used to summarize the main features of the proposition below):

552 **Proposition 8** *In the polygynous as well as in the monogamous mating system the optimal foraging strategies are as follows:*

553 *Case A. If $1 - \theta + \theta g \geq (1 - g)^{1/2}$:*

- 554 A1. $a^*(g) = b^*(g) = 0$ iff $F/H \geq 2(1 - \theta + \theta g)$
555 A2. $a^*(g) > b^*(g) = 0$ iff $2(1 - \theta + \theta g) > F/H \geq 2(1 - \theta - g)^{1/2}$
556 A3. $a^*(g) > 0$ and $b^*(g) > 0$ iff $2(1 - \theta - g)^{1/2} > F/H$.

557 *Case B. If $(1 - g)^{1/2} \geq (1 - \theta - g)^{1/2} \geq 1 - \theta + \theta g$:*

- 558 B1. $a^*(g) = b^*(g) = 0$ iff $F/H \geq 2(1 - g)^{1/2}$
559 B2. $b^*(g) > a^*(g) = 0$ iff $2(1 - g)^{1/2} > F/H \geq 2(1 - \theta + \theta g)$
560 B3. $b^*(g) > 0$ and $a^*(g) > 0$ iff $2(1 - \theta + \theta g) > F/H$.

561 *Case C. If $(1 - g)^{1/2} \geq 1 - \theta + \theta g \geq (1 - \theta - g)^{1/2}$:*

- 562 C1. $a^*(g) = b^*(g) = 0$ iff $F/H \geq 2(1 - g)^{1/2}$
563 C2. $b^*(g) > a^*(g) = 0$ iff $2(1 - g)^{1/2} > F/H \geq 2(1 - \theta + \theta g)$
564 C3. $a^*(g) > b^*(g) = 0$ iff $2(1 - \theta + \theta g) > F/H \geq 2(1 - \theta - g)^{1/2}$.
565 C4. $a^*(g) > 0$ and $b^*(g) > 0$ iff $2(1 - \theta - g)^{1/2} > F/H$.

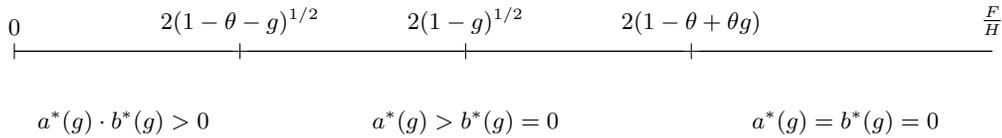


Fig. S4. optimal foraging strategies in Case A of Proposition 8

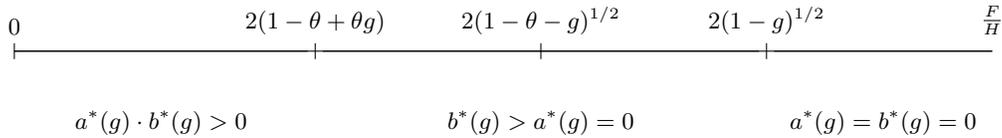


Fig. S5. optimal foraging strategies in Case B of Proposition 8

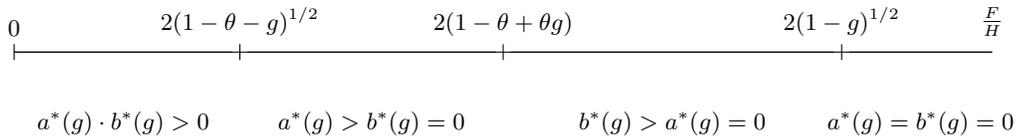


Fig. S6. optimal foraging strategies in Case C of Proposition 8

566 As can be seen from Figures S4-S6, we first note that for any values of g and θ (such that $1 - \theta - g \geq 0$), both males and
567 females refrain from extracting food when the nutritional value of collected relative to extracted foods (F/H) is high enough,
568 and they engage in extractive foraging when F/H is small enough. Second, for intermediate values of F/H only one of the
569 sexes engages in extractive foraging, and this depends on the mate-guarding parameter g (which dampens male extractive
570 foraging by reducing the male's time budget) and the food theft parameter θ (which disincentivizes female extractive foraging).
571 Thus, if θ is small enough (as in Case A), females extract while males don't for intermediate values of F/H (see Figure S4),
572 while if θ is large enough (as in Case B), males extract while females don't for intermediate values of F/H (see Figure S5).
573 Case C is similar to Case B in that males are the ones who start extracting when F/H falls below a certain threshold; however,
574 as F/H falls sufficiently for females also to start extracting, males stop extracting because of the reduction in the time budget
575 that food theft thus implies. However, for even lower values of F/H , males start extracting again (see Figure S6). We finally
576 note that for $g = 0$ the results coincide with those in the promiscuous system, as they should.

577 **C. Sharing in the strictly polygynous system ($k \geq 2, g \in [0, 1]$).**

578 **C.1. Sharing when neither females nor males engage in extractive foraging.** We begin with a characterization result for parameter
579 constellations such that $a^*(g) = b^*(g) = 0$:

580 **Proposition 9** *Under strict polygyny, for parameter values such that neither females nor males engage in extractive foraging,*
581 *a female shares some food with her pair-bonded male if and only if he engages in some mate-guarding ($g > 0$), while a male*
582 *does not share food with his females.*

583 **Proof.** Recalling the expressions in Eq. (49) and Eq. (50), we obtain, for $a^*(g) = 0$:

- 584 • $s^* > 0$ and $t^* = 0$ iff $x^*(g) > y^*(g)$
- 585 • $s^* = 0$ and $t^* = 0$ iff $kx^*(g) \geq y^*(g) \geq x^*(g)$
- 586 • $s^* = 0$ and $t^* > 0$ iff $y^*(g) > kx^*(g)$.

587 Since $a^*(g) = b^*(g) = 0$ implies $x^*(g) = F$ and $y^*(g) = (1 - g)^{1/2} \cdot F$, we find that:

- 588 • $x^*(g) > y^*(g)$ for any $g \in (0, 1]$;
- 589 • $y^*(g) = x^*(g)$ for $g = 0$.

590 Taken together, these observations imply the stated result.

591 The intuition for this result is as follows: when neither females nor males engage in extractive foraging, the male's foraging
592 time budget is smaller than the female's whenever he spends time on mate-guarding. If this is the case, the female acquires
593 more food than her pair-bonded male, and since her reproductive success is higher the more equal is her energy intake to his
594 (see Eq. (35)), she then shares some of her food with him to reduce the inequality; this also explains why the male does not
595 share food with his females, since his reproductive success is determined by theirs. Note that by contrast to the promiscuous
596 system, the female shares here because the benefit of doing so is not diluted across more than one male: here she gives food
597 exclusively to her pair-bonded male.

598 **C.2. Sharing when only males engage in extractive foraging.** Next, we turn to parameter regions where only males engage in extractive
599 foraging ($a^*(g) = 0$ and $b^*(g) > 0$). The following proposition refers to this threshold value:

$$600 \quad \tilde{g}(m) = 1 - \frac{F}{H} \left(m - \frac{F}{4H} \right), \quad [62]$$

601 where $m \in \{1, k\}$.

602 **Proposition 10** *Under strict polygyny, for parameter values such that only males engage in extractive foraging, a female*
603 *shares some food with her pair-bonded male if and only if he spends a large enough amount of time on mate-guarding ($g > \tilde{g}(1)$),*
604 *while a male shares food with his females if and only if he spends a small enough amount of time on mate-guarding ($g < \tilde{g}(k)$).*

605 **Proof.** Recalling the expressions in Eq. (49) and Eq. (50), we obtain, for $a^*(g) = 0$:

- 606 • $s^* > 0$ and $t^* = 0$ iff $x^*(g) > y^*(g)$
- 607 • $s^* = 0$ and $t^* = 0$ iff $kx^*(g) \geq y^*(g) \geq x^*(g)$
- 608 • $s^* = 0$ and $t^* > 0$ iff $y^*(g) > kx^*(g)$.

609 Since $a^*(g) = 0$ implies $x^*(g) = F$ and $b^*(g) > 0$ implies $y^*(g) = \frac{F^2}{4H} + (1 - g)H$, we find that:

- 610 • $x^*(g) > y^*(g)$ iff $g > 1 - \frac{F}{H} \left(1 - \frac{F}{4H} \right)$;
- 611 • $kx^*(g) \geq y^*(g) \geq x^*(g)$ iff $1 - \frac{F}{H} \left(1 - \frac{F}{4H} \right) \geq g \geq 1 - \frac{F}{H} \left(k - \frac{F}{4H} \right)$;
- 612 • $y > kx^*(g)$ iff $1 - \frac{F}{H} \left(k - \frac{F}{4H} \right) > g$.

613 Taken together, these observations imply the stated result.

614 The intuition for why females share is the same as above: a male who engages in a significant amount of mate-guarding
615 collects a smaller amount of energy than the females, although he spends some time in extractive foraging (note that for this to
616 be a relevant case, the food theft parameter θ has to be large enough for females to be discouraged from extracting). Since
617 her reproductive success is higher the more equal is her energy intake to his (see Eq. (35)), she then shares some of her food
618 with him to reduce the inequality. However, if g is small (and θ is large enough for females to be discouraged from extractive
619 foraging), it is the male whose food production is the highest, and he then shares some of his food with his females in order to
620 reduce the inequality between his energy intake and theirs.

621 **C.3. Sharing when females engage in extractive foraging.** Next, we turn to parameter regions when females engage in extractive
 622 foraging ($a^*(g) > 0$). Whether or not males also extract food, Eq. (49) and Eq. (50) imply:

- 623 • $s^* > 0$ and $t^* = 0$ iff $x^*(g) > y^*(g) + \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}$
- 624 • $s^* = 0$ and $t^* = 0$ iff $kx^*(g) - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1} \geq y^*(g) \geq x^*(g) - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}$
- 625 • $s^* = 0$ and $t^* > 0$ iff $y^*(g) > kx^*(g) - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}$.

626 The expressions being highly involved, we illustrate them in graphs rather than derive general results. Thus, Figures S7 and
 627 S8 show the parameter regions for which sharing is evolutionarily stable, for two different group sizes ($N = 18$ and $N = 36$,
 628 respectively). In both figures, the left three panels correspond to a lower polygyny rate than the three right panels ($k = 2$ and
 629 $k = 9$, respectively). Likewise, in both figures the rows of figures correspond to different mate guarding intensities ($g = 0$,
 630 $g = 0.25$, and $g = 0.5$, respectively).

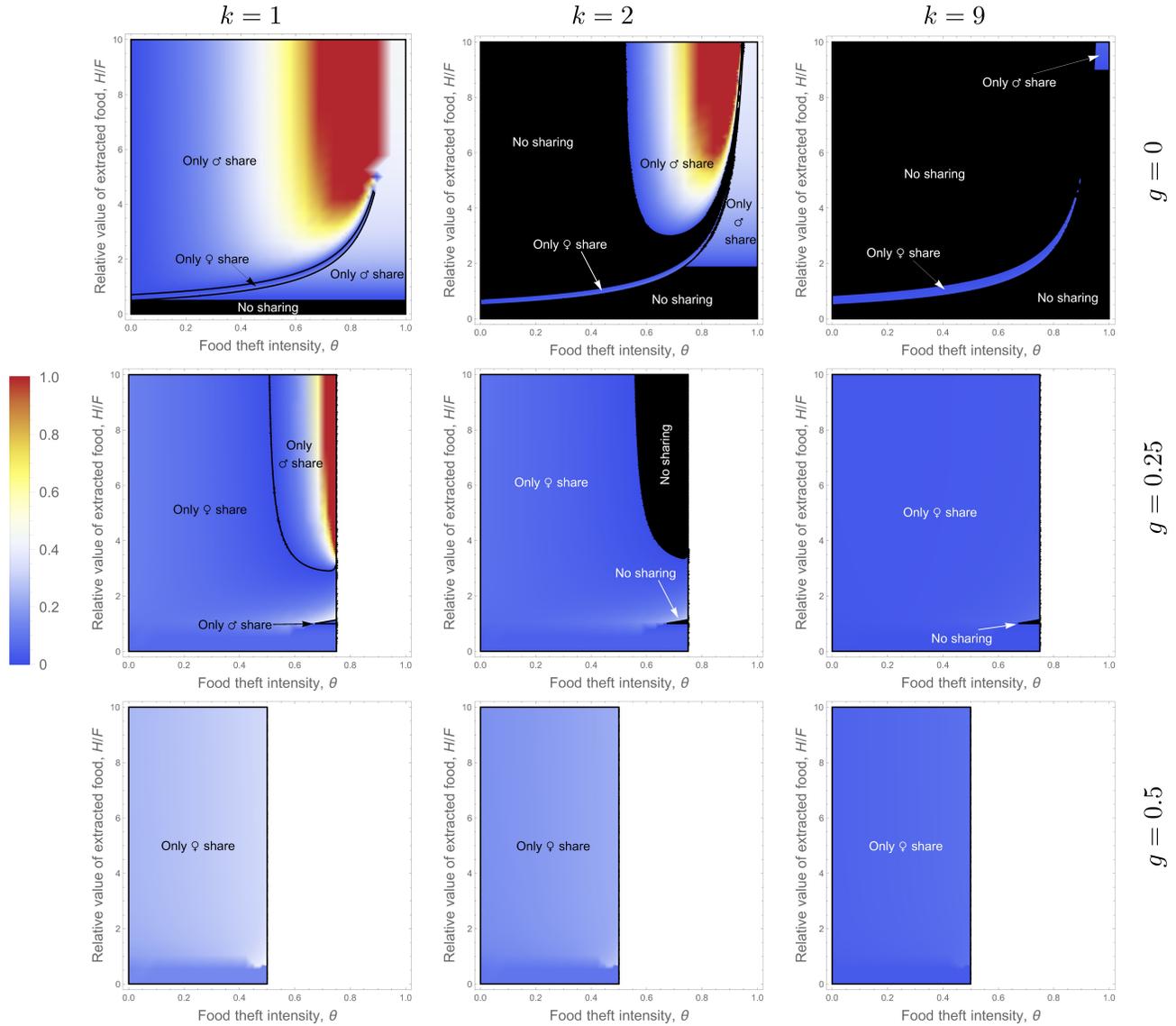


Fig. S7. Regions of parameter space in the monogamous and polygynous mating systems corresponding to the three possible types of ES sharing pairs, (s^*, t^*) , described in Prop. 3. The shading indicates the exact value of s^* or t^* , when it is not 0. Black regions are where both $(s^*, t^*) = (0, 0)$. Note that the white regions represent non-relevant parameter combinations, i.e., $g + \theta > 1$. Parameter values: $N = 18$

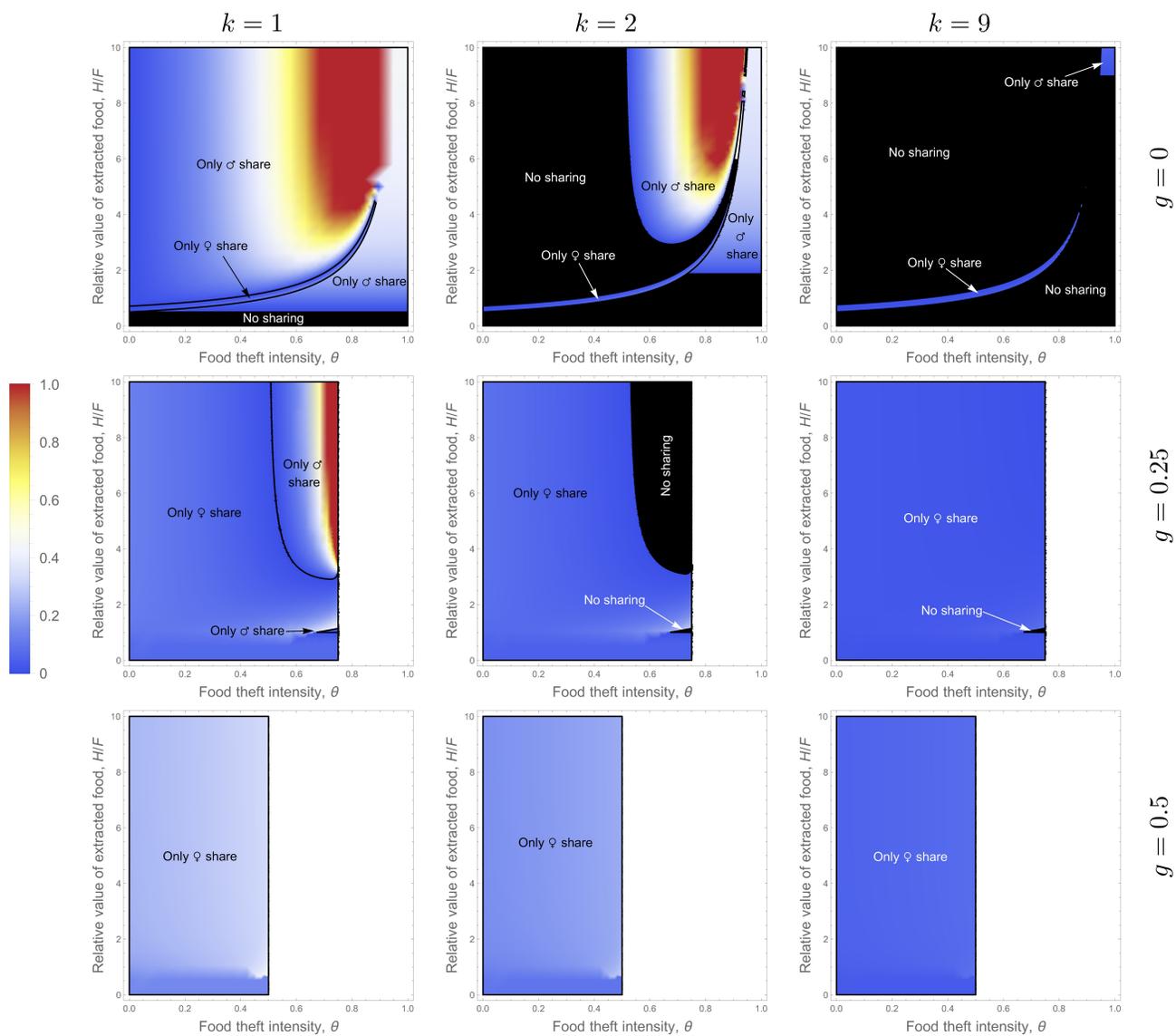


Fig. S8. Same as Fig. S7 but with $N = 36$.

631 **D. Sharing in the monogamous system.** As shown in Proposition 5, whenever possible, in the monogamous system sharing
 632 will equalize the female's and the male's energy intakes, i.e., $X(a^*(g), s^*, b^*(g), t^*) = Y(b^*(g), t^*, a^*(g), s^*)$. Since we have
 633 assumed that the male does not share food that he steals from other females (since he eats it on the spot), such equalization is
 634 impossible to achieve when the amount of stolen food is so large that he would still have more energy than her if he shares
 635 all the collected and extracted food with her, i.e., when $\theta(1-g)a^*(g)H > x^*(g) + y^*(g)$. In that case, $(s^*, t^*) = (0, 1)$ and
 636 $Y(b^*(g), t^*, a^*(g), s^*) > X(a^*(g), s^*, b^*(g), t^*)$.

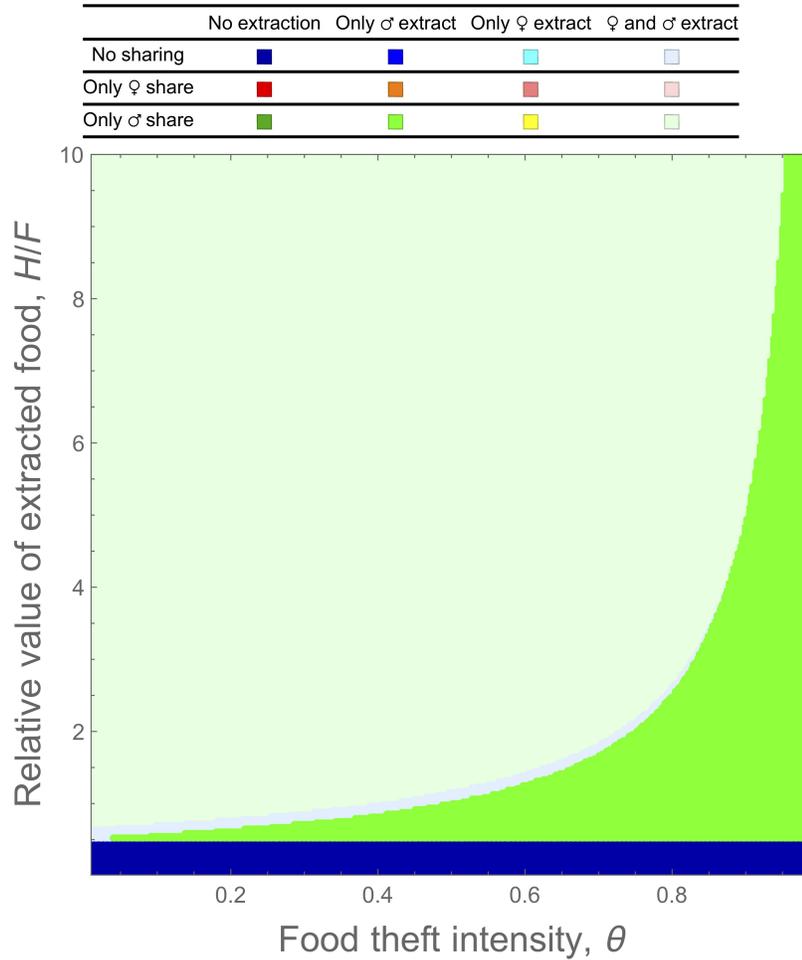


Fig. S9. Sex differences in food production and sharing in the promiscuous mating system. The plotted regions correspond to the three possible types of ES sharing pairs, (s^*, t^*) , and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend.

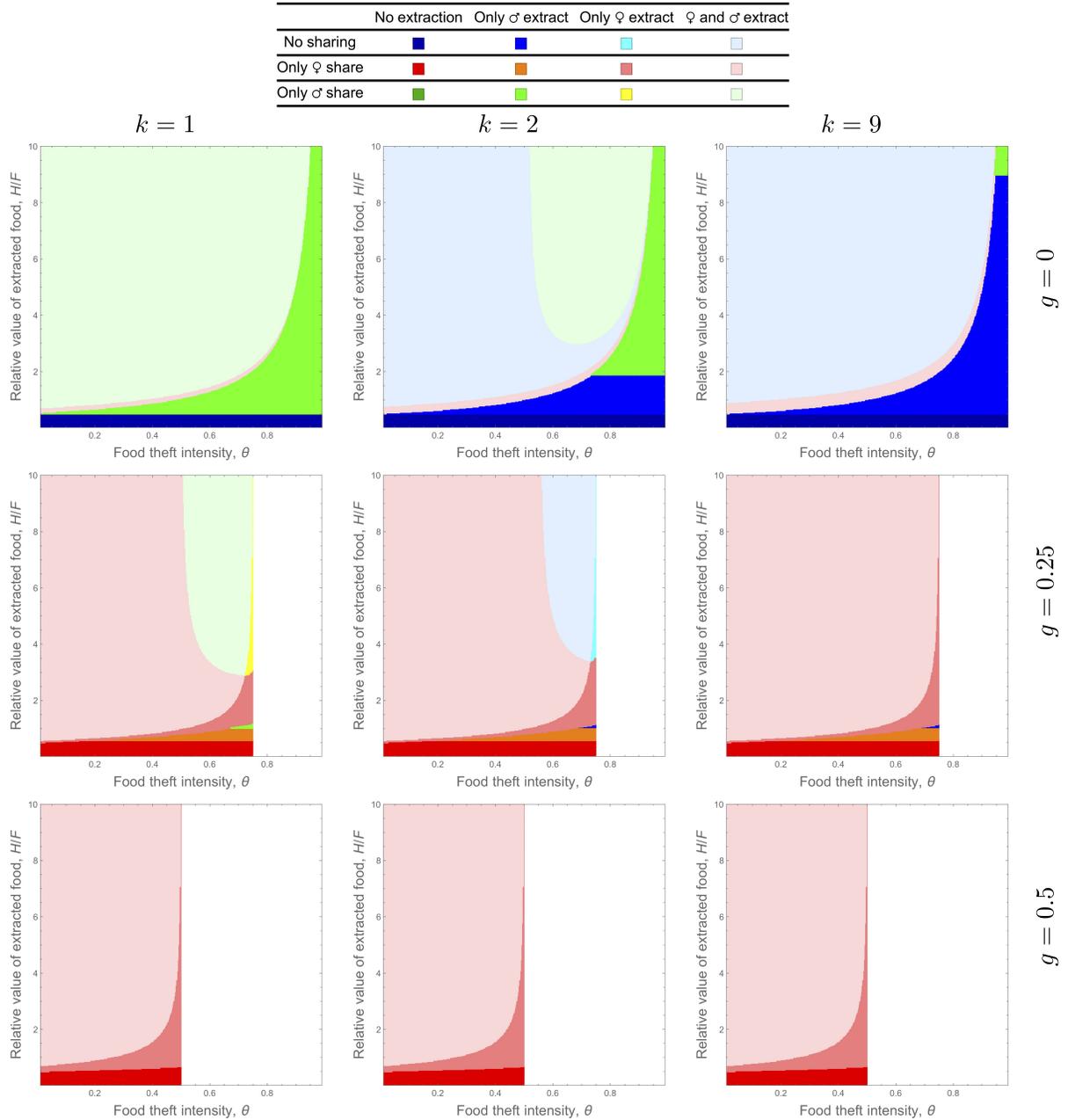


Fig. S10. Sex differences in food production and sharing in the strictly polygynous mating system. The plotted regions correspond to the three possible types of ES sharing pairs, (s^*, t^*) , and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend. $N = 18$.

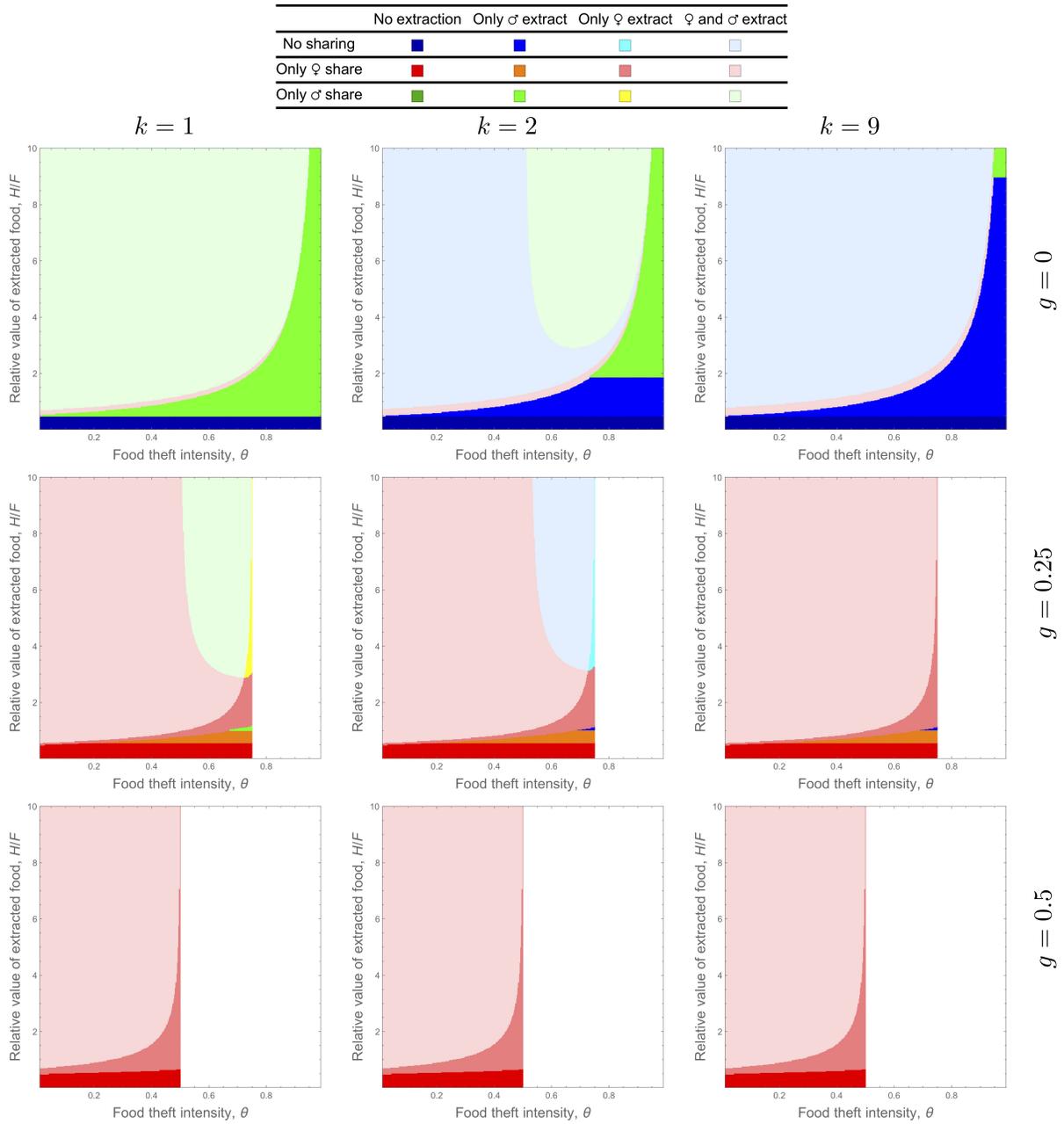


Fig. S11. Same as Fig. S10 for $N = 36$

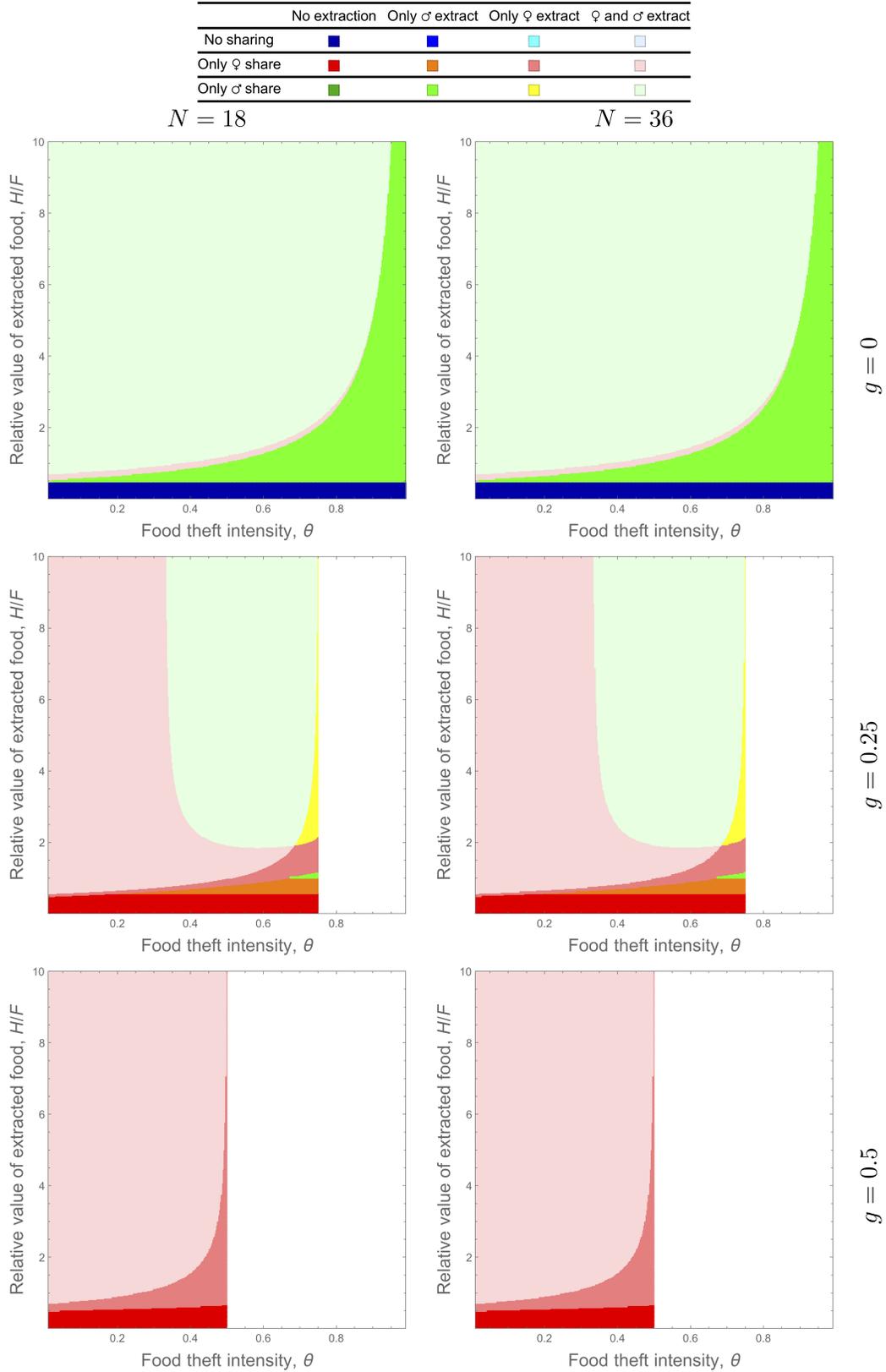


Fig. S12. Sex differences in food production and sharing in the monogamous mating system. The plotted regions correspond to the three possible types of ES sharing pairs, (s^*, t^*) , and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend.

637 **References**

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