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The evolution of early hominin food production and sharing[*]

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Abstract

How did humans evolve from individualistic foraging to collective foraging with sex differences in food production and widespread sharing of plant and animal foods? While current models of food sharing focus on meat or cooking, considerations of the economics of foraging for extracted plant foods (e.g., roots, tubers), inferred to be important for earlier hominins ($\sim$ 6–2.5 mya), suggest that hominins shared such foods. Here we present a conceptual and mathematical model of early hominin food production and sharing, prior to the emergence of frequent scavenging, hunting and cooking. We hypothesize that extracted plant foods were vulnerable to theft, and that male mate-guarding protected females from food theft. We identify conditions favoring plant food production and sharing across mating systems (i.e., monogamy, polygyny, promiscuity), and we assess which mating system maximizes female fitness with changes in the energetic 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 whenever these 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

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mating systems with pair-bonds (monogamous or polygynous), sharing of extracted plant foods by females occurred long before scavenging, hunting and cooking. Such cooperation may have enabled early hominins to expand into more open, seasonal habitats, and provided a foundation for the subsequent evolution of unique human life histories.

Keywords: evolution, food production, sharing, mating systems

1 Introduction

Before agriculture, humans lived by hunting and gathering, a collective foraging strategy that involves sex differences in production and exceptional levels of cooperation [48, 35, 44]. This pattern of subsistence is likely both a cause and consequence of distinctively human life history traits [35, 50, 41, 27]. Among contemporary foragers, hunting and fishing — mainly by men — provide a majority of the calories consumed [41, 54]. As a result, considerable attention has been focused on the evolution of food sharing by males [50, 22, 2]. Nonetheless, extracting, preparing and sharing plant foods — which among contemporary foragers are performed mainly by women — also constitute important economic strategies, which differ strikingly from production, processing and sharing strategies observed in other primates [55, 79, 92, 91]. Forager diets in high latitudes may consist largely of meat and fish obtained by men ([53], but in warmer climates, where early hominins evolved, women contribute substantially to the food supply (median 30.5% of calories provided by adults; range: 15.9–57.0%, n = 9 populations; [42]. Meat is unlikely to have constituted a large part of the diet for early hominins, such as *Australopithecus*, whose teeth and jaws appear adapted for processing extracted plant foods [81, 77]. Early hominins likely lacked sophisticated projectile weapons for hunting (e.g. stone-tipped spears), for which the earliest evidence dates to 500,000 years ago [86]. Recent studies have also challenged long-held views that an increase in meat eating accompanied the origin and subsequent evolution of the genus *Homo* (2.6-1.2 mya; [6]), prompting a need to reconsider whether and how ecological change shaped behavior during hominin evolution. Compared to nonhuman primates, humans engage in an exceptional degree of extractive foraging and active sharing of the foods they obtain [44, 37]. This paper proposes a possible scenario for the evolutionary origins of extractive foraging and the sharing of plant foods.

Extractive foraging involves obtaining foods embedded in substrates, such as deeply buried underground storage organs (USOs) of plants (e.g. roots, tubers) that can be obtained with digging sticks, or hard-shelled nuts that can be smashed open with stones [79]. Because such foods can be large, difficult to obtain, and/or nutrient dense, their acquisition may make sharing economically feasible [60]. 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 [37]), forager women regularly share foods they acquire with nuclear kin and others (e.g., [30, 60, 26]. Sharing with offspring provides direct fitness benefits and thus requires little additional explanation [72], but sharing with unrelated adults poses more of an explanatory challenge, which we address here. Because the extraction and sharing of plant foods is rare among nonhuman primates and produces scant archaeological evidence,

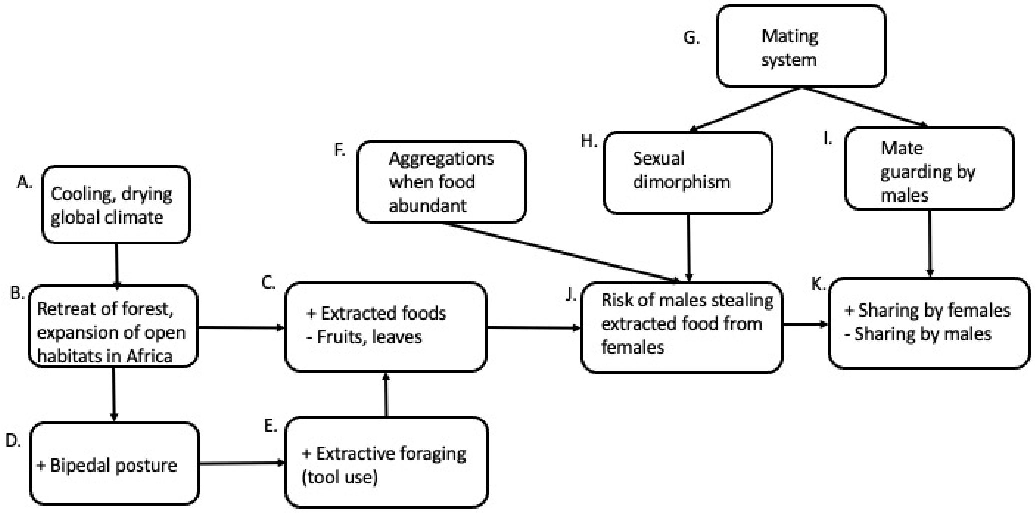

Figure 1: Conceptual framework for the origins of extractive foraging and food sharing by female hominins.

we employ mathematical modeling to identify socio-ecological factors likely to promote these activities among early hominins, and perhaps even their ape ancestors.

Efforts to explain the origin of hominin plant food sharing in particular focus on surplus production by grandmothers [29, 60] and cooking, particularly by females [91]. Grandmothers indeed can contribute to their fitness by provisioning descendants [39], but women extract and share plant foods throughout their adult lives. Cooking likely impacted human evolution profoundly [91, 89], but as we discuss below, several lines of evidence suggest that hominins shared extracted plant foods even before they learned to control fire. We therefore consider in our model the possibility that sharing of extracted plant foods originated in hominins ($\sim$ 6–2.5 mya), before meat and cooking came to predominate hominin diets.

1.1 Conceptual model

Findings from paleoclimatology, paleoanthropology, primatology and human behavioral ecology provide a framework for our conceptual model (Fig. 1). Key factors explaining the evolution of extractive foraging and sharing of plant foods can be categorized broadly as ecological (towards the left of Fig. 1) and social (towards the right).

Ecological change

The ape ancestors of hominins likely lived in forests and consumed mostly easy-to-acquire, collected plant foods that required little extrasomatic processing, similar to present-day *Pan* and *Gorilla* [51]. 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 [14]). 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 modern hunter-gatherer behavior suggest that early hominins increasingly relied on hidden and protected foods including USOs, nuts, and seeds from fruits with hard shells, such as baobabs (Fig. 1C; [79, 46, 53, 53, 51]). Ecological change toward more open, seasonal habitats potentially created selection pressure for bipedal posture and locomotion (Fig. 1D), a defining hominin trait; bipedality may have evolved for feeding on the small trees and shrubs that predominate in open habits [33], wading to obtain protein-rich aquatic foods [90, 58], or for other reasons. As hominins evolved effective bipedal locomotion, this increased their ability to travel between widely dispersed food sources [68, 74, 45]. Increasingly bipedal posture also freed the hands to use tools and carry food [15]. In more open habitats, decreased abundance of fruits and leaves and increased abundance of hidden and protected plant foods would have increased both the relative value of extractive foraging (Fig. 1E) and reliance on culturally transmitted tools and knowledge (e.g., [82, 17]. The discoveries that some populations of modern chimpanzees use stones to crack nuts [9] and sticks to dig for USOs [31] indicate that these extractive foraging strategies likely would have been feasible for early hominins. When cracking nuts, female chimpanzees actively and passively share nut meat with their young offspring [20].

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 modern chimpanzees and bonobos, early hominin mothers likely shared more difficult-to-acquire foods with their offspring [72, 55, 92]. Whether and why hominins evolved to share plant foods with non-kin, including mates in different potential mating systems that may have characterized early hominin social groups, 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 including hunted meat (e.g., [40, 36]. Efforts to explain the origins of hominin food sharing therefore have focused largely on sharing in the context of mating relationships, as a means by which males either invest in offspring in exchange for paternity certainty [22], increase extra-pair mating opportunities by widely broadcasting signals of phenotypic quality [28], or by which both sexes provide complementary resources in a reciprocal fashion to maximize the pair's economic efficiency and fitness [35, 42, 2].

These scenarios typically propose simultaneous changes in mating system and food sharing, mediated either by male provisioning of mates and offspring [35, 41, 22], group-wide signaling of male quality [28], or the cooking of food by females [91]. However, evolutionary sequences consisting of a sequential series of small changes are more likely to occur than simultaneous, large changes in multiple traits [16, 13]. We therefore seek to explore a sequence of events that does not require simultaneous evolutionary changes of both mating system and sharing behaviors.

The mating systems of early hominins and their ape ancestors remain unknown [64, 65]. Nonhuman apes today typically exhibit one of three mating systems: gibbons and siamangs (*Hylobatidae*) are mostly monogamous; gorillas are (*Gorilla*) mostly polygynous, and the rest are promiscuous (*Pongo*, *Pan*; [83]. The mating system 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 occurs in promiscuous and polygynous systems (e.g., [3]), males can evolve to be much larger than females [64, 65]. Such sexual dimorphism in body size may enable males to take food from females with impunity (Fig. 1*H* and 1*J*), as occurs in modern chimpanzees [23] and hamadryas baboons [78]. Given evidence of substantial body size sexual dimorphism for many hominin species, Wrangham et al. [91] proposed that when female hominins began regularly cooking (∼1-2 mya), females established pair-bonds with specific males to protect the food obtained by a given female from theft by other males. But long before hominins began regularly cooking, the extracted plant foods upon which they relied presumably were vulnerable to theft, as is observed among modern nonhuman primates.

Compared to collected foods such as leaves or fruits, extracted plant foods face greater vulnerability to theft for at least 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 some of the labor undertaken to acquire them. For example, among olive and yellow baboons (*Papio anubis* and *P. cynocephalus*, respectively), higher-ranking individuals commonly supplant lower-ranking individuals when feeding on the pea-sized corms of grasses and sedges, which are buried just under the surface [7, 38]. Modern hunter-gatherers in Africa acquire deeply buried USOs that, compared to corms, are bigger, contain more energy, and take longer to acquire [46, 53]. These characteristics may make such foods even more vulnerable to supplanting, scrounging and other forms of theft (Fig. 1*J*). But modern hunter-gatherer women generally forage in small cooperative groups while men hunt elsewhere [53]. Baboons, lacking both sex differences in food production and whatever psychological mechanisms promote reliable collective foraging, may provide a more relevant model than modern hunter-gatherers for understanding foraging competition in early hominins.

We consider "theft" to include transfers of food resulting from a range of behaviors, including supplanting individuals at feeding sites, harassment, co-feeding, 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 [76]. Risk of theft would depend not only on whether a given food item is extracted or collected but also on the degree of sexual dimorphism in body size (Fig. 1*H* and 1*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 sexual pair-bonds determines whether a female can expect to benefit from the presence of one particular male versus that of several males.

First, as Wrangham et al. [91] propose for cooking, risk of food theft may reduce incentives for females to produce a surplus from extractive foraging, including for offspring (Fig. 1*J*). If, however, males guard females from mating attempts by rival males, as occurs widely in primates [1], then guarding males also would thwart potential food thieves and enhance female willingness and ability to extract plant foods (Fig. 1*I* and 1*K*). Any benefits females accrue from such mate guarding should be greater in species with pair-bonds, either monogamous or polygynous, because in these species males guard females throughout their reproductive cycle, whereas in promiscuously mating species, males guard females mainly when they are receptive to mating [57, 25].

Second, in addition to facilitating female extractive foraging, mate-guarding males can also provide benefits to females through support in intergroup conflict [21, 52, 70], territorial competition [87, 49], and protection from predators [56] and infanticide [75, 80] Fig. 1*I*).

2 Mathematical Model

We designed our mathematical model to investigate how the relative value of extracted foods and risk of food theft affect both the evolution of extractive foraging and of sharing in different potential mating systems that may have characterized early hominins.

In our model, males and females can choose either to collect foods of lower nutrient value (i.e., leaves or fruits), or forage using extractive techniques for higher value food items (e.g., tubers and nuts). Both sexes can also choose to share some of their acquired food with some adult(s) of the opposite sex. Males can also steal the higher value extracted food items from females. In modern primates, theft and other forms of feeding competition commonly occur among same-sex individuals, but for simplicity's sake, here we do not attempt to model feeding competition including food theft among same-sex individuals. We compare the evolution of food production and sharing behaviors in three mating systems, which differ in male mate-guarding and the extent to which male presence can benefit females and their offspring.

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.

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 is cultural, but occurs on two distinct time scales. On the time scale of an individual's lifespan, foraging strategies are individually learned and we assume that 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 culturally transmitted from one generation to the next, and we identify *culturally stable sharing strategies.*

There is a mating system in place, which does not evolve. We compare optimal foraging and culturally stable sharing strategies in three different mating systems: *promiscuity* (pair-bonding is absent), *monogamy* (each male has one pair-bonded mate), and *polygyny* (some males have $k \geq 2$ pair-bonded mates while others have none). The promiscuous mating system differs from the non-promiscuous ones in two key ways.

First, in the two systems with pair-bonding, males guard their (pair-bonded) female(s) continuously, in all reproductive states (as in hamadryas baboons, *Papio hamadryas* and gelada monkeys, *Theropithecus gelada*, [25]), rather than just when females are sexually receptive. We presume that efficient mate-guarding requires attention, which imposes a trade-off for males between mate-guarding and extractive foraging. Continuous mate-guarding will be seen to drive 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.

Second, in all the mating systems female reproductive success is an increasing function of both own energy intake and the energy 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, which will take different forms depending on the mating system.

2.1 Foraging behavior

Each female divides her foraging time budget (net of other activities such as 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). Letting each female's foraging time budget be 1, $a \in [0, 1]$ is the time a female spends extracting, while the remainder of the foraging time, $1 - a$, is spent collecting. A female who uses foraging behavior a and who lives in a group where males spend time g on mate-guarding, acquires total energy

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

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 non-evolving 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 vs. 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:

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

where $\delta_a \in \{0,1\}$ is a dummy variable that equals one if there is some extracted food to be stolen from females, and zero otherwise. Males and females are equally efficient at collecting and extractive foraging, and they have the same total time budget net of activities not considered in the model (e.g., mating, sleeping, etc.). However, males have less time at their disposal 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.

2.2 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 behaviors by both males and females determine the total amount of energy available in the group and how this energy is distributed among the adults in the group.

The promiscuous mating system [i.e. no pair-bonds]

In a promiscuous mating system there are no pair-bonds, and 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. Likewise, if a male shares, he gives the same amount to all the N females in his group. After food transfers occur—both through food theft and food 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 given by

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

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

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

The last term represents the energy obtained by way of food theft: each male steals a share $\theta \in [0,1]$ of the food extracted by one female, $a^* H$.

Each female transmits her cultural sharing trait faithfully to all her female offspring, except for the rare case in which a cultural innovation (mutation) arises spontaneously. Assuming that the sex ratio is balanced at birth and independent of the mother's sharing behavior, a female's cultural reproductive success equals (half of) the expected number of her biological offspring that survive to sexual maturity. We take the number of offspring to depend on the female's own energy, and the survival probability of offspring to depend also on the male presence, and hence on their energy. In a population where resident females share s and resident males share t, the reproductive success of a mutant female who shares $\hat{s}$ takes the following form:

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

The first term is the female's energy. The last term is the average male energy in the group. The parameter $p \in [\frac{1}{N},1]$ measures how much the female benefits from services provided by the males in her group, such as assistance in competition over resources and protection against predators and infanticidal males. For example, $p = 1/N$ means that she may expect one male to come and 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 the 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 reproductive success

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

The monogamous and polygynous mating systems (i.e. including pair-bonds)

In a polygynous mating system some males (exactly N/k of them) reproduce exclusively 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 she shares 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 he shares 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

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

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

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

where we assumed 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 reproductive success of a mutant female who shares $\hat{s}$ takes the following form:

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

By contrast to the promiscuous mating system, here the female only receives male services of protection (from predators and infanticidal males) and assistance in resource competition from her pair-bonded male. The parameter $q \in [\frac{1}{k}, 1]$ measures how much she benefits from these services provided by her pair-bonded male. 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 unit 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 reproductive success is simply determined by the number of females k to whom he is pair-bonded:

$$\hat{v}(\hat{t}, t; s) = k \cdot \hat{X}(s, \hat{t}) \cdot q\hat{Y}(\hat{t}, s; s) \tag{10}$$

We do not account for extra-pair matings: all the male offspring of the females to whom the focal male is pair-bonded are exposed to him as a cultural model, and a male will thus transmit his cultural trait to the offspring of his pair-bonded females, whether or not he is their biological father.

2.3 Cultural stability

In order to find the *Culturally Stable* (CS) pair of food sharing strategies (s^*, t^*), we use the assumptions of adaptive dynamics, but for cultural traits. Namely, innovations (or mutations) 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 a culturally stable pair of sharing strategies (s^*, t^*), a mutant female's reproductive success is maximized for s^*, given that all other females share according to s^* and all males according to t^*, and a mutant male's reproductive success must be maximized for t^*, given that all other females share according to s^* and all males according to t^*:

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

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

3 Results

3.1 Pair-bonds depress male extractive foraging but promote female extractive foraging

The amount of time that males and females spend foraging on different foods depends on: (1) the relative value of extracted versus collected foods (H/F); (2) the risk of food theft (θ), and (3) whether males mate-guard (g). Fig. 7 shows, for three different values of g, the optimal extractive foraging time for each sex, as a function of H/F and θ. As might be expected, both males and females 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 take place. First, females reduce time spent on extractive foraging 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 the non-promiscuous mating systems, where $g > 0$, females are somewhat protected from food theft by other males thanks to the mate-guarding by their pair-bonded male, and this induces higher levels of female extractive foraging. Second, food theft and mate-guarding are time-consuming activities that reduce time spent in extractive foraging 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 as soon as H/F is large enough. See Propositions 6 and 8 in the Appendix.

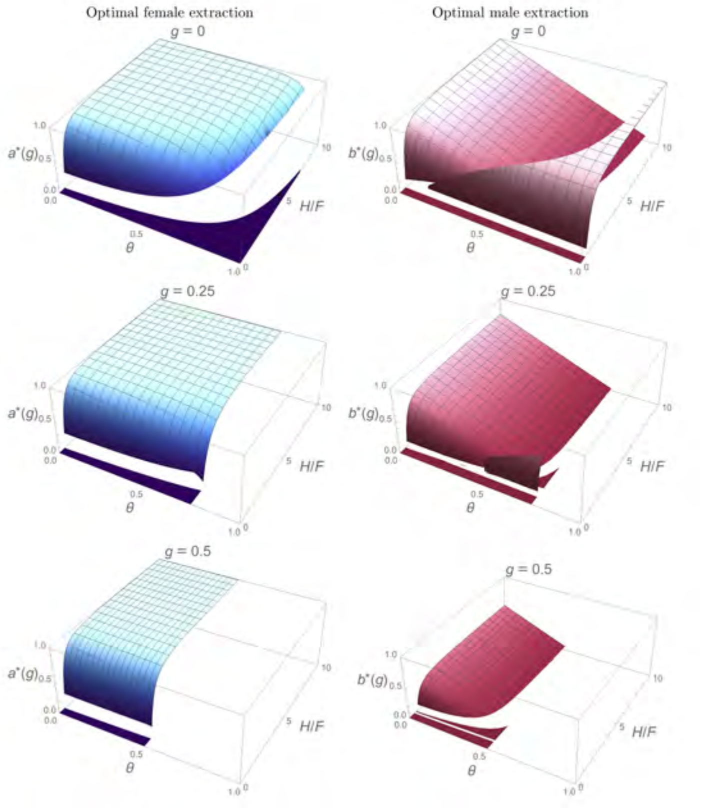

Figure 2: Optimal strategies of extractive foraging by sex. The left (respectively right) column of figures shows, for three different values of mate guarding, g (from top to bottom, $g = 0$, $g = 0.25$, and $g = 0.5$), the optimal amount of time that females ($a^*(g)$) (respectively males ($b^*(g)$)) 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 $\theta + g + b^*(g) \leq 1$.

3.2 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. 14; Proposition 7 in the Appendix). 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.

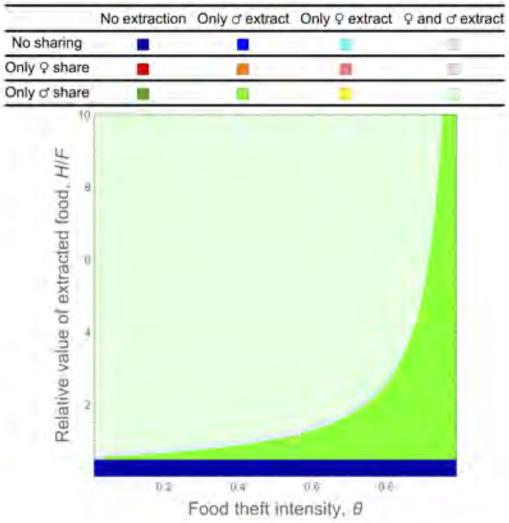

Figure 3: Sex differences in food production and sharing in the promiscuous mating system. The plotted regions correspond to the combinations of three possible types of culturally stable sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table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

In contrast, when pair-bonds exist, females share food with males under a broad range of conditions including varying H/F values (see Fig. 15, and Propositions 5, 9, and 10 in the Appendix). Two factors explain this. First, the benefit from giving up one's 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, each female typically collects and extracts 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. 15 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 engage in mate-guarding. A noticeable difference between the polygynous and the 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 (θ) is high enough for him to accumulate excess energy compared to his pair-bonded female.

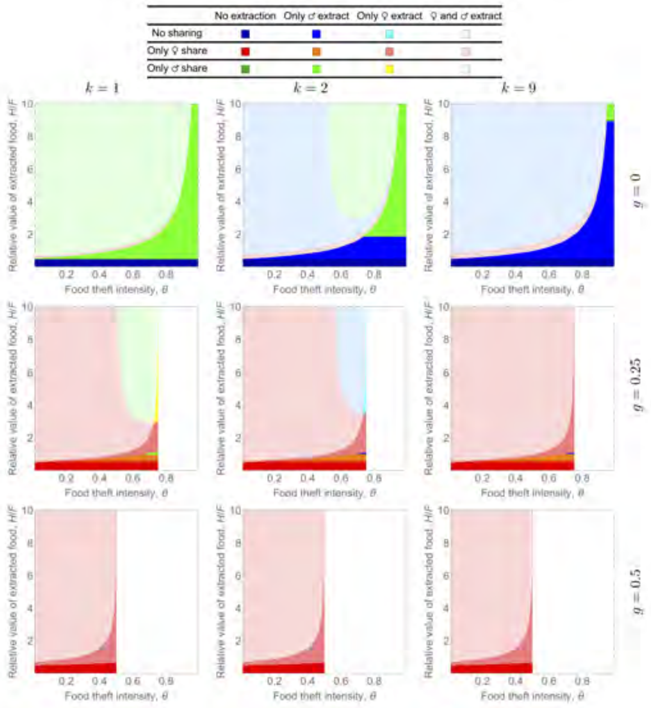

Figure 4: Sex differences in food production and sharing in the monogamous and polygynous mating systems. The plotted regions correspond to the combinations of the three possible types of culturally stable sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend. $N = 18$.

3.3 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. It thus suggests a possible rationale for this combination of sex differences in food production and sharing. For a a complete lack of male extractive foraging to arise, the relative energetic value of extracted versus 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 Prop. 8 in the Appendix; Fig. 15). 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 (section C.3 in the Appendix); 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 non-promiscuous system, since females never share in the promiscuous one; and (2) female investment in extractive foraging relative to the male investment is more pronounced in the non-promiscuous systems, due to the time that males invest in mate-guarding in these systems (see Fig. 1).

3.4 Ecological and social factors affect fitness advantages conferred by sex differences in food production and sharing

Here we use our model to assess how a change in the energetic value of extracted versus collected foods (H/F), which presumably increased starting in the late Miocene (Fig. 1A-E), influences the relative efficiency of promiscuous and non-promiscuous mating systems; by "efficiency" we mean the average female reproductive success obtained for a given amount of time spent on foraging.

Thus, Fig. 5 compares variation in female reproductive success given optimal foraging and culturally stable sharing strategies under the promiscuous mating system ($g = 0$) 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 reproductive success per unit of adult time devoted to 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 (see (28)). Hence, we divide female reproductive success by $1 + N(1 - \delta\theta)$. In the non-promiscuous 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 (see (46)). Hence, we divide female reproductive success 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, and assistance in competition over resources) provided by one male, by setting $p = 1/N$ in the promiscuous system and $q = 1$ in the non-promiscuous systems.

Two interesting findings are shown in Fig. 5. First, an increase in the relative energetic value of extracted versus collected foods (H/F) generally has a non-monotonic effect on the advantage that pair-bonds (*cum* mate-guarding) confer on female reproductive success compared to the promiscuous system. As H/F reaches values triggering extractive foraging (i.e., for values of H/F slightly below 1; see Figure 7), there is first a reduction in the fitness advantage of the non-promiscuous system over the promiscuous one. However, as H/F increases further, the fitness advantage of the non-promiscuous 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 non-promiscuous system enhances its fitness advantage over the promiscuous system (the ratio is higher in the bottom than in the top row of Fig. 5). In fact, comparing the fitness advantage for the highest values of H/F with those for which no extractive foraging occurs, we see that the higher level of mate-guarding confers a more pronounced fitness advantage of the non-promiscuous system over the promiscuous one.

4 Discussion

In summary, our model identifies a range of conditions that promote extractive foraging (Fig. 7) and food sharing (Fig. 14, Fig. 15) by males and females. Both males and females extract foods when doing so 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.

Mating system profoundly affects food sharing strategies. Under promiscuous mating, males share with females under a broad range of conditions, but females do not share with males (Fig. 14). When males and females have pair-bonds, either monogamous or polygynous, food sharing tends to flow from females to their pair-bonded males (Fig. 15). Pair-bonded males rarely share with females, except when they spend little time mate-guarding (e.g., Fig. 15, $g = 0$, $k = 1$), or when the value of extracted foods is extremely high (e.g., Fig. 15, $g = 0.25$, $k = 1$, $\theta > 0.5$). The overall pattern of results differs greatly between societies with and without pair-bonds, but differs little as the number of females per male (k) varies from 1 to 9.

Females share with their pair-bonded males even when no theft occurs (θ=0), provided males invest in mate guarding. Compare, for example, the row corresponding to g=0.25 to that corresponding to g=0 in Fig. 15. Why would females share with males if there is no risk of theft? Males provide other benefits to females, including protection from infanticide

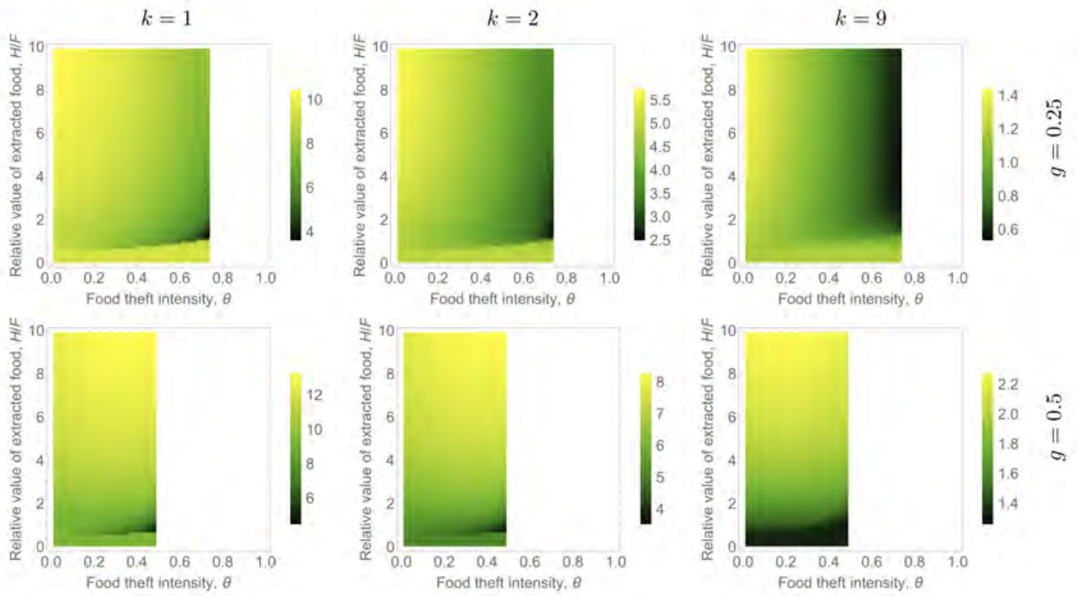

Figure 5: Comparison of reproductive success between the promiscuous mating system vs. monogamous (leftmost column) and polygynous systems (middle and rightmost column). The shading represents the ratio of the reproductive success per unit of adult time devoted to foraging evaluated at the culturally stable state in either monogamous or polygynous systems (numerator) over the fitness per unit of adult time devoted to foraging in the promiscuous system (denominator), i.e., $\dfrac{\hat{w}(s^*, s^*; t^*)/(2 - \delta\theta - g)}{\hat{w}_P(s^*_P, s^*_P; t^*_P)/(1 + N(1 - \delta\theta))}$, where the index P indicates the promiscuous system, for $\hat{w}_P(s^*_P, s^*_P; t^*_P)$ see (28) and for $\hat{w}(s^*, s^*; t^*)$ see (46); we used the values $p = 1/N$ and $q = 1$ (so that each female gets services (protection from predators and infanticidal males, and assistance in competition over resources) provided by one male in each system). The shading scale is panel-dependent; see the panel-specific legend to the right of each panel. $N = 18$.

and predators, but in providing these benefits, they pay costs of mate guarding. Under these conditions, females gain fitness benefits by providing some food to males to offset their mate-guarding costs.

These results suggest that sharing from females to males may have emerged early in hominin evolution, before scavenging, hunting, or cooking became important for hominin subsistence. The pattern of plant food sharing observed in present-day hunter-gatherers thus may have ancient roots. These findings differ from existing scenarios in which sharing by males and females emerges simultaneously, when males began hunting (as [41] seem to imply). Our model shows that females could benefit from sharing food with males, even if males shared no food with them.

In our model, females do not share under conditions of 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 [91]. 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 females would be willing to share food with males.

Under a broad range of conditions, our model finds that with profitable extractive foraging, females have higher fitness with pair-bonds than promiscuity (Fig. 5), and that this advantage becomes more pronounced as the relative value of extractive to non-extractive foraging increases. This suggests that if pair-bonds existed in early hominins or their ape ancestors, the presence of mate-guarding males may have 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 discuss evidence from paleoanthropology and primatology relevant to the model's assumptions, results, and novel predictions, as well as evidence that could be obtained by future studies. The final sections discuss this model in relation to other models of the origins of food sharing in hominins.

4.1 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 outlined in our conceptual model (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) male-female 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 consider evidence available for each of these conditions, as well as potential sources of evidence that could be obtained by future studies.

Profitability of Extractive Foraging

We currently lack detailed knowledge of the diets of early hominins, making it difficult to assess the profitability of extracted versus collected food items with any confidence. However, it is likely that as the climate of late Miocene Africa became cooler and drier, fruits and leaves became seasonally scarce in many habitats [19, 11]. The seasonal scarcity of such resources is thought to be the main factor limiting the distribution of nonhuman apes in Africa today [84]. 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 [46, 8]. Among present-day hunter-gatherers, the Hadza of Tanzania prefer foods such as meat, honey, and berries to tubers [8]. 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 [47], are highly prized by foragers [8, 47]. While early hominins surely did not process foods as extensively as do modern humans, observations of chimpanzees cracking nuts [10] and evidence that they dig for USOs [31] suggests that early hominins also could obtain such foods. It therefore seems likely that hominins relied to a considerable extent on extracted foods, which were more profitable than collected foods in many circumstances, particularly in seasons with few fruits and leaves available.

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 versus extracted foods eaten by apes and hunter-gatherers in Africa would also be informative.

Vulnerability of Extracted Foods to Theft

Whether hominins faced a risk of theft when obtaining and eating extracted foods likely depended on qualities of the particular food, such as the relative quality and the extent to which it could be monopolized. Behavioral observations of nonhuman primates provide useful insights.

In *Pan*, female food acquisition efforts can indeed vary depending on the risk of theft by males. Chimpanzee females hunt less often than males, whereas bonobo females hunt at least as often as males. This difference appears to depend mainly on the risk of food theft: chimpanzee males outrank females and steal from them with impunity, whereas bonobo females often outrank males and face little risk of food theft [23]. When chimpanzees crack nuts, offspring beg for nut meat from their mothers [20], but other individuals do not attempt to steal nut meat, perhaps because nuts are abundant (Wittig, pers. comm.). Chimpanzee food theft thus mainly consists of males stealing animal products from females [23].

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 extracted corms than other foods [7]. Yellow baboons (*Papio cynocephalus*) also frequently supplant one another when extracting fever tree gum [66]. 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” [66].

Hominin Mating Systems

We modeled three different mating systems for early hominins because we do not know the mating system(s) of these species. 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 of body size and canine height. In primates, males are larger than females, and have longer canines, in mating systems characterized by intense contest competition among males: polygyny and promiscuity [63]. Fossil evidence indicates that in early hominins [24], and in many of the apes that lived before hominins evolved [4], males were larger than females, to a greater extent than in either modern humans or chimpanzees (see 67 for an opposing view). If estimates that hominin males were substantially larger than females are correct, this would suggest a mating system in which males needed to be large to compete successfully — more like polygynous gorillas than monogamous gibbons or promiscuous chimpanzees [32].

In contrast to this evidence of substantial sexual dimorphism in body size, canine size differed only moderately between the sexes [63]. Some argue that this indicates that monogamy characterized hominins [85]. Others, however, have argued that being bipedal, hominins fought with their hands and perhaps also weapons, rather than their teeth [15], which freed them to optimize their teeth and jaws for feeding efficiency [34].

Second, a key indicator of mating system in extant primates is the presence of swellings of the ano-genital skin, which provide a graded signal of fertility, and are more common in multi-male mating systems [59]. Gibbons exhibit small sexual swellings, consistent with behavioral evidence that female gibbons infrequently mate with multiple males [5]. The presence of large sexual swellings in chimpanzees and bonobos, but not other apes, suggests that frequent multi-male 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 multi-male mating system [18, 59].

Third, some of the largest genetic changes inferred to have taken place in *Pan* since the divergence of *Pan* and *Homo* are associated with features of male reproduction, including sperm production [12, 32]. 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, than male-female bonds would be an ancestral rather than derived trait of hominins.

Effects of pair bonds

Our model tests a prediction from [91] that in hominins, alliances between males and females were a central factor promoting female investment in food production. However, if (as noted above) polygyny was an ancestral trait for hominins, then bonds between males and females may have supported the emergence of extractive foraging and food sharing, rather than evolving as a consequence of these behaviors.

In our model, in when pair-bonds exist, female fitness depends directly on the male's energy ($\hat{Y}(t, \hat{s}; s)$). This term is meant to capture the benefits that female primates may obtain from male services, including protection from infanticide and predators, and help during intergroup conflict, which can result in more access to resources. The model assumes that those benefits are higher when pair-bonds ensure that females have 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. So long as female 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 (*Papio hamadryas*).

The extent to which mate guarding by males 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 [69, 88, 21], in which male efforts to defend mates from rival males provide protection of food resources as a byproduct. For example, female chimpanzees reproduce more quickly when the size of the territory defended by males is larger [87]. Swedell ([78] notes that female hamadryas baboons (*Papio hamadryas*), 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 [78, 71]. Among olive baboons (*Papio anubis*), feeding competition was the most common context of aggression between males and their female "friends" [73]. Whether females gain net feeding benefits from their association with males is an open question.

The role of males in improving access to specific food resources requires further study. Detailed observations on species such as gelada monkeys (*Theropithecus gelada*) and hamadryas baboons that live in multi-level societies, in which males and females form enduring breeding bonds, would be particularly relevant.

4.2 Comparison with existing models of food sharing

Our model differs from existing models in that it focuses on (i) sharing of plant foods rather than meat (cf., [41, 43]); (ii) sharing by females rather than males (cf., [50, 22, 2]); (iii) sharing by all adult females, rather than just grandmothers (cf., [29, 60]); (iv) sharing before the invention of cooking (cf., [91]); and (v) sharing as a consequence of mating system, rather than a cause of changes in the mating system (cf., [91]). We view our findings as complementary to many of these previous studies; if females began sharing plant foods early in hominin evolution, this seems likely to support, rather than undermine, the eventual importance of males, meat, grandmothers, and cooking for the collective foraging strategies documented among modern hunter-gatherers. Insofar as sharing plant foods promoted the evolution of psychological traits promoting food sharing, the sharing of plant foods by females that we focus on here may have promoted the later evolution of food sharing by males.

4.3 Hunting and meat sharing

In our model, males share extracted foods only in promiscuous mating systems. This result may seem surprising, given in modern foragers — characterized mainly by monogamous and polygynous mating — males share extensively with females. However, in our model, 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) which 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. Indeed, in our model, promiscuous mating results in a similar pattern to what has been documented 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 [23]. 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 according to which female extraction and sharing evolved before men began to hunt in a coordinated manner. Our model is thus complementary to existing models, which focus on male meat hunting and sharing (e.g., [2]).

Early hominins likely did not have the weapons needed to kill big game, since this requires sophisticated technology, such as spears, which didn't come along until much later. Additionally, in modern humans, men and women forage separately. Earlier hominins presumably lacked language, and therefore lacked socio-linguistic means to monitor mating behavior. Separate foraging by men and women therefore would impose severe trade-offs between hunting and paternity certainty, and seems unlikely to occur.

Another key difference between our model and the embodied capital model of Kaplan et al. [41] is that in our model, increasing dietary reliance on extracted foods and sexual cooperation is not necessarily accompanied by increased brain size. We show that as the relative profitability of extractive foraging increases (due to ecological changes that are independent of cognitive capacities per se), 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 may have 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 model findings accord with existing fossil evidence indicating that early hominins occupied diverse habitats long before observed increases in hominin cranial capacity.

4.4 Surplus production

One additional question that arises from our model is: if female fitness generally depends on male energy, and females benefit to a greater extent from this when pair-bonded with a particular male — why don't females more often share food with males? As noted in a review of food sharing in primates [37], "Sharing from females to males was too rare to test." The answer may be that primates generally can't produce surplus food efficiently. Extractive foraging, however, may provide means to produce surpluses at low marginal costs. When digging up tubers, for example, digging up a tuber large enough to share with others may require little more effort than digging up a smaller tuber.

Primates that gain access to food stored by people provide informative illustrations of what can happen upon the invention of methods to gain access to rich food supplies. For example, at Gombe National Park, Tanzania, many baboons have learned to open doors of park and research staff by turning the door hands, and thereby gain access to food stored in the houses. People then began locking their doors, but leaving the key in the lock, because risk of theft by humans in this small community was low. One female baboon, *Harina*, learned to unlock doors by turning the key. She was followed around by males who took advantage of her door opening skills (MLW, personal observation).

A broader comparative perspective provides cases where females that are able to produce surplus food do share with males. For example, group hunting by lions permits the capture of large prey *Panthera leo*. Females permit males to take food from them without a fight, at least in part because males are 40 percent larger than females [61]. Additionally, females benefit from other services males provide, such as territory defense and protection from infanticidal males [62], and so benefit from investing in the well-being of males, much as we propose here for early hominins.

4.5 Conclusions

Our findings indicate that hominins may have begun sharing plant foods long 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 males, provided they had access to surplus foods. In this case, the invention of digging sticks and other extractive tools provided the keys needed to a storehouse of food surpluses.

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Appendix

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

A Mathematica notebook containing all the code necessary to produce the figures can be accessed at the following address: `https://www.wolframcloud.com/obj/slimane.dridi0/Published/The%20evolution%20of%20early%20hominin%20food%20production%20and%20sharing.nb`

A Model

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

We assume that the female (and respectively male) food sharing trait is transmitted vertically from mother to daughters (and respectively from fathers to sons). This can be interpreted as a cultural learning process where adult individuals that have more offspring are more likely to be copied by juveniles in the group. Foraging on the other hand is considered to be learned during an individual's lifespan, and we will assume that each individual reaches the optimal foraging strategy quickly enough for the learning period to be ignored. We will see below that we could also interpret this optimization process as frequency-independent cultural evolution of the trait.

Formally, consider a population subdivided into groups, all consisting of the same number of adult males and adult females, denoted N. Pair-bonds may exist between males and females within each group. We assume that a limited number of males are pair-bonded. Conditional on there being some pair-bonded males at all, each such male is pair-bonded with k females, while the remaining males ($N - N/k$) are mateless (note that all females are distributed equally across the pair-bonded males). 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 are no mateless females. Under these assumptions the parameter k fully defines the mating system, which can be monogamous ($k = 1$), polygynous ($1 < k < N$), or promiscuous ($k = 0$) (see Fig. 6). We rule out polyandry by assumption, since this mating system is rarely documented in great apes and likely did not characterize mating systems of early hominins. Importantly, N and k are exogenously given parameters, i.e., we do not model the evolution of group size and mating systems. Moreover, for simplicity we ignore reproductive skew by assuming that all pair-bonded males have the same number of mates k.

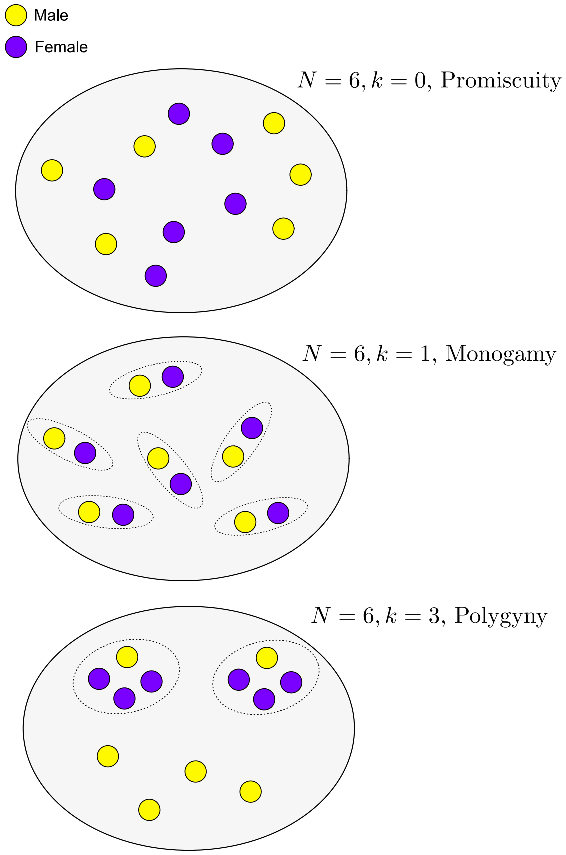


Figure 6: The different types of mating systems captured by our model.

Foraging behavior is modeled as the allocation of time between collecting easily accessible foods of lower nutritional value (e.g., leaves and fruits) and extracting more difficult to acquire foods of higher nutritional value (e.g., nuts and tubers). Letting 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 access; henceforth, this will simply be referred to as *extracting*. The remainder of the foraging time, $1 - a_i$, represents the time spent collecting easily accessible foods. Males allocate their time budget, which is also normalized to 1, between guarding their pair-bonded mates (in proportion g), and extracting and collecting foods; moreover, if females extract food, males can spend a 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 spends on extracting foods. The time spent on mate-guarding, g, and the time spent on stealing extracted food from females, θ, are both taken to be exogenously given parameters.

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 $t_j \in [0,1]$ denote the share of his acquired food that male j gives to some female(s) (more on this below).

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

B Foraging

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

Let $F > 0$ denote the expected nutritional value of collected foods and H the expected nutritional value of extracted foods (the expected values of H and F capture the possibility that the search for food may be unsuccessful; however, we disregard 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) spends time g on mate-guarding, acquires the following total energy:

$$x_i = x(a_i, g) = (1 - a_i)^{1/2} \cdot F + a_i \cdot [1 - (1 - g)\theta] \cdot H. \tag{12}$$

The first term in (12) is the total energy of collected foods acquired, given that the female spends time $1 - a_i$ on this activity; we take the square root of $1 - a_i$ to capture the fact that there are 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 expected energy of extracted foods acquired. She spends the share a_i of 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 than her pair-bonded mate; this *food theft intensity* is a non-evolving 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. Note that the returns to extracting are constant instead of decreasing. This reflects the idea that once an individual starts extractive foraging (e.g. digging for tubers), either there are food items to be found or not; in other words, the probability of finding specific extracted food items does not depend on the amount of time spent in extractive foraging, but rather on whether the individual started extractive foraging in the right place or not.

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 $a^*(g)$ denote the value of a_i that maximizes $x(a_i, g)$, we have:

$$a^*(g) = \max\left\{0, 1 - \left(\frac{F}{2\left[1 - (1 - g)\theta\right] H}\right)^2\right\}. \tag{13}$$

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

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 steal from some female(s) in the group, and zero otherwise. Then the amount of time available for him to forage is $1 - \delta_a \cdot \theta - g$. 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 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:

$$y_j = y(b_j, g) = (1 - \delta_a \cdot \theta - g - b_j)^{1/2} \cdot F + b_j \cdot H. \tag{14}$$

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 $y(b_j, g)$:

$$b^*(g) = \max\left\{0, 1 - \delta_a \cdot \theta - g - \left(\frac{F}{2H}\right)^2\right\}. \tag{15}$$

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

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

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

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

$$x^*(g) \equiv x(a^*(g), g) = [1 - a^*(g)]^{1/2} \cdot F + a^*(g) \cdot [1 - (1-g)\theta]\, H \tag{16}$$

$$y^*(g) \equiv y(b^*(g)) = [1 - \delta_a \cdot \theta - g - b^*(g)]^{1/2} \cdot F + b^*(g) \cdot H. \tag{17}$$

C Food sharing

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 foraging strategy $b^*(g)$, and all females use the same foraging strategy $a^*(g)$ (see (16) and (17)). A female i may give 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 we determine the equilibrium values of such transfers in each mating system.

As mentioned in the model description, we consider that food sharing evolves on a cultural timescale, and that females inherit their sharing strategies from their mothers while males inherit their sharing strategies from their fathers. This assumption implies that evolution occurs in parallel in the female and the male population. We use the technique of adaptive dynamics to determine the *Culturally Stable (CS)* food sharing strategies in females and in males. In adaptive dynamics, one assumes that mutations occur very rarely, and that when a mutant appears, it quickly either gets lost or fixates in the population; in the latter case, the mutant strategy then becomes the resident one. These assumptions can be used in cultural evolution, but now new traits do not appear by mutation but by innovation. To make the connection clear between our approach and traditional adaptive dynamics, 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

$$W(s,t) = \left.\frac{\partial \hat{w}(\hat{s}, s; t)}{\partial \hat{s}}\right|_{\hat{s}=s}, \tag{18}$$

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 residents have trait s and the male population is monomorphic for trait t. The invasion fitness for females is evaluated for a monomorphic male population because the assumption of rare mutations implies that it is very unlikely that a mutant appears simultaneously in both the female and the male populations. While sharing is a cultural trait—which can thus be transmitted to "cultural offspring" who may differ from biological offspring—in our analysis we will take the fitness function $\hat{w}$ to coincide with biological reproductive success. We do this for two reasons. First, to the extent that biological offspring tend to remain in the proximity of their mother, it is natural to assume a high probability that they would copy their mother's trait; for simplicity we take this probability to equal 1. Second, we argue that it is reasonable to use biological reproductive success as a proxy for 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 cultural fitness.

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

$$V(s,t) = \left.\frac{\partial \hat{v}(\hat{t}, t; s)}{\partial \hat{t}}\right|_{\hat{t}=t}. \tag{19}$$

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 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 coincide with biological reproductive success. The exact expressions for the fitness functions $\hat{w}$ and $\hat{v}$ will be defined precisely 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

$$\begin{aligned} \dot{s} &= \mu_s W(s,t) \\ \dot{t} &= \mu_t V(s,t) \end{aligned} \tag{20}$$

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 derivative of s and t, respectively. A rest point (s^*, t^*) of eq. 20 corresponds to a candidate *Culturally Stable* (CS) pair of sharing strategies. A rest point that lies in the interior of the considered set, i.e., a rest point such that $(s^*, t^*) \in (0,1)^2$, satisfies the system of first-order conditions

$$\begin{cases} W(s^*, t^*) = 0 \\ V(s^*, t^*) = 0. \end{cases} \tag{21}$$

A sufficient condition for such a singular state (s^*, t^*) to be a *Culturally Stable Strategy Profile* (CSSP) 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:

$$\frac{\partial^2 \hat{w}(\hat{s}, s^*; t^*)}{\partial \hat{s}^2} < 0 \quad \text{for all} \quad \hat{s} \in [0,1] \tag{22}$$

$$\frac{\partial^2 \hat{v}(\hat{t}, s^*; t^*)}{\partial \hat{t}^2} < 0 \quad \text{for all} \quad \hat{t} \in [0,1]. \tag{23}$$

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 $\hat{t} = t^*$ the unique and global maximum of the invasion fitness $\hat{v}(\hat{t}, s^*; t^*)$. Turning finally to any (s^*, t^*) such that both $\hat{s} = s^*$ 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 $[0,1]^2$, we note that these two second-order conditions are also sufficient for (s^*, t^*) to be a CSSP.

C.1 Promiscuous mating system

In a promiscuous mating system there are no pair-bonds between males and females, and 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 paternity; however, he would not guard her once her offspring are born, and this is the mate-guarding that matters in our model). Females may still share some food with the males in her group, and *vice versa*. We posit that if a female shares, she 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 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, so that all the females in any given group thus obtain the same energy via the transfers from the males. Let $\boldsymbol{a} = (a_1, a_2, ..., a_N)$ denote the vector of the foraging strategies and $\boldsymbol{s} = (s_1, s_2, ..., s_N)$ the vector of the sharing strategies used by the females in the focal group. Likewise, let $\boldsymbol{b} = (b_1, b_2, ..., b_N)$ be the vector of the foraging strategies and $\boldsymbol{t} = (t_1, t_2, ..., t_N)$ the vector of the sharing strategies used by the males in the focal group. Then the total energy that female i has at her disposal equals

$$X(a_i, s_i, \boldsymbol{b}, \boldsymbol{t}) = (1 - s_i) \cdot x(a_i, 0) + \sum_{j=1}^{N} \left[\frac{t_j}{N} \cdot y(b_j, 0) \right], \tag{24}$$

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

$$Y(b_j, t_j, \boldsymbol{a}, \boldsymbol{s}) = (1 - t_j) \cdot y(b_j, 0) + \sum_{i=1}^{N} \left[\frac{s_i}{N} \cdot x(a_i, 0) \right] + \frac{\theta}{N} \sum_{i=1}^{N} a_i H, \tag{25}$$

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

In order to find an expression for invasion fitness, it is useful to rewrite (24) in a population where there is one focal female with trait $\hat{s}$, one focal male trait $\hat{t}$, while all other $N-1$ males share t. This leads to:

$$\hat{X}(\hat{s}, \hat{t}; t) = (1 - \hat{s}) \cdot x(a^*, 0) + \left(\frac{\hat{t}}{N} + \frac{N-1}{N} t \right) \cdot y(b^*, 0), \tag{26}$$

where we also assume that all females in the population employ the optimal foraging strategy a^* and all males employ b^*. Similarly, we rewrite (25) for a focal male who shares $\hat{t}$ in a group where a focal female shares $\hat{s}$, while all other $N-1$ females share s, and thus obtain:

$$\hat{Y}(\hat{t}, \hat{s}; s) = (1 - \hat{t}) \cdot y(b^*, 0) + \left(\frac{\hat{s}}{N} + \frac{N-1}{N} s \right) \cdot x(a^*, 0) + \theta a^* H. \tag{27}$$

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

$$w((a_i, \boldsymbol{a}_{-i}), (s_i, \boldsymbol{s}_{-i}), \boldsymbol{b}, \boldsymbol{t}) = X(a_i, s_i, \boldsymbol{b}, \boldsymbol{t}) \cdot p \cdot \sum_{j=1}^{N} Y(b_j, t_j, (a_i, \boldsymbol{a}_{-i}), (s_i, \boldsymbol{s}_{-i})), \tag{28}$$

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 example, $p = 1/N$ means that she may expect one male to come and protect her, should her offspring be attacked by predators; at the other extreme, if $p = 1$, she benefits from the protection of all males. In this expression the vectors $\boldsymbol{a}$ and $\boldsymbol{s}$ are written $(a_i, \boldsymbol{a}_{-i})$ and $(s_i, \boldsymbol{s}_{-i})$, respectively, to show clearly how the reproductive success of the focal female i depends on the foraging and sharing strategies of the other females in her group. From (28) and using (26)–(27), invasion fitness of a female who shares $\hat{s}$ in a population where resident females share s and resident males share t takes the form

$$\hat{w}(\hat{s}, s; t) = \hat{X}(\hat{s}, t; t) \cdot p \cdot N \cdot \hat{Y}(t, \hat{s}; s), \tag{29}$$

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

$$\begin{aligned} v((b_j,\boldsymbol{b}_{-j}),(t_j,\boldsymbol{t}_{-j}),\boldsymbol{a},\boldsymbol{s}) &= \frac{1}{N}\sum_{i=1}^{N} w((a_i,\boldsymbol{a}_{-i}),(s_i,\boldsymbol{s}_{-i}),(b_j,\boldsymbol{b}_{-j}),(t_j,\boldsymbol{t}_{-j})) \qquad (30) \\ &= \frac{1}{N}\sum_{i=1}^{N}\left[X(a_i,s_i,(b_j,\boldsymbol{b}_{-j}),(t_j,\boldsymbol{t}_{-j}))\cdot p\cdot\sum_{\ell=1}^{N} Y(b_\ell,t_\ell,(a_i,\boldsymbol{a}_{-i}),(s_i,\boldsymbol{s}_{-i}))\right]. \end{aligned}$$

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

$$\hat{v}(\hat{t},t;s) = \hat{X}(s,\hat{t};t)\cdot p\cdot\left[\hat{Y}(\hat{t},s;s)+(N-1)\hat{Y}(t,s;s)\right]. \tag{31}$$

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

Proof. **[Proof of Claim 1.]** Starting with female foraging behavior, suppose—to the contrary of Claim 1—that some female 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 in her group, $(\boldsymbol{a}_{-i},\boldsymbol{s}_{-i})$, and any given vector of strategies used by the males in her group, $(\boldsymbol{b},\boldsymbol{t})$, she would then fail to maximize her reproductive success (see (28)), since both $X(a_i,s_i,\boldsymbol{b},\boldsymbol{t})$ and the sum in this expression are non-decreasing in $x(a_i,0)$, and at least one of them is strictly increasing. A contradiction is reached. Turning now to male foraging behavior, 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, any given vector of strategies used by the other males in his group, $(\boldsymbol{b}_{-j},\boldsymbol{t}_{-j})$, and any given vector of strategies used by the females in his group, $(\boldsymbol{a},\boldsymbol{s})$, he would then fail to maximize his reproductive success (see (30)), since both $X(a_i,s_i,\boldsymbol{b},\boldsymbol{t})$ and $Y(b_\ell,t_\ell,(a_i,\boldsymbol{a}_{-i}),(s_i,\boldsymbol{s}_{-i}))$ for $\ell = j$ are non-decreasing in $y(b_j,0)$, and at least one of them is strictly increasing. A contradiction is reached. ■

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 sharing strategies (see equations (18) and (19)), we first write the full expressions for the partial derivative of the focal female's reproductive success with respect to her sharing strategy, and likewise for the focal male (to keep the notation as simple as possible, we write $\boldsymbol{a^*(0)}$ for the N-dimensional vector with all components equal to $a^*(0)$, and $\boldsymbol{b^*(0)}$ for the N-dimensional vector with all components equal to $b^*(0)$):

$$\begin{aligned} \frac{\partial w(\boldsymbol{a^*(0)},(s_i,\boldsymbol{s}_{-i}),\boldsymbol{b^*(0)},\boldsymbol{t})}{\partial s_i} &= \frac{\partial X(a^*(0),s_i,\boldsymbol{b^*(0)},\boldsymbol{t})}{\partial s_i}\cdot p\cdot\sum_{j=1}^{N} Y(b^*(0),t_j,\boldsymbol{a^*(0)},(s_i,\boldsymbol{s}_{-i})) \qquad (32) \\ &+ X(a^*(0),s_i,\boldsymbol{b^*(0)},\boldsymbol{t})\cdot p\cdot\sum_{j=1}^{N}\frac{\partial Y(b^*(0),t_j,\boldsymbol{a^*(0)},(s_i,\boldsymbol{s}_{-i}))}{\partial s_i} \end{aligned}$$

$$\begin{aligned}\frac{\partial v(\boldsymbol{b}^*(\mathbf{0}),(t_j,\boldsymbol{t}_{-j}),\boldsymbol{a}^*(\mathbf{0}),\boldsymbol{s})}{\partial t_j} &= \frac{p}{N}\sum_{i=1}^{N}\left[\frac{\partial X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),(t_j,\boldsymbol{t}_{-j}))}{\partial t_j}\cdot\sum_{\ell=1}^{N}Y(b_\ell,t_\ell,\boldsymbol{a}^*(\mathbf{0}),\boldsymbol{s})\right] \\ &+ \frac{p}{N}\sum_{i=1}^{N}\left[X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),(t_j,\boldsymbol{t}_{-j}))\cdot\frac{\partial Y(b^*(0),t_j,\boldsymbol{a}^*(\mathbf{0}),\boldsymbol{s})}{\partial t_j}\right].\end{aligned}\tag{33}$$

Writing $\mathbf{s}^{(N)}$ (respectively $\mathbf{t}^{(N)}$) for the N-dimensional vector whose components all equal s (respectively t), and recalling the notation for $x^*(0)$ and $y^*(0)$ (see (16) and (17)) from these expressions we obtain (upon simplification):

$$\begin{aligned}W(s,t) &= \frac{\partial w(\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i}),\boldsymbol{b}^*(\mathbf{0}),\mathbf{t}^{(N)})}{\partial s_i}\Big|_{(s_i,\boldsymbol{s}_{-i})=\mathbf{s}^{(N)}} \\ &= p\cdot x^*(0)\cdot\left[X(a^*,s,\boldsymbol{b}^*,\mathbf{t}^{(N)})-N\cdot Y(b^*,t,\boldsymbol{a}^*,\mathbf{s}^{(N)})\right]\end{aligned}\tag{34}$$

$$\begin{aligned}V(s,t) &= \frac{\partial v(\boldsymbol{b}^*(\mathbf{0}),(t_j,\boldsymbol{t}_{-j}),\boldsymbol{a}^*(\mathbf{0}),\mathbf{s}^{(N)})}{\partial t_j}\Big|_{(t_j,\boldsymbol{t}_{-j})=\mathbf{t}^{(N)}} \\ &= p\cdot y^*(0)\cdot\left[Y(b^*,t,\boldsymbol{a}^*,\mathbf{s}^{(N)})-X(a^*,s,\boldsymbol{b}^*,\mathbf{t}^{(N)}))\right].\end{aligned}\tag{35}$$

One might notice a difference between the definitions of $W(s,t)$ and $V(s,t)$ in (18)–(19) and their respective definitions here in (34)–(35), which stems only from two different approaches, but lead to the same result. In (34)–(35) we track all individuals in the group, an approach more widespread in game theory, while in (18)–(19) we focus on a mutant in a group where all other individuals are residents, an approach more known to students of adaptive dynamics. In order to keep track of these two different approaches, we have used hat notation for all functions that take the standpoint of a focal mutant in a group of residents. Next we show that a female's reproductive success is strictly concave in her own sharing strategy, and that a male's reproductive success is strictly concave in his own sharing strategy. Recall from above (see (21) and (23)) that such strict concavity is sufficient for any candidate CS pair of sharing strategies to indeed be CS.

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

Proof. We prove the lemma by proving that the relevant second-order partial derivatives are strictly negative. From (32) we obtain:

$$\begin{aligned}\frac{\partial^2 w(\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i}),\boldsymbol{b}^*(\mathbf{0}),\boldsymbol{t})}{\partial s_i^2} &= \frac{\partial^2 X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),\boldsymbol{t})}{\partial s_i^2}\cdot p\cdot\sum_{j=1}^{N}Y(b^*(0),t_j,\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i})) \\ &+ \frac{\partial X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),\boldsymbol{t})}{\partial s_i}\cdot p\cdot\sum_{j=1}^{N}\frac{\partial Y(b^*(0),t_j,\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i}))}{\partial s_i} \\ &+ \frac{\partial X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),\boldsymbol{t})}{\partial s_i}\cdot p\cdot\sum_{j=1}^{N}\frac{\partial Y(b^*(0),t_j,\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i}))}{\partial s_i} \\ &+ X(a^*(0),s_i,\boldsymbol{b}^*(\mathbf{0}),\boldsymbol{t})\cdot p\cdot\sum_{j=1}^{N}\frac{\partial^2 Y(b^*(0),t_j,\boldsymbol{a}^*(\mathbf{0}),(s_i,\boldsymbol{s}_{-i}))}{\partial s_i^2},\end{aligned}\tag{36}$$

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

$$\frac{\partial^2 w(\boldsymbol{a^*(0)},(s_i,\boldsymbol{s}_{-i}),\boldsymbol{b^*(0)},\boldsymbol{t})}{\partial s_i^2} = 2p\cdot\frac{\partial X(a^*(0),s_i,\boldsymbol{b^*(0)},\boldsymbol{t})}{\partial s_i}\sum_{j=1}^{N}\frac{\partial Y(b^*(0),t_j,\boldsymbol{a^*(0)},(s_i,\boldsymbol{s}_{-i}))}{\partial s_i} \tag{37}$$

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

From (33) we obtain:

$$\begin{aligned}\frac{\partial^2 v(\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}),\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j^2} &= \frac{p}{N}\sum_{i=1}^{N}\left[\frac{\partial^2 X(a^*(0),s_i,\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}))}{\partial t_j^2}\cdot\frac{\sum_{\ell=1}^{N}Y(b_\ell,t_\ell,\boldsymbol{a^*(0)},\boldsymbol{s})}{N}\right] \\ &+ \frac{p}{N}\sum_{i=1}^{N}\left[\frac{\partial X(a^*(0),s_i,\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}))}{\partial t_j}\cdot\frac{1}{N}\frac{\partial Y(b_t,t_j,\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j}\right] \\ &+ \frac{p}{N}\sum_{i=1}^{N}\left[\frac{\partial X(a^*(0),s_i,\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}))}{\partial t_j}\cdot\frac{1}{N}\frac{\partial Y(b^*(0),t_j,\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j}\right] \\ &+ \frac{p}{N}\sum_{i=1}^{N}\left[X(a^*(0),s_i,\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}))\cdot\frac{1}{N}\frac{\partial^2 Y(b^*(0),t_j,\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j^2}\right].\end{aligned} \tag{38}$$

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

$$\frac{\partial^2 v(\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}),\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j^2} = \frac{2p}{N}\sum_{i=1}^{N}\left[\frac{\partial X(a^*(0),s_i,\boldsymbol{b^*(0)},(t_j,\boldsymbol{t}_{-j}))}{\partial t_j}\cdot\frac{1}{N}\frac{\partial Y(b_t,t_j,\boldsymbol{a^*(0)},\boldsymbol{s})}{\partial t_j}\right], \tag{39}$$

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

$$\sigma(t)=\frac{x^*(0)+Nty^*(0)-N[(1-t)y^*(0)+\theta a^*(0)H]}{x^*(0)(N+1)}. \tag{40}$$

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

$$\tau(s)=\frac{(2s-1)x^*(0)+y^*(0)+\theta a^*(0)H}{2y^*(0)}. \tag{41}$$

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

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

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 $W(1, t^*) \geq 0$. In both cases, $W(s^*, t^*) \geq 0$. From (34), and since $x^*(0) > 0$, the inequality $W(s^*, t^*) \geq 0$ implies $X(a^*, s^*, \boldsymbol{b^*}, \boldsymbol{t^*}) \geq N \cdot Y(b^*, t^*, \boldsymbol{a^*}, \boldsymbol{s^*})$. Hence, for any $N \geq 2$, $Y(b^*, t^*, \boldsymbol{a^*}, \boldsymbol{s^*}) - X(a^*, s^*, \boldsymbol{b^*}, \boldsymbol{t^*}) < 0$; but since $y^*(0) > 0$, this implies $V(s^*, t^*) < 0$ (see (35)). By strict concavity of v (see Lemma 1), and given that t^* must lie in the interval $[0, 1]$, it follows that $t^* = 0$.

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 $V(s^*, 1) \geq 0$. In both cases, $V(s^*, t^*) \geq 0$. From (35), and since $y^*(0) > 0$, the inequality $V(s^*, t^*) \geq 0$ implies $Y(b^*, t^*, \boldsymbol{a^*}, \boldsymbol{s^*}) \geq X(a^*, s^*, \boldsymbol{b^*}, \boldsymbol{t^*})$. Hence, for any $N \geq 2$, $X(a^*, s^*, \boldsymbol{b^*}, \boldsymbol{t^*}) - N \cdot Y(b^*, t^*, \boldsymbol{a^*}, \boldsymbol{s^*}) < 0$; since $x^*(0) > 0$, this implies $W(s^*, t^*) < 0$ (see (34)). By strict concavity of w (see Lemma 1), and given that s^* must lie in the interval $[0, 1]$, it follows that $s^* = 0$. ■

Next we establish existence and uniqueness of CS pair of sharing strategies.

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

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

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

Second, if parameter values are such that $(s^*, 0)$ is CS for some $s^* \in (0, 1]$, then there exists no $t^* \in (0, 1]$ such that $(0, t^*)$ is CS. To see this, suppose that $(s^*, 0)$ is CS for some $s^* \in (0, 1]$. Then, $\sigma(0) > 0$ (see (40)) and $s^* = \min\{\sigma(0), 1\}$. Now, 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 culturally stable pair of sharing strategies.

Likewise, if parameter values are such that $(0, t^*)$ is CS for some $t^* \in (0, 1]$, then there exists no $s^* \in (0, 1]$ such that $(s^*, 0)$ is CS. To see this, suppose that $(0, t^*)$ is CS for some $t^* \in (0, 1]$. Then, $\tau(0) > 0$ (see (41)) and $t^* = \min\{\tau(0), 1\}$. Now, note 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 a culturally stable pair of sharing strategies. ■

C.2 Monogamous and polygynous mating systems

We now consider a polygynous mating system where some males (exactly N/k of them) reproduce exclusively with a fixed number of k females each, while the remaining males are mateless (monogamy will be the special case where $k = 1$). We assume that each female shares food only with her pair-bonded mate (if she shares 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 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 the females he is pair-bonded with. Let $\boldsymbol{s_j} = (s_{1j}, s_{2j}, ..., s_{Nj})$ denote the vector of the sharing strategies used by the females 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 pair-bonded male uses the amount g of mate-guarding, equals

$$X(a_{ij}, s_{ij}, b_j, t_j) = (1 - s_{ij}) \cdot x(a_{ij}, g) + t_j \cdot \frac{y(b_j, g)}{k}, \tag{42}$$

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

$$Y(b_j, t_j, \boldsymbol{a}, \boldsymbol{s_j}) = (1 - t_j) \cdot y(b_j, g) + \sum_{i=1}^{k} [s_{ij} \cdot x(a_{ij}, g)] + \frac{\theta(1-g)}{N-1} \sum_{d \neq j} \left(\sum_{\ell=1}^{k} a_{\ell d} H \right). \tag{43}$$

The last term reflects the assumption that each male garners a fraction $1/(N-1)$ of any food stolen from each female who 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).

Just as in the promiscuous system, we rewrite (42) and (43) to find an expression for invasion fitness focusing on a focal mutant in a monomorphic population of residents. The total 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 $\hat{t}$, equals

$$\hat{X}(\hat{s}, \hat{t}) = (1 - \hat{s}) \cdot x(a^*, g) + \hat{t} \cdot \frac{y(b^*, g)}{k}. \tag{44}$$

Similarly, rewriting (43) for a focal male who shares $\hat{t}$ has at his disposal, given that a focal female in his unit shares $\hat{s}$ while his other pair-bonded females share s, gives

$$\hat{Y}(\hat{t}, \hat{s}, s) = (1 - \hat{t}) \cdot y(b^*, g) + [(k-1)s + \hat{s}] \cdot x(a^*, g) + \frac{N-k}{N-1} \theta(1-g) a^* H. \tag{45}$$

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

$$w\left((a_{ij}, \boldsymbol{a}_{-ij}, \boldsymbol{a}_{-j}), (s_{ij}, \boldsymbol{s}_{-ij}), b_j, t_j\right) = X(a_{ij}, s_{ij}, b_j, t_j) \cdot q \cdot Y(b_j, t_j, (a_{ij}, \boldsymbol{a}_{-ij}, \boldsymbol{a}_{-j}), (s_{ij}, \boldsymbol{s}_{-ij})). \tag{46}$$

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 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 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 can without loss of generality drop it to determine the stable sharing strategies. Using (44)–(45) and starting from (46), we can write the invasion fitness of a mutant female who shares $\hat{s}$ in a group where all other females use the resident sharing strategy s and all males (including her pair-bonded male) share t, as

$$\hat{w}(\hat{s}, s, t) = \hat{X}(\hat{s}, t) \cdot q \cdot \hat{Y}(t, \hat{s}, s). \tag{47}$$

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

$$\begin{aligned} v((b_j, \boldsymbol{b}_{-j}), (t_j, \boldsymbol{t}_{-j}), \boldsymbol{a}, \boldsymbol{s}, \boldsymbol{g}) &= [1-\phi(1-g)] \cdot \sum_{i=1}^{k} w((a_{ij}, \boldsymbol{a}_{-ij}, \boldsymbol{a}_{-j}), (s_{ij}, \boldsymbol{s}_{-ij}), b_j, t_j) \qquad (48) \\ &+ \frac{1}{N-1} \sum_{d \neq j} \sum_{\ell=1}^{k} (1-g)\phi \cdot w((a_{\ell d}, \boldsymbol{a}_{-\ell d}, \boldsymbol{a}_{-d}), (s_{\ell d}, \boldsymbol{s}_{-\ell d}), b_d, t_d). \end{aligned}$$

In the first term, the expression inside the square brackets is the expected proportion of offspring born to females in his unit for which he is the biological father. The second term represents the expected number of paternities that he can steal from females outside his own unit: of all the extra-pair copulations by females outside his unit that are not protected by these females' pair-bonded males, the focal male gets a share $1/(N-1)$. We indeed assume that for any given female, each male besides her pair-bonded male gets an equal share of her extra-pair copulations. From (48) and using (44)–(45), we can write the invasion fitness of a mutant male who shares $\hat{t}$ in a group where all other males use the resident sharing strategy t and all females share s as

$$\hat{v}(\hat{t}, t, s) = k \cdot \hat{X}(s, \hat{t}) \cdot q \cdot \hat{Y}(\hat{t}, s, s). \qquad (49)$$

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

Proof. [Proof of Claim 1.] Starting with female foraging behavior, suppose—to the contrary of Claim 1—that some female 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 females in her group, $(\boldsymbol{a}_{-i}, \boldsymbol{s}_{-i})$, and any given vector of strategies used by the males in her group, $(\boldsymbol{b}, \boldsymbol{t})$, she would then fail to maximize her reproductive success (see (46)), since both $X(\cdot)$ and $Y(\cdot)$ in this expression are non-decreasing in $x(a_{ij}, 0)$, and at least one of them is strictly increasing. A contradiction is reached. Turning now to male foraging behavior, 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, any given vector of strategies used by the other males in his group, $(\boldsymbol{b}_{-j}, \boldsymbol{t}_{-j})$, and any given vector of strategies used by the females in his group, $(\boldsymbol{a}, \boldsymbol{s})$, he would then fail to maximize his reproductive success (see (48)). To see this, note first that his reproductive success is strictly increasing in the reproductive success of each female in his unit (i.e., in $w((a_{ij}, \boldsymbol{a}_{-ij}, \boldsymbol{a}_{-j}), (s_{ij}, \boldsymbol{s}_{-ij}), b_j, t_j)$ for all $i = 1, ..., k$), and that this in turn is strictly increasing in b_j (since both $X(\cdot)$ and $Y(\cdot)$ in (46) are non-decreasing in b_j and at least one is strictly increasing). A contradiction is reached. ■

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 sharing strategies (see equations (18) and (19)), we first write the full expressions for the partial derivative of the focal female's reproductive success with respect to her sharing strategy, and likewise for the focal male, in a population where all males apply mate-guarding amount g (we write $\boldsymbol{a^*(g)}$ for the N-dimensional vector with all components equal to $a^*(g)$, and $\boldsymbol{b^*(g)}$ for the N-dimensional vector with all components equal to $b^*(g)$):

$$\begin{aligned}\frac{\partial w\left(\boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}), b^*(g), t_j\right)}{\partial s_{ij}} &= \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij})) \\ &+ X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial s_{ij}}\end{aligned} \tag{50}$$

$$\frac{\partial v(\boldsymbol{b^*(g)}, (t_j, \boldsymbol{t}_{-j}), \boldsymbol{a^*(g)}, \boldsymbol{s}, \boldsymbol{g})}{\partial t_j} = [1-\phi(1-g)] \cdot \sum_{i=1}^{k} \frac{\partial w(\boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}), b^*(g), t_j)}{\partial t_j} \tag{51}$$

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

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

$$\begin{aligned} W(s,t) &= \frac{\partial w\left(\boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}), b^*(g), t\right)}{\partial s_{ij}}\Big|_{(s_{ij}, \boldsymbol{s}_{-ij}) = \mathbf{s}^{(k)}} \\ &= x^*(g)\left[X(a^*(g), s, b^*(g), t) - Y(b^*(g), t, \boldsymbol{a^*(g)}, \mathbf{s}^{(k)})\right]\end{aligned} \tag{52}$$

$$\begin{aligned} V(s,t) &= \frac{\partial v(\boldsymbol{b^*(g)}, (t_j, \boldsymbol{t}_{-j}), \boldsymbol{a^*(g)}, \mathbf{s}^{(N)}, \boldsymbol{g})}{\partial t_j}\Big|_{(t_j, \boldsymbol{t}_{-j}) = \mathbf{t}^{(N)}} \\ &= [1-\phi(1-g)]\, y(b^*(g)) \left[Y(b^*(g), t, \boldsymbol{a^*(g)}, \mathbf{s}^{(k)}) - k \cdot X(a^*(g), s, b^*(g), t)\right].\end{aligned} \tag{53}$$

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

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

Proof. We prove the lemma by proving that the relevant second-order partial derivatives are strictly negative. From (50) we obtain:

$$\begin{aligned} \frac{\partial^2 w\left(\boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}), b^*(g), t_j\right)}{\partial s_{ij}^2} &= \frac{\partial^2 X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}^2} \cdot Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij})) \\ &+ \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial s_{ij}} \\ &+ \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial s_{ij}} \\ &+ X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial^2 Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial s_{ij}^2}. \end{aligned} \tag{54}$$

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

$$\frac{\partial^2 w\left(\boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}), b^*(g), t_j\right)}{\partial s_{ij}^2} = 2 \cdot \frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial s_{ij}} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial s_{ij}} \tag{55}$$

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

From (51) we obtain that $\frac{\partial^2 v(\boldsymbol{b^*(g)}, (t_j, \boldsymbol{t}_{-j}), \boldsymbol{a^*(g)}, \boldsymbol{s}, \boldsymbol{g})}{\partial t_j^2}$ has the same sign as (since $[1 - \phi(1-g)] > 0$):

$$\begin{aligned} &\sum_{i=1}^{k} \cdot \left[\frac{\partial^2 X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j^2} \cdot Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))\right] \\ + &\sum_{i=1}^{k} \cdot \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial t_j}\right] \\ + &\sum_{i=1}^{k} \cdot \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial t_j}\right] \\ + &\sum_{i=1}^{k} \cdot \left[X(a^*(g), s_{ij}, b^*(g), t_j) \cdot \frac{\partial^2 Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial t_j^2}\right]. \end{aligned} \tag{56}$$

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

$$2 \cdot \sum_{i=1}^{k} \cdot \left[\frac{\partial X(a^*(g), s_{ij}, b^*(g), t_j)}{\partial t_j} \cdot \frac{\partial Y(b^*(g), t_j, \boldsymbol{a^*(g)}, (s_{ij}, \boldsymbol{s}_{-ij}))}{\partial t_j}\right] \tag{57}$$

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

$$\sigma(t) = \frac{x^*(g) - y^*(g) + \frac{ty^*(g)(1+k)}{k} - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{(1+k)x^*(g)}. \tag{58}$$

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

$$\tau(s)=\frac{y^*(g)+(2s-1)kx^*(g)+\frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{2y^*(g)}. \tag{59}$$

Again, let (s^*,t^*) denote a pair of sharing strategies (s,t) that is culturally 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.

C.2.1 Strict polygyny

The following proposition establishes that under strict polygyny there exists no CS such that both males and females share food.

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

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 $W(1,t^*)\geq 0$. In both cases, $W(s^*,t^*)\geq 0$. From the expression in (52), and since $x^*(0)>0$, the inequality $W(s^*,t^*)\geq 0$ implies $X(a^*,s^*,\boldsymbol{b^*},\boldsymbol{t^*})\geq Y(b^*,t^*,\boldsymbol{a^*},\boldsymbol{s^*})$. Hence, for any $k\geq 2$, $Y(b^*,t^*,\boldsymbol{a^*},\boldsymbol{s^*})-k\cdot X(a^*,s^*,\boldsymbol{b^*},\boldsymbol{t^*})<0$; but since $y^*(0)>0$, this implies $V(s^*,t^*)<0$ (see (53)). By strict concavity of v (see Lemma 2), and given that t^* must lie in the interval $\in[0,1]$, it follows that $t^*=0$.

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 $V(s^*,1)\geq 0$. In both cases, $V(s^*,t^*)\geq 0$. From the expression in (53), and since $y^*(0)>0$, the inequality $V(s^*,t^*)\geq 0$ implies $Y(b^*,t^*,\boldsymbol{a^*},\boldsymbol{s^*})\geq k\cdot X(a^*,s^*,\boldsymbol{b^*},\boldsymbol{t^*})$. Hence, for any $k\geq 2$, $X(a^*,s^*,\boldsymbol{b^*},\boldsymbol{t^*})-Y(b^*,t^*,\boldsymbol{a^*},\boldsymbol{s^*})<0$; since $x^*(0)>0$, this implies $W(s^*,t^*)<0$ (see (52)). By strict concavity of w (see Lemma 2), and given that s^* must lie in the interval $\in[0,1]$, it follows that $s^*=0$. ■

Next we establish existence and uniqueness of CS under strict polygyny.

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

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

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

Second, if parameter values are such that $(s^*,0)$ is CS for some $s^*\in(0,1]$, then there exists no $t^*\in(0,1]$ such that $(0,t^*)$ is CS. To see this, suppose that $(s^*,0)$ is CS for some

$s^* \in (0,1]$. Then, $\sigma(0) > 0$ (see (58)) and $s^* = \min\{\sigma(0), 1\}$. Now, 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 culturally stable pair of sharing strategies.

Likewise, if parameter values are such that $(0, t^*)$ is CS for some $t^* \in (0,1]$, then there exists no $s^* \in (0,1]$ such that $(s^*, 0)$ is CS. To see this, suppose that $(0, t^*)$ is CS for some $t^* \in (0,1]$. Then, $\tau(0) > 0$ (see (59)) and $t^* = \min\{\tau(0), 1\}$. Now, note 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 a culturally stable pair of sharing strategies. ■

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

$$\sigma(0) = \frac{x^*(g) - y^*(g) - \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{(1+k)x^*(g)}, \tag{60}$$

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

$$\tau(0) = \frac{y^*(g) - kx^*(g) + \frac{\theta(1-g)(N-k)a^*(g)H}{N-1}}{2y^*(g)}, \tag{61}$$

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

Finally, we turn to the monogamous system.

C.2.2 Monogamy

We obtain the following result:

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

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

Proof. Plugging $k = 1$ into (52) and (53), we see that either both $W(s,t) = V(s,t) = 0$, or $W(s,t)$ and $V(s,t)$ have 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 fitness function w, maximization of w is compatible with a strictly positive selection gradient if and only if s is at its maximum value, 1; likewise, by strict concavity of the invasion fitness function v, maximization of v is compatible with a strictly negative 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 be that $t = 1$ and $s = 0$. To examine whether such corner solutions are relevant for any parameter constellations, we now 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 that (see (52) and (53)):

$$X(a^*(g), s, b^*(g), t) = Y(b^*(g), t, \boldsymbol{a^*(g)}, s). \tag{62}$$

Using (42) and (43), this equality becomes

$$(1-s)x^*(g) + ty^*(g) = (1-t)y^*(g) + sx^*(g) + \theta(1-g)a^*(g)H. \tag{63}$$

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 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 (63). Any such pair is CS, 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 (63) is strictly smaller than the RHS for any $(s,t) \in [0,1]^2$. In other words, $Y(b^*(g), t, \boldsymbol{a^*(g)}, s) < X(a^*(g), s, b^*(g), t)$, and the observation above implies that the unique CS 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., $X(a^*(g), s^*, b^*(g), t^*) = Y(b^*(g), t^*, \boldsymbol{a^*(g)}, s^*)$. 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, $Y(b^*(g), t^*, \boldsymbol{a^*(g)}, s^*) > X(a^*(g), s^*, b^*(g), t^*)$.

D Characterization of optimal foraging and CS sharing strategies

In the preceding sections we proved the existence and (sometimes) uniqueness of optimal foraging strategies and culturally 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

$$a^*(g) = \max\left\{0, 1 - \left(\frac{F}{2(1-\theta+\theta g)H}\right)^2\right\} \tag{64}$$

and

$$b^*(g) = \max\left\{0, 1 - \delta_a \cdot \theta - g - \left(\frac{F}{2H}\right)^2\right\}, \tag{65}$$

we obtain

$$x^*(g) = \begin{cases} F & \text{if} \quad a^*(g) = 0 \\ \frac{F^2}{4(1-\theta+\theta g)H} + (1-\theta+\theta g)H & \text{otherwise} \end{cases} \tag{66}$$

and

$$y^*(g) = \begin{cases} (1 - \delta_a \cdot \theta - g)^{1/2} \cdot F & \text{if} \quad b^*(g) = 0 \\ \frac{F^2}{4H} + (1 - \delta_a \cdot \theta - g)H & \text{otherwise.} \end{cases} \tag{67}$$

In Fig. 7 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.

D.1 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* $F/H \geq 2$*;*

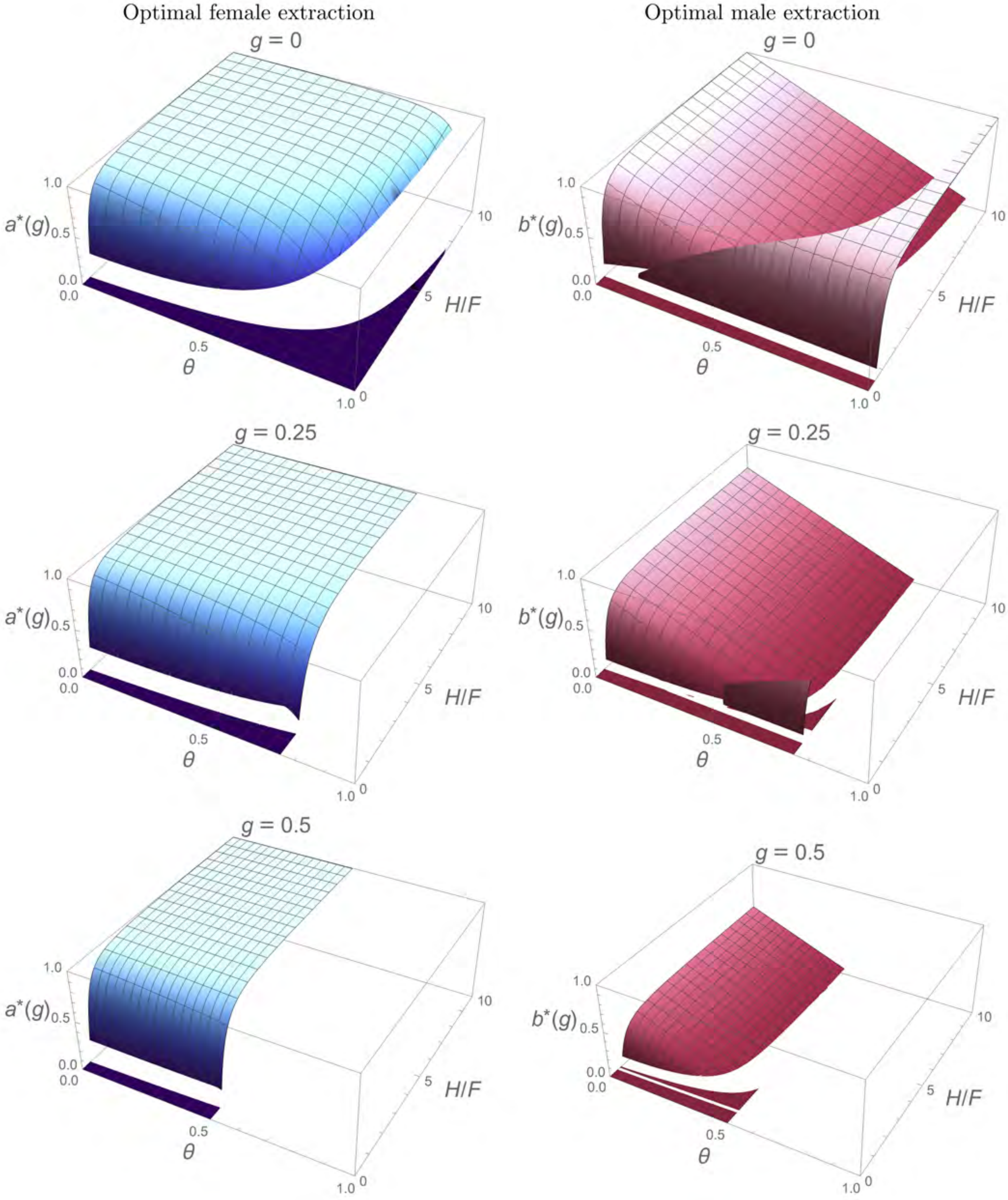
(Case B) $a^*(0) = 0$ *and* $b^*(0) > 0$ *iff* $2 > F/H \geq 2(1-\theta)$*;*

(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).



Optimal female extraction

Optimal male extraction

$g = 0$

$g = 0.25$

$g = 0.5$

Figure 7: 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 $\theta + g + b^*(g) \leq 1$.

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:
    - 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. 7. 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. 40:

$$\sigma(0) = \frac{x^*(0) - N[y^*(0) + \theta a^*(0)H]}{x^*(0)(N+1)}. \tag{68}$$

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

$$\frac{x^*(0)}{y^*(0) + \theta a^*(0)H} > N. \tag{69}$$

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 (69) 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 (69) can thus be interpreted as the synergy factor of this public goods game. The condition in (69) 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 (41):

$$\tau(0) = \frac{y^*(0) - x^*(0) + \theta a^*(0)H}{2y^*(0)}. \tag{70}$$

Hence, $t^* > 0$ iff

$$y^*(0) > x^*(0) - \theta a^*(0)H, \tag{71}$$

and $t^* < 1$ iff

$$x^*(0) + y^*(0) > \theta a^*(0) H. \tag{72}$$

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 (69) nor (71) holds. We use these conditions to prove the following results:

Proposition 7 *In the promiscuous system:*

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

Proof. The proof is based on the necessary and sufficient conditions derived above for $s^* > 0$ (see (69)), for $t^* > 0$ (see (71)), and for $t^* < 1$ (see (72)). 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 (69) and (71), 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 (69) and (71), 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).

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 (69) and (71), we obtain:

- 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 inequality as $\left[1 - N(1-\theta)\right] F^2 > 4(N-1)(1-\theta)^2 H^2$, we see that it is violated for any $N \geq \frac{1}{1-\theta}$; for $N < \frac{1}{1-\theta}$, the 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 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 $N \geq 2$;

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

■

Proposition 7 shows that in a promiscuous system:

1. Female sharing does not arise for any parameter constellations. This is because when males do not spend any time on mate-guarding, they always have at least as much food as females do: when both females and males extract, males have more food because they steal food from females, and when only males extract they have more food than females (as explained above). The synergy factor in the public goods game between the females (see inequality (69) and the comment below it) is therefore always smaller than 1 and thus fails to trigger any sharing by females.
2. If both males and females extract, males share only if θ is small enough.
3. If females do not extract, then food theft does not impact the CS sharing of males.

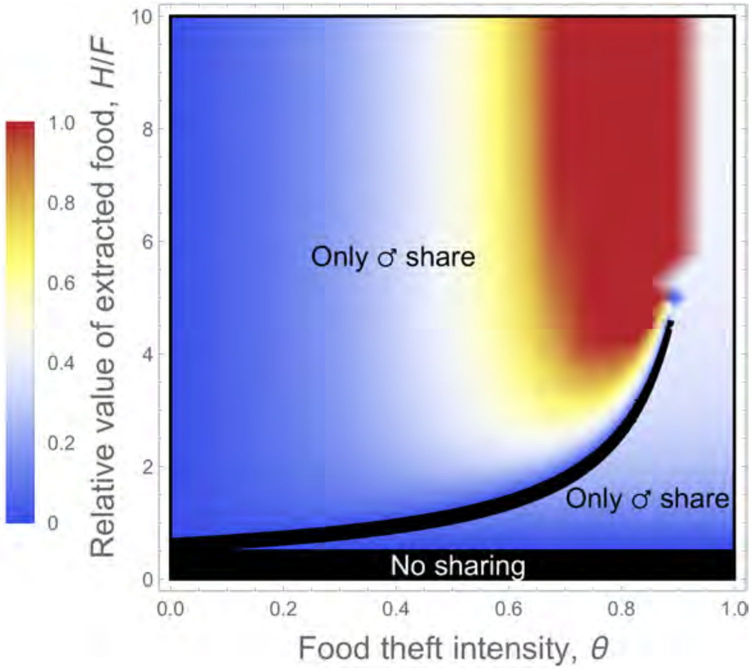


Figure 8: Regions of parameter space in the promiscuous mating system corresponding to the two possible types of CS sharing pairs, (s^*, t^*), described in Prop. 7. In regions labelled "Only males (♂) share", we have $s^* > 0$ and $t^* = 0$, while in regions labelled "No sharing" we have $s^* = 0$ and $t^* = 0$. The shading indicates the exact value of t^*, when it is not 0 ($s^* > 0$ is never CS as shown in Prop. 7) .

Proposition 7 is displayed in Fig. 14. Moving leftward in the figure, the first black region corresponds to parameter values such that neither males nor females extract, and hence do not share. In the first blue region, only males extract. In the second black region, both males and females extract, and males steal extracted food from females; however, because males now spend time on food theft, their own food production is below that of females, and because the food theft yields only a small return (since females do not spend much time on extraction), males end up having a total amount of food that is still smaller than that of females, and hence they do not share food with them. Finally, in the leftmost region, males do share, and they share more the more they steal from females.

D.2 Foraging in the polygynous and the monogamous systems

Recall that $a^*(g) = 0$ iff $F/H \geq 2(1-\theta+\theta g)$ and $b^*(0) = 0$ 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 illustrated in Figures 9-11, which will also be used to summarize the main features of the proposition below):

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

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

A1. $a^*(g) = b^*(g) = 0$ *iff* $F/H \geq 2(1-\theta+\theta g)$

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

A3. $a^*(g) > 0$ *and* $b^*(g) > 0$ *iff* $2(1-\theta-g)^{1/2} > F/H$.

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

B1. $a^*(g) = b^*(g) = 0$ *iff* $F/H \geq 2(1-g)^{1/2}$

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

B3. $b^*(g) > 0$ *and* $a^*(g) > 0$ *iff* $2(1-\theta+\theta g) > F/H$.

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

C1. $a^*(g) = b^*(g) = 0$ *iff* $F/H \geq 2(1-g)^{1/2}$

C2. $b^*(g) > a^*(g) = 0$ *iff* $2(1-g)^{1/2} > F/H \geq 2(1-\theta+\theta g)$

C3. $a^*(g) > b^*(g) = 0$ *iff* $2(1-\theta+\theta g) > F/H \geq 2(1-\theta-g)^{1/2}$.

C4. $a^*(g) > 0$ *and* $b^*(g) > 0$ *iff* $2(1-\theta-g)^{1/2} > F/H$.

As can be seen from Figures 9-11, we first note that for any values of g and θ (such that $1-\theta-g \geq 0$), both males and females refrain from extracting food when the nutritional value of collected relative to extracted foods (F/H) is high enough, and they engage in extractive foraging when F/H is small enough. Second, for intermediate values of F/H only one of

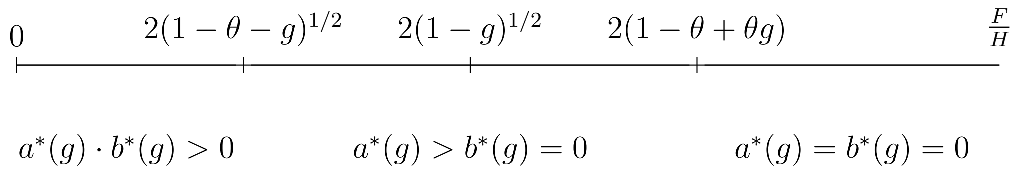


Figure 9: optimal foraging strategies in Case A of Proposition 8

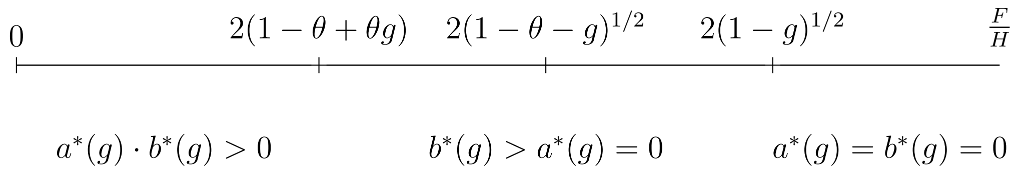


Figure 10: optimal foraging strategies in Case B of Proposition 8

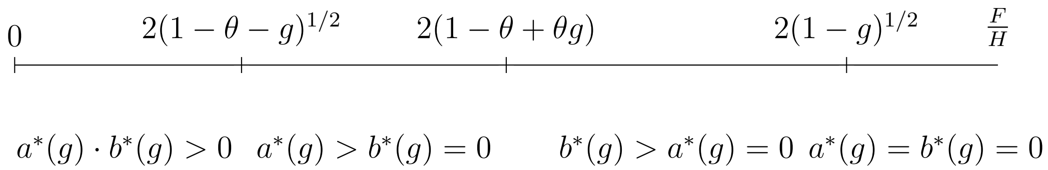


Figure 11: optimal foraging strategies in Case C of Proposition 8

the sexes engages in extractive foraging, and this depends on the mate-guarding parameter g (which dampens male extractive foraging by reducing the male's time budget) and the food theft parameter θ (which disincentivizes female extractive foraging). Thus, if θ is small enough (as in Case A), females extract while males don't for intermediate values of F/H (see Figure 9), while if θ is large enough (as in Case B), males extract while females don't for intermediate values of F/H (see Figure 10). 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, as F/H falls sufficiently for females also to start extracting, males stop extracting because of the reduction in the time budget that food theft thus implies. However, for even lower values of F/H, males start extracting again (see Figure 11). We finally note that for $g = 0$ the results coincide with those in the promiscuous system, as they should.

D.3 Sharing in the strictly polygynous system ($k \geq 2$, $g \in [0,1]$)

D.3.1 Sharing when neither females nor males engage in extractive foraging

We begin with a characterization result for parameter constellations such that $a^*(g) = b^*(g) = 0$:

Proposition 9 *Under strict polygyny, for parameter values such that neither females nor males engage in extractive foraging, 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 does not share food with his females.*

Proof. Recalling the expressions in (60) and (61), we obtain, for $a^*(g) = 0$:

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

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

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

Taken together, these observations imply the stated result. ■

The intuition for this result is as follows: when neither females nor males engage in extractive foraging, the male's foraging time budget is smaller than the female's whenever he spends time on mate-guarding. If this is the case, the female acquires more food than her pair-bonded male, and since her reproductive success is higher the more equal is her energy intake to his (see (46)), she then shares some of her food with him to reduce the inequality;

this also explains why the male does not share food with his females, since his reproductive success is determined by theirs. Note that by contrast to the promiscuous system, the female shares here because the benefit of doing so is not diluted across more than one male: here she gives food exclusively to her pair-bonded male.

D.3.2 Sharing when only males engage in extractive foraging

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

$$\tilde{g}(m) = 1 - \frac{F}{H}\left(m - \frac{F}{4H}\right), \tag{73}$$

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

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

Proof. Recalling the expressions in (60) and (61), we obtain, for $a^*(g) = 0$:

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

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:

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

Taken together, these observations imply the stated result. ■

The intuition for why females share is the same as above: a male who engages in a significant amount of mate-guarding collects a smaller amount of energy than the females, although he spends some time in extractive foraging (note that for this to be a relevant case, the food theft parameter θ has to be large enough for females to be discouraged from extracting). Since her reproductive success is higher the more equal is her energy intake to his (see (46)), she then shares some of her food with him to reduce the inequality. However, if g is small (and θ is large enough for females to be discouraged from extractive 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 reduce the inequality between his energy intake and theirs.

D.3.3 Sharing when females engage in extractive foraging

Next, we turn to parameter regions when females engage in extractive foraging ($a^*(g) > 0$). Whether or not males also extract food, (60) and (61) imply:

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

The expressions being highly involved, we illustrate them in graphs rather than derive general results. Thus, Figures 12 and 13 show the parameter regions for which sharing is culturally stable, for two different group sizes ($N = 18$ and $N = 36$, respectively). In both figures, the left three panels correspond to a lower polygyny rate than the three right panels ($k = 2$ and $k = 9$, respectively). Likewise, in both figures the rows of figures correspond to different mate guarding intensities ($g = 0$, $g = 0.25$, and $g = 0.5$, respectively).

D.4 Sharing in the monogamous system

As shown in Proposition 5, whenever possible, in the monogamous system sharing will equalize the female's and the male's energy intakes, i.e., $X(a^*(g), s^*, b^*(g), t^*) = Y(b^*(g), t^*, \boldsymbol{a^*(g)}, s^*)$. Since we have assumed that the male does not share food that he steals from other females (since he eats it on the spot), such equalization is impossible to achieve when the amount of stolen food is so large that he would still have more energy than her if he shares 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 $Y(b^*(g), t^*, \boldsymbol{a^*(g)}, s^*) > X(a^*(g), s^*, b^*(g), t^*)$.

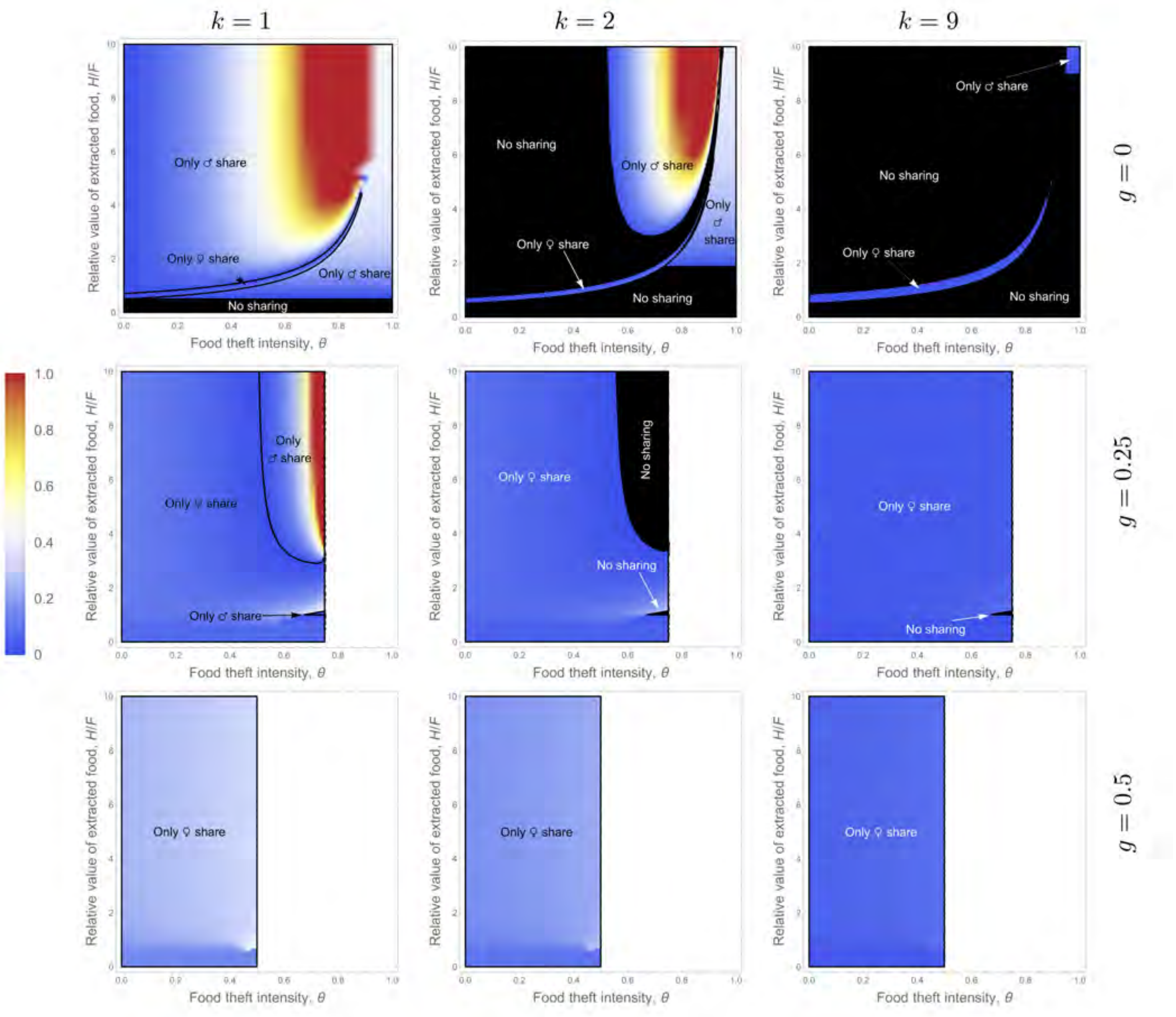


Figure 12: Regions of parameter space in the monogamous and polygynous mating systems corresponding to the three possible types of CS sharing pairs, (s^*, t^*), described in Prop. 3. The shading indicates the exact value of s^* or t^*, when it is not 0. Black regions are where both $(s^*, t^*) = (0, 0)$. Note that the white regions represent non-relevant parameter combinations, i.e., $g + \theta > 1$. Parameter values: $N = 18$

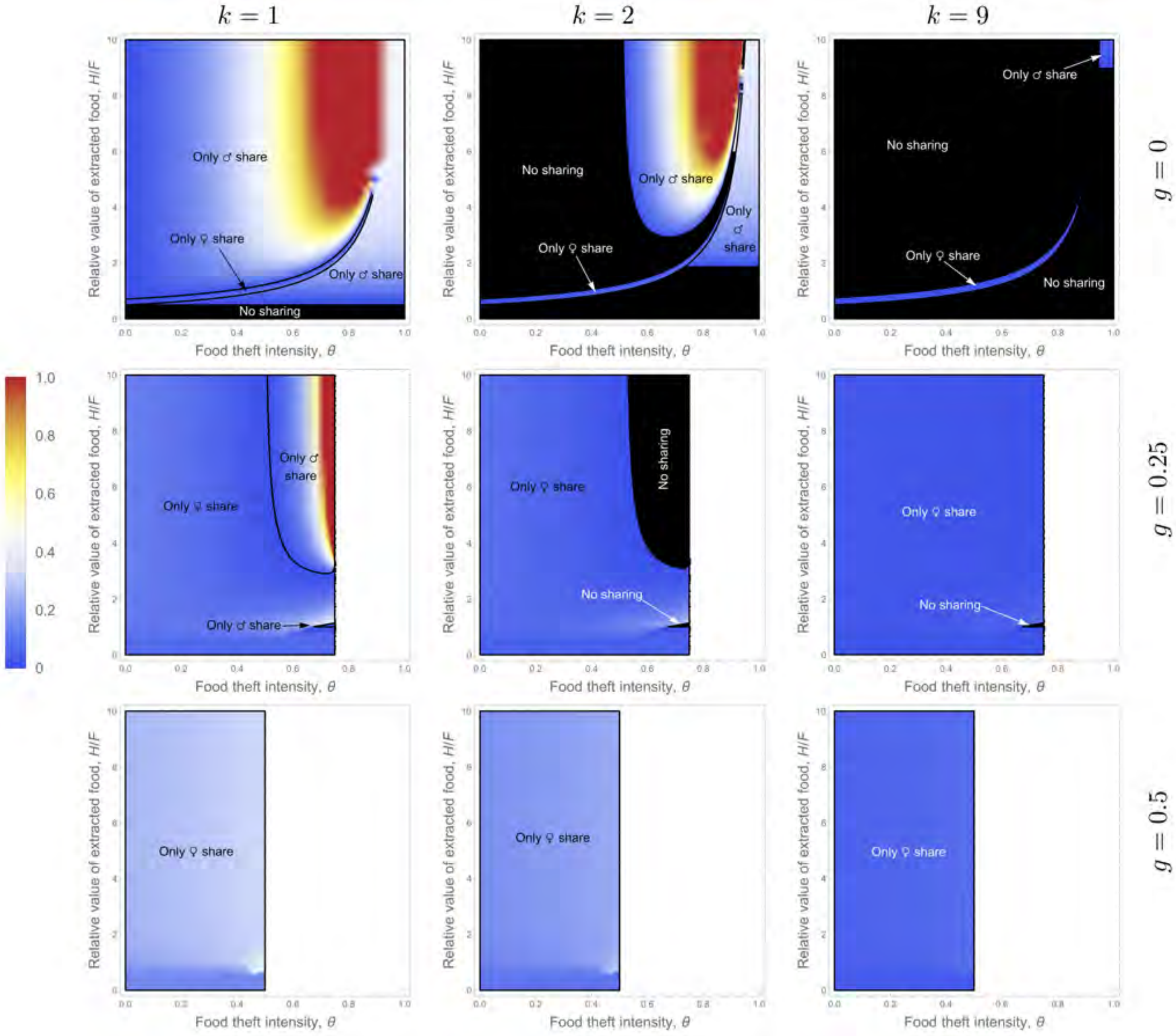


Figure 13: Same as Fig. 12 but with $N = 36$.

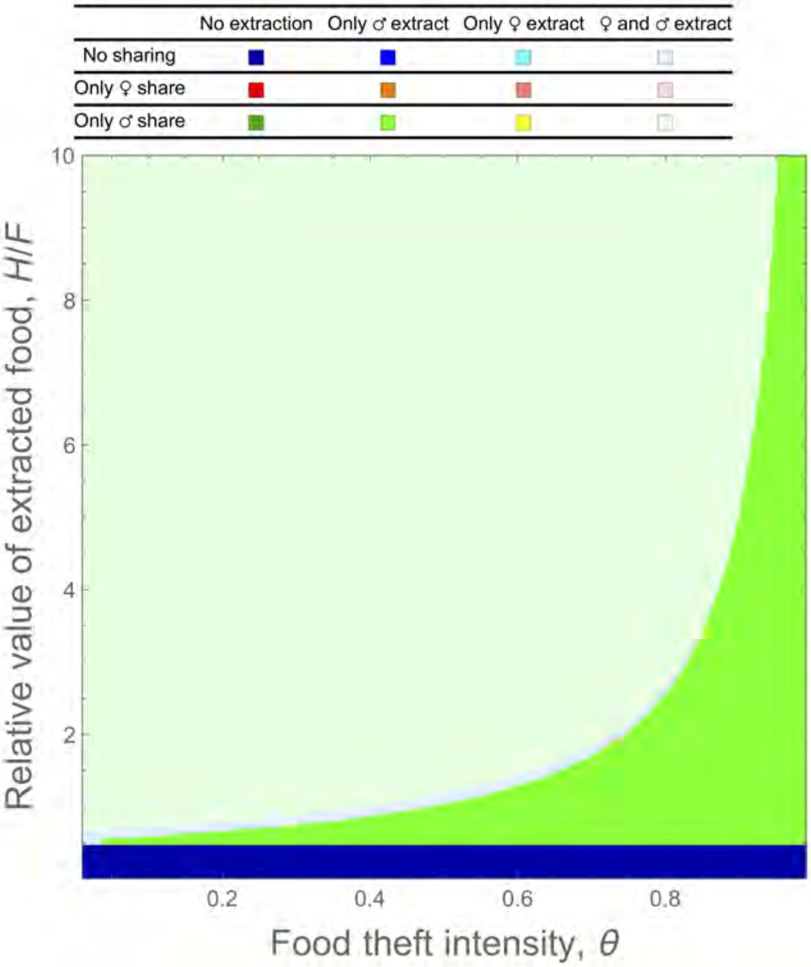


Figure 14: Sex differences in food production and sharing in the promiscuous mating system. The plotted regions correspond to the three possible types of CS sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend.

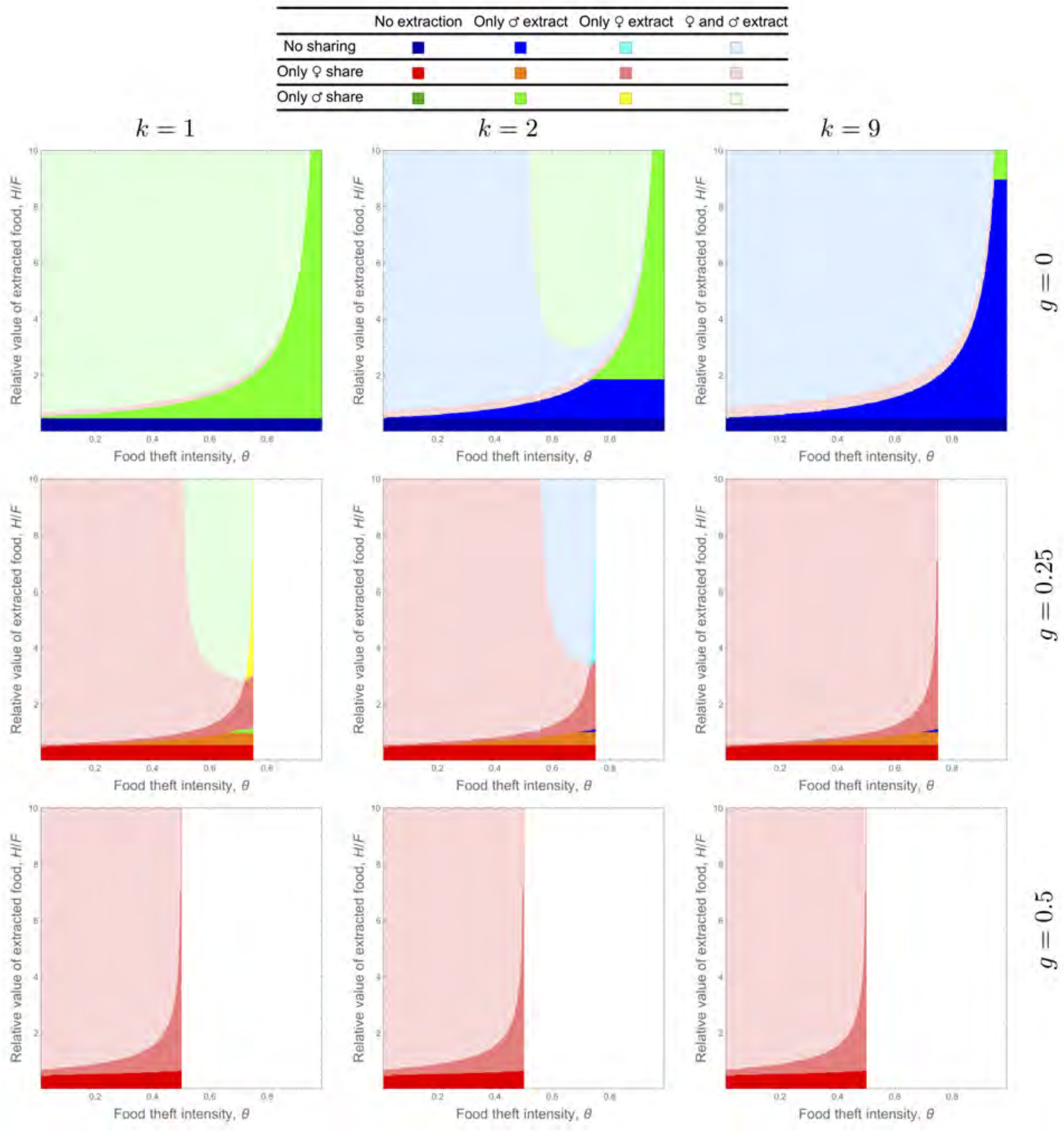


Figure 15: Sex differences in food production and sharing in the strictly polygynous mating system. The plotted regions correspond to the three possible types of CS sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend. $N = 18$.

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

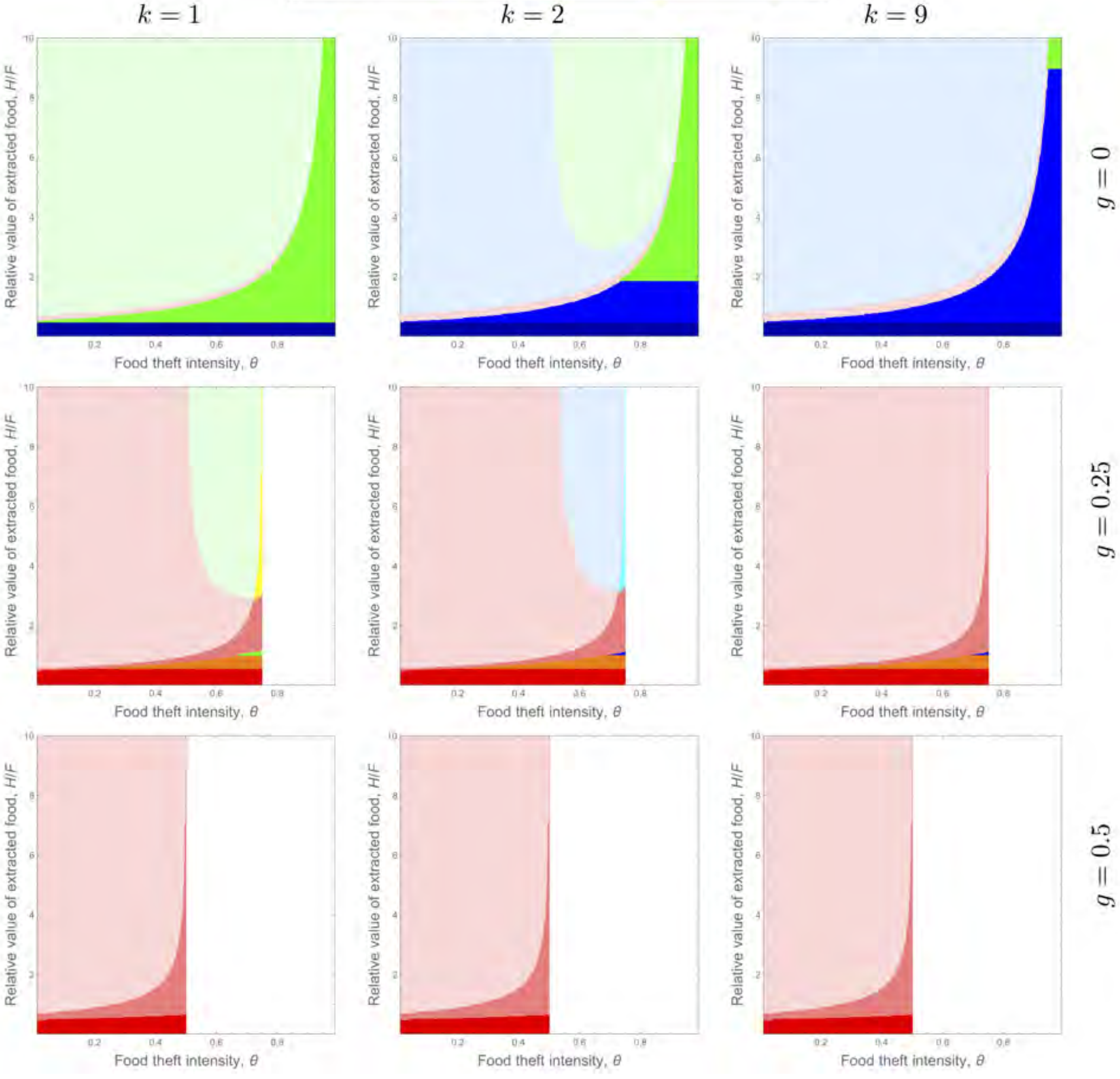


Figure 16: Same as Fig. 15 for $N = 36$

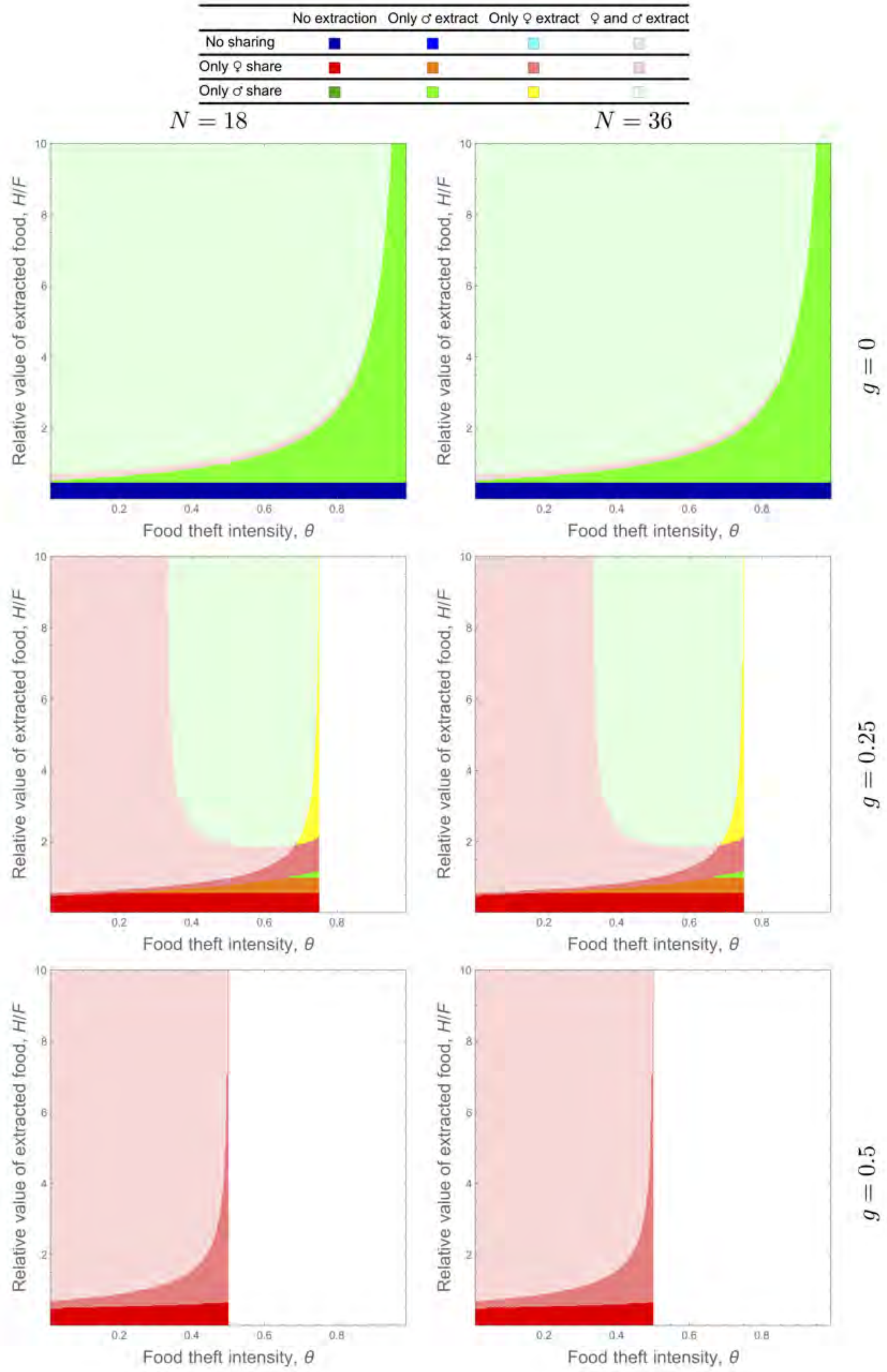


Figure 17: Sex differences in food production and sharing in the monogamous mating system. The plotted regions correspond to the three possible types of CS sharing pairs, (s^*, t^*), and the four possible types of optimal foraging strategies $(a^*(g), b^*(g))$. The table at the top is the legend.