

Cooperation and Conflict: The Behavioral Ecology of the Sexual Division of Labor

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When it comes to subsistence, men and women in almost all societies do it differently. One long-standing explanation for this sexual division of labor is that men and women pair up to provision offspring and specialize in subsistence activities in order to maximize household productivity. This model of cooperative parental provisioning has generally been supported by the proposal that both male and female reproductive success is maximized by provisioning current offspring rather than deserting them in order to seek new mating opportunities. But recent analyses of bird behavior have often failed to support this premise. We now know that among many species conflicting reproductive strategies between males and females often result in less than optimal compromises with regard to mating and parenting. This new focus on the role of sexual selection in creating compromise and conflict between the sexes has the potential to illuminate many puzzling aspects of human partnerships between men and women. To demonstrate its potential, I compare the explanatory power of a cooperative provisioning model of sex difference in human foraging and food sharing with a model incorporating conflicting reproductive goals.

On the island of Mer at the edge of the Coral Sea, a man and a woman go foraging on the reef flat at low tide. The man walks out near the edge of the reef with a large bamboo spear, pokes around in a shallow lagoon, then stands on a coral head and watches the water for signs of spine-foot, squid, giant trevally, sweet lip, and sea mullet. Seeing the wake of a giant trevally, he crouches, stalks, and throws the spear nearly twenty meters. He misses. He picks up the spear, adjusts the prongs, and walks, search-

ing, until he sees another fish. He throws, and on the end of his spear quivers a fish just larger than his hand. He continues in this way and spears another fish before the tide starts to deepen the lagoon and makes walking awkward. While he is spearing, his wife is walking on the dry reef carrying a basket, a knife, and a hammer. She picks up a tridacnid (giant) clam and cuts out the meat, putting it in her basket. She picks up a spidershell conch, cracks the shell, puts the meat in her basket. She carries a small spear, but she uses it mostly for balance. If she sees a small fish or octopus at close range, she might spear it. The tide begins to flood the reef flat and, when the man and woman meet on the beach, her basket is full of meat, but he has only two medium-sized fish. He carries the fish home on a stringer attached to the spear slung over his shoulder. When they return home, he gives one fish to his wife and the other to his neighbor. The wife cooks fish and shellfish meat for supper. The family eats.

When we observe human subsis-

tence behavior, we often see patterns such as this: females and males moving through the same habitat, making strikingly different decisions about how to obtain resources within that habitat, and often returning to a central location with the results of their labor. Agta men and women hunt game with bows in the Philippine rain forest, but women hunt smaller game using dogs, and only women plant gardens.¹⁻³ Hiwi men in Venezuela spend most of their time traveling by canoe, searching for large game and fish and collecting loads of oranges, while women spend their time traveling on foot to dig roots, pound palm starch, pick legumes, and collect honey.⁴⁻⁶ In the neotropical forest of Paraguay, Ache men spend almost seven hours daily hunting forest game such as pacas, armadillos, deer, and peccary, while women spend most of their time in the forest following male hunting parties and opportunistically collecting fruit, digging roots, collecting insects, hunting armadillos, and pounding palm starch.⁷⁻¹⁰ Hadza women and men of the Eastern Rift, Tanzania, show little overlap in foraging activities, with men almost exclusively hunting large game animals and collecting plants mostly for their own consumption, while women almost exclusively collect berries, nuts, and fruit and dig roots.¹¹⁻¹⁴ !Kung men of Botswana hunt large game, as do Hadza men, but often bring home small game and nuts, fruits, or roots.¹⁵ In the arid center of the Australian continent, both male and female foragers hunt small game animals and collect and process grass seed, but usually only men hunt kangaroos.^{16,17} Among many marine subsistence foragers and gardeners in island Oce-

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Figure 1. The differences between men's foraging and women's foraging on Mer Island. A: Two men displaying their catch of spanish mackerel outside the shop on Mer. B: A woman catches some small long-tom for lunch on the beach.

ania, women spend most of their time collecting shellfish on the reef flats and fishing and trapping in the lagoons and foreshore. Men tend to fish in open waters for tuna, mackerel, and other pelagic fish, hunt large marine mammals and sea turtles, and spear and dive in the shallow waters on the reef top.^{18–28} In almost all of these cases, the items women tend to focus on are commonly acquired, come in smaller sizes, have a relatively low risk of pursuit failure, and are often associated with high processing costs. The resources men prefer generally are more rarely acquired, larger, have higher risk of pursuit failure, and are associated with lower processing costs (Fig. 1).

COOPERATION

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human societies in different ecological contexts? One explanation is that adult males and females within a

household group are cooperatively acquiring food for their dependent children.^{29–38} By specializing in different forms of resource acquisition, they are able to maximize consumption benefits to the household in a way they could not if both were to cooperate in the same task or set about similar tasks separately. The hypothesis that cooperative provisioning by mated pairs maximizes the reproductive success of both sexes in a partnership was proposed by David Lack³⁹ to explain why monogamous mating systems were observed in 90% of all bird species. Cooperative provisioning might be required where members of a species depend on resources that are hard to locate, such as insects. In order to provision a brood successfully, two parents must cooperate in food acquisition. This mutualism, in which both

Box 1. Cooperative Provisioning Trade-Offs in Birds

Among monogamously mated sunbirds, the provisioning of offspring by both parents is crucial to nestlings' growth and survival.⁴⁷ Yet males fail to work as hard as females at provisioning and do not make up for the lack of a female's provisioning effort if that effort is experimentally reduced. Male birds face tremendous fitness-related trade-offs in allocating time to provision nestlings. When they undertake provisioning, they leave the nest unprotected and forgo the opportunity to seek extra-pair copulations with the nearest available female. When males do supply parental care, they may be more likely to invest in types of care

that have fewer trade-offs between parenting effort and mating competition. Nest protection is an important paternal behavior that protects offspring from nest predators and parents from brood parasitism. Yet providing protection offers the potential for mating pay-offs in ways that provisioning does not. Females are attracted to males on territories. Accordingly, a male that remains on its territory stands the best chance of attracting another female to mate with, presumably while his current mate is out foraging for food for their offspring.

The solution to a male's trade-off often depends on both the characteris-

tics of the male (his attractiveness to females as a mate) and the opportunities for seeking extra-pair copulations or guarding his current mate. For example, zebra finch males that are attractive to females as partners for extra-pair copulation invest less in parental care and provisioning than other males do.⁴³ Blackbird males with fertile partners realize high benefits from guarding and spend less time provisioning nestlings.⁴⁸ Males thus do not cooperate with females to provision even when parenting pays because other forms of parental investment either do not conflict with or actually provide mating competition pay-offs.

parties immediately benefit to a greater extent than if they acted separately, ensures the stability of the partnership. Where food is more abundant and more easily located as, for example, where fruits and seeds are an important part of the diet, so that one sex is able to provision a brood successfully on its own, cooperation might break down.

CONFLICT

When researchers began testing the paternity of offspring of monogamously mated birds, they discovered potential problems with the Lack hypothesis: monogamous matings did not often benefit both sexes equally, extra-pair copulations were common, and offspring were frequently sired on the mates of other males.^{40–43} Paternal care did not seem to correlate consistently with either monogamy or probability of paternity.^{44–46} In addition, males who were seemingly investing in paternal care often were not cooperating completely with their partners^{47,48} or gaining additional matings as a product of their investment (Box 1).

Male birds rarely benefit most from a reproductive strategy involving cooperative parenting: Monogamy often results from compromise and offspring provisioning from either poor mating prospects or attempts to enhance mating prospects. We might have pre-

dicted this outcome with sexual selection theory. Where variability in male reproductive success is higher than variability in female reproductive success, the increase in the fitness-related benefits males could acquire by stuff-

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ing more food into offspring are predicted to be lower than the pay-offs of more sex with more partners. Male and female strategies are likely to conflict if parenting and mating investment activities trade off; that is, if parenting requires lost mating opportunities and vice versa.^{49,50} When fathering reduces mating pay-offs, even

though offspring might eat less and grow more poorly without their help, the temptation to compete to gain more in other reproductive arenas can lure males away from fathering and toward philandering or mate guarding.⁵¹

Conflict may also arise over types of investment when a certain amount of fathering pays off. Males may invest in types of fathering that do not conflict with seeking more partners or that actually provide new opportunities to mate, but also provide fewer benefits to their current offspring than females would like. Theory suggests that females rarely gain as many pay-offs as males do from investing in mating competition. However, if males control access to resources females need for reproduction, females may attempt to mate with as many males as possible in order to secure access to those resources and, at the same time, attempt to keep their current mates from mating with other females.⁵² If males supplied nothing but genetic material, females might choose mates based on their quality and be less concerned about their partners' philandering. Because in that case, females would supply all parental care to offspring, they would face strong parenting tradeoffs and questions such as whether to forage for their children or guard them from harm or whether to try to do both effectively.

The Lack hypothesis has been instrumental in the acceptance of a cooperative provisioning model of the human sexual division of labor. Challenges to the hypothesis based on the behavior of birds raise questions about its applicability to humans. Are sex differences in foraging the result of mutualistic cooperative provisioning or do sex differences arise because one sex gains greater benefits from investing in mating effort than in provisioning?

COOPERATIVE PROVISIONING: LET'S FEED THE KIDS?

If men and women specialize in order to maximize their provisioning efficiency, the pressure to become specialized occurs where there are strong fitness-related benefits for efficient provisioning and where males gain more from provisioning in terms of enhanced offspring growth rate and lowered mortality than they could obtain by more matings. This suggests three primary testable predictions: 1. Gender specialization should increase foraging income relative to nonspecialization, with more food being delivered to the household more predictably; 2. resource sharing by men should favor their own households over others; 3. where men and women are very specialized, men should have high payoffs for fathering.

A Sexual Division of Labor Should Increase or Stabilize Household Income

We would expect that by dividing their efforts, men and women can better and more reliably provision their offspring and partners. But many studies demonstrate that if men's subsistence strategies are simply about supplying energy to the household, they have plenty of room for improvement. Hurtado and Hill⁵ have demonstrated that Hiwi women, especially postreproductive women, work hard digging roots while they are in season. Indeed, these women's seasonal return rate on roots is higher than men's hunting returns, yet men do not switch to root-digging during this time. In addition, men stop hunting to collect mangoes in distant groves (which women do not do), again accepting lower energetic returns by doing so. In one of the

best documented cases, Hill and collaborators⁹ have shown that in terms of their return rate while foraging, Ache men lose out by focusing exclusively on hunting: men consistently fail to collect the palm starch that women do, even though it provides greater on-encounter returns than does the continuing search for game.

We find similar patterns in Melanesia. Meriam men in the Torres Strait choose to spear fish on the reef at low tide rather than collect shellfish as women do, a choice which nets them half the return rate of shellfishing and a 20% risk of coming home empty-handed.²⁸ Yams are an important part of horticultural subsistence in both men's and women's gardens throughout Melanesia, but men compete to grow outsized roots, sometimes spending days preparing a single hole, while women plant dozens of "table" yams in

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smaller holes. The huge "feasting" yams grown in such competitions are displayed at public gatherings and often are too fibrous to eat. Instead, they are distributed as suckers for others to plant in their gardens.^{53,54}

A common explanation for men's avoidance of women's resources is that a household requires both energy and proper nutrients. The nutrient complementarity hypothesis suggests that men pass over carbohydrates with higher energetic return rates because they value the protein or fat return rates from hunting game, primarily because women's resources are almost entirely carbohydrate.^{10,55} While it is obvious that over the long term individuals need to consume a relatively balanced diet, cooperative nutrient complementarity fails as an explanation for the sexual division of labor.

This hypothesis cannot explain why sex differences exist where both men and women forage for meat nor why it necessarily is men who obtain protein. For example, men and women forage on reefs throughout the tropical Pacific, but men consistently choose to hunt large game, especially pelagic fish and marine turtles, while women consistently focus on small game such as shellfish and resident fish.^{27,28} Elsewhere, women sometimes hunt terrestrial animals and cooperate with men in some forms of hunting.⁵⁶⁻⁵⁹ But even when women bring home fat and protein-rich plant foods, there are still sex differences in foraging: !Kung men hunt even though !Kung women bring home mongongo nuts.¹⁵

Is Big Game Shared Too Widely to Provide Well for a Household?

Because people often return with large quantities of food to a central place and consume it socially, there are many opportunities for food to be transferred between individuals.⁶⁰ One common pattern of human food sharing is that men share more than women do. Men tend to search for resources that come in uncontrollably large packages or spend a lot of time acquiring more food than their households can eat. Women tend to spend their time searching for items for which package size can be controlled and more rarely spend the time acquiring more than their families can eat.⁶⁰⁻⁶⁵

If big-package hunting is primarily about fathering and provisioning, hunter-fathers must keep at least as much meat for their own households as they might if they had chosen small-package hunting.^{64,66} Little cross-cultural data is available to test this prediction. Although Hill and Kaplan⁶¹⁻⁶³ reported that Ache hunters may keep a large proportion of their prey, Ache households receive no more food when large rather than small game is targeted because large game are shared more. Data based on foraging experiments among the Hadza suggest that hunters would return food to their households more predictably and in greater abundance if they focused on small game rather than large game.¹² When Meriam men hunt marine turtles, the amount of meat they keep

for their households varies according to the number of other households in close proximity. More than 60% of the time, households keep fewer calories of turtle than they might acquire by spending the same amount of time and energy netting sardines.⁶⁵

Does a Sexual Division of Labor Mean Men are Fathering?

It is possible that short-term measures of foraging success fail to capture the longer-term benefits to offspring if parents specialize and divide provisioning tasks. Hadza and !Kung foragers live in similar environments with similar prey types available to provision their households, but the sexual division of labor among the Hadza seems stronger than that among the !Kung. Lee¹⁵ reported that !Kung men often spend time gathering when hunting returns have been poor and will often seek small game when they have been unsuccessful in the pursuit of large game. Hadza men rarely do any collecting except for their own consumption on hunts and do not seek small game to return to wives and children when the hunt fails.¹²

Are these disparities in foraging strategy between Hadza men and women the result of a cooperative partnership between husband and wife? If Hadza men hunt because they strongly benefit from fathering, we might expect them to face many of the conditions that make fathering pay off. For example, a high cost might be attached to investing in mating competition. Offspring might be so much better off when fathers are attentively provisioning that fathers actually benefit more from provisioning than they would from investing in new mating opportunities. But what we actually see is the Hadza data chipping relentlessly away at the hypothesis of fathering hunters. The operational sex ratio is quite good from the male perspective, so that finding additional mates is unlikely to be costly for the Hadza.⁶⁷ Hadza men who desert their families face no statistically significant reduction in their offsprings' survival chances.⁶⁷ And Hadza partnerships are comparatively unstable: 24% of Hadza marriages that lasted for more than 10 years ended in divorce within the subsequent 5 years, while among the

!Kung only 8% of marriages that had reached 10 years failed in the next 5 years.⁶⁷ Although this is not a definitive test of the cooperation model, it suggests that strong differences like those seen among the Hadza, with men focused on big-game hunting and women harvesting and collecting of plants and small game, might not always mean that men are hunting to be good fathers to their wives' children.

CHILD CARE CONSTRAINTS

Cooperation alone cannot explain why a sexual division of labor takes the shape it does. Men and women could conceivably work together, as they sometimes do, in both collecting and hunting, if this is most efficient. The cooperation hypothesis relies

One constraint that might be common to all women is the trade-off between contact care of infants and children and foraging to feed those children. Because men typically invest less in contact care than females do, and rarely take children foraging, they may rarely face this trade-off.

solely on nutrient complementarity to explain why men seem to avoid cooperative collecting with wives when it might benefit the household for them to do so; yet it incorporates both nutrient complementarity and constraints to explain women's general reluctance to hunt larger game as their mates do. One constraint that might be common to all women is the trade-off between contact care of infants and children and foraging to feed those children.^{6,30,32,68} Because men typically invest less in contact care than females do, and rarely take children foraging, they may rarely face this trade-off. Perhaps the trade-off between contact

care and foraging for women and the absence of this trade-off for men constrains women from hunting and makes hunting pay for men.

Does Contact Care Trade Off With Foraging to Make Hunting a Poor Option?

Women do face childcare trade-offs

Hurtado and coworkers⁶ examined the role of child-care trade-offs in female foraging decisions among the Ache and Hiwi. Sex differences in foraging are strong among the Ache, but even stronger among the Hiwi. Hiwi women never capture game and work very little when roots are not in season. Ache women spend most of their time following male hunting parties, spending only two hours a day collecting fruit, digging roots, looking for insects, pounding palm starch, and capturing the occasional opportunistically encountered animal prey. Based on these sex differences in foraging, we might predict that child-care trade-offs would affect Hiwi women more than Ache women.

Hurtado and colleagues⁶ found that both Ache and Hiwi women seemed sensitive to the changing benefits of foraging and child care, but that child care trade-offs did not seem to affect Hiwi women to the extent that they did the foraging strategies of Ache women. When foraging was less productive, and during seasons when pests and other dangers could be avoided only by vigilance, women in both groups spent more time caring for their children than foraging. During seasons when return rates were greater, they spent more time foraging. Yet the competing demands of care and foraging seemed easier for Hiwi women to fulfill simultaneously. Hiwi women with multiple children acquired more food and at a faster rate than did Ache women with multiple children, perhaps because the presence of more children caused more interruptions in Ache women's foraging than was the case among the Hiwi women. It is also possible that Hiwi children themselves were more productive foragers than were Ache children. Even nursing Hiwi women did not differ significantly from other women in time allocation or the amount of calories

acquired, and increased their time allocation and calories harvested per day when high-ranked resources (roots) become available.

Women who avoid trade-offs do not hunt more

Hurtado and coworkers⁶ proposed that one explanation for the difference between responses of Ache and Hiwi women was the presence of many suitable alternative caretakers among the Hiwi but few among Ache camping groups. Presumably this is because the few elderly Ache who survived the postcontact period are likely to be left in the village during week-long foraging forays. In addition, the short duration of Hiwi foraging trips makes it possible to leave children with grandmothers or to bring grandmothers along. Women with greater access to substitute caretakers would be released from some of the constraints placed on them by the need to care for children while they forage. But variability in child-care trade-offs does not seem to affect the degree to which women and men differ in their prey and patch choice, either between Ache and Hiwi or overall. The availability of alternative caretakers is assumed to be high among the Agta, where women spend much time hunting either without their children or with them strapped to their backs.^{1,3} However, Hiwi and !Kung women do no hunting even though many alternative caretakers are available.⁶

Women who are beyond reproductive age also avoid the care-foraging trade-off and appear to work hard, in many cases, to provision their adult offspring and grandchildren. Yet postreproductive Ache, Hiwi, Hadza, and Agta women do not spend more time hunting than younger women do.^{2,4-7,11,14} Among the Hiwi at times when roots are available, postreproductive women and women who are not currently pregnant or lactating work longer and acquire more food than do pregnant or lactating women. These women acquire nearly as many calories per day as men do, with half the variability.^{5,14} The resources such women target are those that predictably supply large harvests with increased work effort. Thus the emphasis on root-digging (rather than

hunting) by the grandmothers of many foraging societies.^{5,7,11,14,15}

CONFLICTING REPRODUCTIVE GOALS: PARENTAL VERSUS MATING INVESTMENT

Women's parenting trade-offs have received the most attention as shapers of the sexual division of labor; men's trade-offs have generally been ignored or assumed not to exist. This assumption seems untenable, especially since theory suggests that trade-offs between parenting and mating are likely to be important determinants of male reproductive strategy. The cooperation model tends to assume little or no trade-off between parenting and mating, whereas a conflict model assumes that parenting and mating are neces-

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sarily conflicting activities and are likely to affect male foraging strategies. A third option, that some parenting activities might conflict with mating more than others do is presented in Box 1. It is worth pointing out that although offspring might profit from a male who performs some activity with multiple benefits, such as caretaking, in order to attract mates⁶⁹ or keep his current mate happy,⁵⁹ this does not necessarily mean that he is parenting. He may take care of offspring as long as the behavior does not reduce his ability to invest in other areas, then cease once that behavior becomes costly.^{59,69} This kind of caretaking does not accord with Trivers' definition of parental investment as an activity that invests in current offspring at the expense of future offspring.⁴⁹

Is Meat Income That Can Be Invested in Both Parenting and Mating?

Big-game hunting is the quintessential male activity, and subsequent sharing of meat could potentially offer hunters both mating and parenting benefits. Meat may be a commodity, with hunters distributing game not only to feed children and wives, but to attract the attention of potential lovers, ensure future shares of game from other hunters, and gain better treatment for their offspring.^{10,34,61-63,70} Big game hunting is thus attractive to men because it supplies large packages that can be distributed down many reproductive avenues. Meat also supplies animal fat, a more valuable commodity than plant nutrients, and one for which there is strong demand and thus, high value in trade.

Smoothing over the bumps in consumption

One problem with relying on hunted meat for household subsistence is that it is a risky resource: Hunters often fail to find and capture game. A single hunter might find such resources too risky as a source of subsistence, but a group of hunters might cooperate to minimize the risk by sharing widely when they are successful and garnering shares from others when they are not.^{71,72} Through conditional sharing networks of hunters (sharing with those who share in return), risky big game can be good for provisioning as long as it is within the optimal diet and as long as hunters keep enough of the resource within their households. The problem is the lack of evidence that hunters have an opportunity to control the destination or size of game portions. In many cases, sharing big game seems to be unconditional and not directed toward those who share in return.^{62,73-76} Without such control, there is tremendous opportunity for free-riding.⁶⁰

Trading meat for sex and children's welfare

Chimpanzees seem to initiate more hunts in the presence of estrous females. Observers also have noted transfers of food between possessors of meat and estrous females prior to mat-

ing.^{77,78} Do similar transactions occur among humans? Among the Ache, better hunters are more often named as lovers and as fathers of children,⁷⁰ but there is little evidence that hunters receive more sex based on the distribution of meat to particular females. Better hunters among the Ache also have children who are well-treated by others.⁷⁰ Children without male protectors seem to fare badly, being subject to mistreatment and infanticide.⁷⁹ But again, specific links between meat distribution and treatment of children have not been investigated. Generally, a hunter can control only little of what could be “traded” for favors. In addition, the long periods between successful hunts, reaching an extreme of nearly 30 days among the Hadza, are also puzzling if a hunter’s aim is to acquire meat currency to invest in reproductive advantages.¹² Other, more predictable ways of acquiring meat would ensure that even poor hunters would always have something to trade (or eat!) in between successful big-game hunts. Hunting must not be simply about acquiring meat, either to eat or to share.

The Puzzle of Unconditional Generosity

Anthropological wisdom assures us that generosity through seemingly altruistic distributions of food—so-called generalized reciprocity—is an important part of human behavior.⁷⁵ There is no doubt that some kinds of food are traded between individuals, sometimes with return benefits coming after some delay. However, what is so striking among humans is that conspicuous resources, particularly those that come asynchronously, in large packages, and with some risk of failure—those that men often target and women avoid—are often distributed widely with little attention paid to recipients or return benefits.^{64,65,73,75,76} This is evident in many ethnographic studies of food sharing after big-game hunting. A big-game hunter often distances himself from the distribution of his catch and has little control over the distribution of shares. Such practices are often institutionalized through rules of butchery specifying which relative of the hunter must cut and distribute the carcass. Hadza game is butch-

ered at the kill site by a number of people from camp, all of whom claim shares and then carry the meat away for secondary distribution; hunters have no control over primary distribution.⁸⁰ Sea turtles captured among the Meriam often are not butchered or distributed by their hunters. When turtles are acquired for public feasts, hunters have nothing to do with butchery and sometimes do not eat any meat at all.⁶⁵ This makes not only hunting the turtle, but sharing it, a costly activity.

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Such unconditional generosity could be elicited by the demands of others that would be too costly to refuse (also known as tolerated theft)^{73,81,82} or by hunters seeking the prestige associated with costly displays of giving (sometimes referred to as costly signaling).^{83,84} Both the tolerated theft and costly-signaling hypotheses are grounded in evolutionary theory, and generate testable alternative predictions about the nature of giving. If largesse is patterned by gift-givers seeking prestige (sharing for recognition), the givers often keep nothing for themselves and indeed, go to great lengths to avoid any expectation of return from the recipients of their meat. Through costly giving of meat a hunter may

signal his quality as a mate or competitor.

But distribution may sometimes be patterned not by the benefits of giving but by the high cost of refusing others (“tolerated theft”).^{64–66,73,81,82} The intrinsic nature of some resources (their size and acquisition asynchrony) draws a hungry audience, making hoarding or controlling distribution of the entire prey very costly and conversely, increasing the likelihood of sharing according to demands or potential demands. Hunters thus end up with small portions that they control outright or at least to the extent that they own the distribution rights, letting hungry neighbors take the rest. By not paying attention to who receives shares, or to how many shares of what size go to which households, a hunter seems to have little interest either in the value of the meat as currency or in controlling for reciprocation among those who could return benefits to him based on his gift. When hunters share according to the cost of refusals, they often end up taking home less than they would have if they had gone after prey that attract less attention, as women often do.^{64,65} Under such circumstances, it is difficult to imagine how big-game hunting can function primarily as a form of paternal investment or how hunters can be trading meat to others who supply them benefits based on their gift.

Hunting As Costly Signaling

If hunters do not hunt to share, we are left with the question of what benefit men receive from spending so much time getting food that goes to others.⁶⁴ One answer to that question might come from costly signaling theory. Hunters do receive benefits, even where they seem to exert little control over distribution of their prey. They are desirable lovers,^{70,79} their children are well-treated,^{70,79} and they are married to harder-working women.^{6,80} Both Hawkes^{64,66} and Bliege Bird and Smith^{83,84} argue that such benefits are not gained through distribution of meat from hunted game that is subject to costly refusal (tolerated theft), but rather through the acquisition of the meat. Hunters may hunt to show off, not to share per se. Men may seek large game not because they can trade

TABLE 1. Cooperative Provisioning and Conflicting Goals Models of the Sexual Division of Labor

	Cooperative Provisioning	Conflicting Goals
Foraging goal		
Women	Maximize long-term average rate of food intake	Maximize provisioning or consumption benefits of resources
Men	Maximize long-term average rate of food intake	Maximize mating competition or signaling pay-offs of resources
Currency		
Women	Energy (carbohydrates)	Energy
		High acquisition synchrony
Men	Energy (protein or fat)	Low acquisition synchrony
		Large package size
		Special skills
Constraints		
Women	Child care tradeoffs	Child care trade-offs
Men	None	Mating investment trade-offs

the meat for prestige and other benefits, but because it requires a particular skill that is a reliable indicator of other characteristics. By hunting, they can broadcast that skill to the large audience that is attracted to the kill. The fact that big game is shared is incidental. The audience comes to claim a share and grants hunters distinction not in exchange for the meat, but because hunting is an honest (costly) signal.⁸⁵ It benefits everyone to pay attention to a hunter's signal: potential mates, competitors, and allies can avoid the high costs of trying to evaluate abilities through drawn-out interaction or confrontation. Small game that is difficult to acquire and that would reliably distinguish one man from a competitor would be just as attractive as a source of prestige if an audience can be assured. This might explain why Meriam men spear small fish, a highly visible activity on the exposed reef, instead of collecting shellfish⁸⁴; why many Melanesian men compete to grow big but inedible yams for public display^{53,54}; and why Hadza men spend a lot of time killing huge animals only to abandon most of the meat to people not only from their own camp, but from other camps as well.⁸⁰ The benefits that hunters' children indirectly acquire from signaling activities may be important, but they do not seem to be driving the system.

CONCLUSIONS

Our ideas about the evolution of the sexual division of labor have often incorporated many assumptions that lack empirical and theoretical support. The first assumption is that the sexual division of labor consists of the husband's big-game hunting and the

wife's plant collecting and the sharing of these resources with each other and their children. As ethnographic accounts demonstrate, this description can hardly be generalized to many places around the world where women hunt and take small game, fish, and shellfish. This assumption also fails to account for the potentially important

The fact that big game is shared is incidental. The audience comes to claim a share and grants hunters distinction not in exchange for the meat, but because hunting is an honest (costly) signal.

effects of extensive sharing beyond the nuclear family. The second assumption is that the function of the sexual division of labor is to maximize labor efficiency for the household in order to provision all members optimally. We now know that in many cases the choices women make bring home more food more consistently than do the choices men make, because men's foods are highly variable and widely shared. In these cases, it would make more sense for a provisioning man to do what women do. The third assumption is that the origins of the sexual division of labor lie in the physiological constraints and trade-offs faced by females with small children, namely birthing, nursing, and transporting children, which force women into rela-

tive immobility. Such trade-offs may explain variability in time allocation to food production according to reproductive status, but they do not explain differences in the resource choice of men and women. Postmodernist critiques of scenarios incorporating such assumptions have already challenged their typification of women as "physically weak, immobilized by nursing children, engrossed in the provisioning of reliable plant foods, redolent with odors that drive away the game, and subject . . . to the axiom that specialization everywhere increases productivity."⁸⁶ From an entirely different standpoint, we can now round out the critique to challenge common representations of male foragers as being free from constraints and engrossed in big-game hunting in order to provision their wives and children with meat.

The puzzling pattern of the human sexual division of labor seems to make more sense as an outcome of conflicts rather than similarities in reproductive goals. By testing competing predictions from the conflict hypothesis and its cooperative alternative, we find that the singular role of cooperation in maintaining a ubiquitous division of labor seems less likely, although this does not mean that cooperation does not exist. The conflict model predicts that sex differences are stronger where men benefit more from investing in mating opportunities, and hence will value resources that enhance these opportunities rather than provisioning ones. That such competition can result in benefits to children may be an important but incidental outcome. Sex differences are predicted to be weaker or more cooperative where both males

Figure 2. Cooperation and conflict on the reef. A: Cooperation: a man and his wife collecting shellfish on the reef at low tide. B: Conflict: a man spearing while his wife collects shellfish some distance away. His bag is full of shellfish meat, collected after his spearing was unsuccessful.



and females gain greater benefits from investing in offspring and their common goals are likely to result in cooperative foraging on resources that provide high consumption benefits. This might occur where large game is not available, where resources are captured more synchronously and predict-

ably or are more narrowly shared (e.g. among net hunters and desert small-game hunters), and where men gain more benefits from provisioning and fewer from competition, including mate guarding. As so much recent research suggests, attention to the conflicts of interest between the sexes and

between closely related individuals can illuminate many perplexing aspects of social dynamics.⁸⁷

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Figure 3. Cooperation and conflict in the water. A: To fish the reef, the boat must be positioned properly. The reef top, where small resident fish feed, cannot be fished at the same time as the reef edge and bottom slope, where larger fish reside. If men get their way, they fish the edge and bottom. If women get their way, they fish the top (shown here). B: Men and women sometimes compromise with anchoring the boat. Here, they've positioned the boat in such a way that the man catches a single large fish at the edge and the women catches a few smaller fish on the top, neither catching as much as they would have had they positioned the boat optimally.



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