

Sexual Division of Labor: Energetic and Evolutionary Scenarios

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ABSTRACT This article examines comparative energetic data on hunter–gatherers in the context of evolutionary scenarios of the sexual division of labor, with respect to both *specific task* allocation and *overall levels* of daily physical activity. The division of labor between men and women, well marked in contemporary foraging societies, was once posited as the “true watershed” for the evolution of the genus *Homo*. Some research on brain-wiring even links sex differences in cognitive and spatial abilities to sex-specific foraging activities. Most recent evolutionary arguments posit that men focus on hunting and women on gathering activities to realize potentially conflicting mating and parenting goals. A range of cooperative strategies (male/female and female/female) for child provisioning is also under investigation. Attention to energetic and reproductive trade-offs has usefully challenged the proposition that women are excluded from big-game hunting due to constraints of foraging ecology and reproduction. Simplistic assumptions about gender roles are thus increasingly questioned in anthropology, as well as in archaeology. Current models in behavioral ecology explore ways in which foraging practices vary with ecological circumstances, aiming to derive testable hypotheses from fine-grained data on the behavior of contemporary hunter–gatherers. Data on overall physical activity levels (PAL) can also serve to evaluate relative male/female workloads in modern groups, reconstruct hominid energy requirements and activity profiles, and examine changes with subsistence intensification. Male/female PAL ratios show that a task-specific division of labor does not readily extrapolate to 24-hour energy expenditure and that male/female differences in workloads were not necessarily reduced with the transition to agriculture. With respect to gender roles and PAL, a shift away from facile stereotypes of human behavior is evident. The challenge is to incorporate a range of behavioral responses to ecological circumstances in reconstructions of our evolutionary past. *Am. J. Hum. Biol.* 14:627–640, 2002. © 2002 Wiley-Liss, Inc.

The division of labor between men and women, encapsulated in the memorable phrase “Man the Hunter, Woman the Gatherer” (Lee and DeVore, 1968; Dahlberg, 1981), is a well-known and much-debated feature of foraging societies. In particular, the portrayal of subsistence activities, whereby men hunt big game while women procure vegetable foods and small game is a consistent feature of the allocation of tasks in modern (and past) foragers. This portrayal has hardened into a stereotypic view of what men and women do in foraging societies, a view which does little justice to the historically and culturally specific ways in which modern foraging societies organize daily work responsibilities (Balme and Beck, 1993; Brightman, 1996; Endicott, 1999).

The sexual division of labor was once posited as a key behavior propelling the course of human evolution (Lancaster and Lancaster, 1983). It was then associated with a “package” of behaviors related to food sharing, food provisioning, and even pair bonding (see Zihlman, 1991). The nature of a “package” driving the course of

hominid evolution and the success of hunter–gatherer ways of life has been debated many times (Wrangham et al., 1999; Lancaster et al., 2000; Kaplan et al. 2000, 2002; Panter-Brick et al., 2001; Stanford and Bunn, 2001). Such reconstructions of human evolution draw directly upon evidence from modern foragers: thus big-game hunting in the Upper Paleolithic has been portrayed in the mirror image of hunting activities by San men (Bernaldo de Quirós, 1987). A stereotypic view of subsistence activities has often been conveyed in evolutionary scenarios of male and female activities, despite more nuanced data from foragers to the contrary.

This article evaluates the extent to which evolutionary scenarios regarding the sexual division of labor have been informed by current energetic data. It considers research on both *specific task* allocation and *overall*

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levels of daily physical activity. Recent evolutionary theories as to why males specifically hunt and women usually gather, framed in terms of trade-offs between mating and parenting goals, draw heavily upon energetic data from contemporary foragers to show how foraging activities are finely tuned to ecological circumstances. Similarly, reconstructions of hominid activity profiles are reliant upon data on levels of daily energy expenditure in contemporary societies, raising questions about the extent of male/female differences across various subsistence regimes. To a large extent, energetic models of foraging subsistence have moved away from facile stereotypes of gender roles and activity patterns. Following the adoption of more finely grained models of human behavior, they provide a useful range of hypotheses pertaining to the course of human evolution.

EVOLUTIONARY CONSIDERATIONS

Given that no other primate group features a *sexual* division of labor to organize subsistence activities, what explains its origins in humans? When did the sexual division of labor evolve: with protohominids, *Homo erectus*, or *Homo sapiens*? Does the division of labor whereby women are precluded from big-game hunting have anything to do with energetic or biological constraints? And what is the evolutionary significance of a food-sharing behavior predicated on different male and female activities? These are some of the major questions debated in the literature.

Lancaster and Lancaster (1983, p. 36) held the sexual division of labor and food sharing as the "true watershed for differentiating ape from human life ways." Accordingly, "the fundamental platform of behavior for the genus *Homo* was the division of labor between male hunting and female gathering, which focused on a unique human pattern of parental investment—the feeding of juveniles" (p. 51). Indeed, a major difference between human and nonhuman primates is that humans provision their children *after* weaning until about puberty. Lancaster and Lancaster (1983) noted that "in contrast to humans, the juvenile monkey or ape feeds itself," such that child provisioning is a defining trait of human evolutionary history. Bogin (1997, 1998) has argued that the hu-

man reproductive strategy, in contrast to that of living apes and extinct hominids, hinges on the insertion of a new life stage (childhood) between the end of infancy and the juvenile period, namely, after weaning but before the ability to eat human foods (Geary and Bjorklund, 2000). This stage of development is most prolonged in *Homo sapiens* to allow for brain development and social learning. Konner (1991, p. 427) stated this most simply: "*We are the species that takes care of children*" (italics in original).

Male/female activities and brain-wiring scenarios

How this parental investment strategy might relate to the subsistence strategies of men and women is under lively debate. Some research even links sexual dimorphism in the brain to differential male and female activities, based on evidence that men and women use different cognitive strategies to solve navigation tasks. While men activate the left hippocampus, an area of the brain involved in spatial tasks, women activate the right prefrontal cortex (Grön et al., 2000). Such differential brain-wiring would allow men to outperform women on spatial tasks, and women to outperform men on verbal abilities (Falk, 1988, p. 122). While interpretation of this research is contentious,¹ it is important to note, as expressed by Falk (p. 124), that "finely shaded but significant sex differences characterize human behaviors," and then to ask, what might have driven this brain evolution? Falk explicitly proposed that the "cognitive specialities of men and women evolved for reasons to do with classical 'reproductive fitness'—i.e., superior visuospatial skills [in] male ancestors of hominids for finding mates (and the way home)" and superior verbal skills "selected in female ancestors in conjunction with mothering" (p. 133). Falk highlighted that comparative mammalian evidence suggests a deep time-scale for male/female brain

¹ Tongue in cheek, Matt Ridley (1996) thus summarized these sex-related cognitive differences: men are "innately better at throwing things," are ... "more carnivorous ... generally prefer large meals to frequent snacks ... prove consistently better at map reading" (p. 95). In the editorial of *Nature: NeuroScience*, Narasimham (2000), introducing the research by Grön et al., asked whether their findings had to do with "the notorious male reluctance to ask for directions" (p. 306).

asymmetries and their association with differential activities, geared to mating (for males) and parenting (for females).

One evolutionary scenario to explain sex differences in "way-finding" starkly designates itself as the "hunter-gatherer theory of the origin of sex-specific spatial attributes" (Silverman and Eals, 1992; Silverman et al., 2000). It is argued that the ability of men to generate a mental map of unfamiliar environments, in contrast to the ability of women to remember landmarks and the location of objects (male spatial competencies are distinct from female location memory) are related to foraging practices and the sexual division of labor (see Joseph, 2000). This field is well reviewed by Geary (1998a), who argued that sex differences in physical and cognitive skills are more readily understood in terms of sexual selection than the division of labor (Geary, 1998a, 1998b).

Brain-wiring scenarios easily lend themselves to stereotypic views of male/female abilities and patterns of activity, overlooking individual variability. Undoubtedly, human subsistence activities and a sexual division of labor have implications for human evolutionary biology. However, observed differences in brain-wiring can reflect not just biological programming (the action of natural selection on mating and parenting activities) but also training (learned cultural habits). London taxi drivers, for example, have a very large hippocampus, which is larger if they are more experienced (Maguire et al., 1997). The hippocampus presumably develops to help reflect the drivers' extraordinarily large mental map of London geography and navigation skills. As in present-day taxi drivers, a "topographical memory" would have developed in hominid foragers, to develop mental maps of the world to forage for subsistence. Arguably, hunting "is the most learning-intensive foraging strategy practiced by humans" over areas often exceeding 1,000 km² per year (Kaplan et al., 2000: p. 170–171). Whoever foraged over a large habitat would have maximized their way-finding skills. Thus visuospatial skills vary not just by sex and biology, but also by occupation and experience. Interestingly, both nature and culture shape the emergence of sex differences in children's play behaviors said to lay the ground for sex differences in adulthood and to reflect sex differences in

parental investment throughout human evolution (Bjorklund and Shackelford, 1999; Geary and Bjorklund, 2000).

With respect to the activities of present-day and past foragers, two important questions arise: What accounts for the pervasive division of labor by sex? And what is its significance for human evolution? Several hypotheses are currently under examination.

Evolutionary scenarios along mating or parenting goals

One debate in the literature focuses on what started the human evolutionary strategy of provisioning children, and who did it, men by hunting, or women by gathering? Bird (1999) succinctly outlined the two main competing propositions in the field of behavioral ecology, which hinge the division of labor on either cooperation or conflict. The *cooperative parental provisioning model* has men and women dividing subsistence tasks in order to maximize food returns, minimize potential risks, and/or ensure defensible resources, to better provision their offspring. By contrast, the *conflict model* recognizes that men and women can choose very different trade-offs between mating and parenting goals.

Hunting activities have long been interpreted as *male parental provisioning* in contemporary and archaeological settings. However, Hawkes et al. (1997) have forcefully argued that human males hunt primarily to gain mating opportunities, i.e., to maximize mating rather than parenting goals. Evidence from primate, archaeological, and ethnographic material, discredits "the long-standing hypothesis that men hunt primarily to provision their wives and offspring" (p. 30). Thus, in chimpanzees, males hunt for mating opportunities—to share meat with females in estrus, not with dependents. And hunting is overwhelmingly a male activity (Stanford, 1995), possibly evolved for the purposes of "seduction" (Ridley, 1996; Stanford et al., 1994; Stanford, 1996). Second, in *Homo erectus* the evidence for active hunting and central place foraging, featuring transport of food back to home base, has been reevaluated. Last, among modern foragers, big-game hunting can be a rather poor strategy for feeding a family. It is risky and returns are unreliable, compared to gathering or hunting small game (Hawkes et al., 1997). Thus,

male hunting exists for reasons other than paternal provisioning, such as to maximize mating rather than parenting goals. There are situations, of course, where men satisfy both goals (among the Ache, hunting directly benefits families and makes a significant contribution to dietary intake, Kaplan et al., 2000). It is instructive, nonetheless, to explore whether the sexual division of labor results from strategies driven by compromise, cooperation, or conflict (Bird, 1999), or a mix of these.

Effectively downplaying its significance for human evolution, Hawkes and colleagues (O'Connell et al., 1995, 1999) do not view the sexual division of labor as "the key transition in human evolution." Rather, routine mother-child provisioning, in contrast to male hunting, had more powerful evolutionary implications. Thus, where climatic change led to a decline in resources (such as fruit) which juveniles could harvest, provisioning children would have allowed for an expansion of habitat, while help with childcare (notably by grandmothers, rather than fathers) would have increased fertility. Children could have been provisioned, not with meat (by men), but with tubers (by women), a resource that yielded high returns and was reliable, but could only be processed by adults. Emphasis is thus shifted from male/female to female/female cooperative behaviors, and from meat to vegetable sources. This reconstruction is offered as an alternative scenario for the evolution of *Homo erectus* (*ergaster*).

Conversely, Kaplan et al. (2000) emphasize that males actually do most of the provisioning of children and reproductive-age women among contemporary foragers. It is estimated that forager men provide not only all of the protein but also 97% of calories to offspring (Kaplan et al., 2002); no measure of variability across groups is provided. The authors present data on the dietary intakes of 10 groups to demonstrate that "hunting provides the greatest energy component of human diets in many foraging societies" (Kaplan et al., 2000, p. 174), which is interpreted as reflecting parental investment rather than mating effort. The authors also argue that male hunting is fundamental to the human life-history adaptation. It represents, relative to chimpanzees, a change in feeding niche focused on large, high-quality, but difficult-to-acquire foods, which would have driven human

evolution towards increased intelligence, delayed growth and maturation, an exceptionally long lifespan, and male provisioning of females and their offspring (with lower mortality rates and enhanced food sharing). Kaplan et al. (2000, p. 161) thus see "the shift to calorie-dense, large-package, skill-intensive food resources" as responsible for the unique evolutionary trajectory of the genus *Homo*, and the male/female division of labor resulting from essentially cooperative strategies for provisioning children.

Reviewing the literature on paternal investment, Geary (2000, p. 72) also insists that "the most noteworthy feature of human parental care is that many fathers show some degree of direct and indirect investment in their children," a trait remarkable in light of the mammalian reproductive strategy. Among mammals, lactating females can effectively provision an infant, leaving males to focus on mating effort (among chimpanzees and bonobos, males typically provide no paternal investment). For Geary, the evolution (and proximate expression) of paternal care is more strongly related to mating effort than parental effort, as shaped by the nature of male/female reproductive strategies and sexual selection. However, the strategy is flexible, in that social and ecological conditions modify the expression of parental care, and given that individuals may vary emphasis on mating and parenting at different points of their lifespan and in relationships with different partners (Geary, 2000; after Draper and Harpending, 1988). This argument goes beyond reiterating the point of sex differences in the expression of parental care. Future research could usefully move towards modelling the range of circumstances affecting male/female and female/female subsistence strategies and child provisioning behaviors.

Evolutionary scenarios featuring energetic and reproductive constraints

Returning to women's activities, other important questions arise. Do reproductive responsibilities limit the nature or extent of women's foraging activities, and effectively exclude them from large-game hunting? To what extent can women combine their productive and reproductive responsibilities? It is now well known that

the !Kung San walk 2,400 km annually while carrying equipment, food, and a child weighing 3 kg at birth and 11–15 kg at age 4 (Lee, 1979, p. 310; Bentley, 1985; Blurton Jones, 1987). Can they manage to multitask and avoid energetic/reproductive trade-offs altogether?

As Bird (1999, p. 72) stated, a common “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 relative immobility.” She emphasized that “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” (p. 72). This marks a shift of attention away from the largely binary consideration of male/female division of labor in earlier studies (Brown, 1970; Murdock and Provost, 1973; Burton and White, 1977) towards more careful analysis of how reproductive responsibilities affect women *per se*.

For example, Peacock (1991) contended that a test for the “compatibility” between subsistence and reproductive tasks should be based on detailed measures of women’s activities at different stages of their childbearing careers (see Hurtado et al., 1992). Peacock also usefully contrasted energetic with strictly logistic constraints. Evidence from the Efe of the Ituri forest revealed the former type of constraints (on work intensity) during pregnancy and drew attention to cooperative strategies between women (for infant caretaking), namely female/female cooperative behaviors which could have important implications for models of human evolution. In Peacock’s (1991) view, scenarios of the sexual division of labor based on women’s involvement with child-care had hitherto restricted their focus to a narrow range of subsistence tasks, child-care behaviors, and type of constraints.

Evolutionary “narratives” and gender stereotyping

The phrase “the sexual division of labor” refers specifically to lack of big-game hunting by women, but is often misleadingly applied to the gamut of subsistence activities. Although women are said not to “hunt,” women nearly everywhere take

small game, fish, and shellfish, and do so while childbearing. The overlap of male and female subsistence tasks is usually considerable. But (nearly) universally, women do not pursue very large game and are prohibited from touching male hunting weapons (Brightman, 1996).

A famous exception to the rule is the Agta of the Philippines. Agta women hunt wild pig and deer with bows and arrows, accompanied by dogs, although hunting “is reasonably dangerous and arduous” (Estioko-Griffin and Griffin, 1985, p. 71). Moreover, Agta mothers assume main responsibilities for their children, hunting with babies strapped to their backs. In drawing the implications of Agta activities, Estioko-Griffin and Griffin (1985) stated that the Agta offer one perfectly plausible model of human evolution, and consequently argued in favor of pluralistic models of hominid evolution, including ones in which women would have participated in hunting even while childbearing. Examples such as the Agta challenge the assumption that exclusion of women from hunting is a necessary feature of evolutionary biology and foraging ecology. Ethnographic cases of women hunting are rare—it is interesting that Agta women should hunt with the help of dogs, domesticated only since the European Mesolithic, and should profit from trading meat for starch with settled horticulturalists. They are, however, far from insignificant. Among Cheyenne and Mbuti, women participate in communal hunts while Amazonian Mastes women (Romanoff, 1983) hunt with men.

The study of “an engendered past,” based on a careful reconstruction of male/female activities, also has important implications for archaeologists.² The interesting subfield of archaeology devoted to reconstructing gender³ identities from past material has

²For instance, Jackson (1991) argued that women’s economic activities (processing acorn) had critical impact on social change and settlement patterns among the precontact Mono Indians of California, but that evidence for the processing of vegetable matter is often sidelined by archaeologists. Sassaman (1998) argued that perceived changes in lithic technology marking the “transition” from mobile to sedentary prehistoric societies simply reflects the increased visibility of women in the archaeological record.

³The analytical concept of gender (a social construct) is distinct from biological sex (see Sørensen, 2000). There can be more than two genders (consider cultural constructions of hermaphroditism, homosexuality, childhood and old age; see Lesick, 1991).

gathered substantial momentum (Walde and Willows, 1991; Nelson, 1997; Moore and Scott, 1997; Hays-Gilpin and Whitley, 1998; Sassaman, 1998; Armelagos, 1998; Sørensen, 2000). As highlighted by Conkey and Spector (1998, p. 17), it finds the "common assumption of a relatively rigid sexual division of labor" highly questionable. "Although archaeologists are generally cautious about simplistic ethnographic analogies, this has not been true with regard to the subject of gender" (p. 13), such that the interpretation of archaeological material overtly or covertly reflects stereotypic assumptions about task-allocation and activity patterns.⁴ Hurcombe (1997) called this the BIG problem—Biased Interpretations of Gender—while Willoughby (1991) showed that the most popular models of the sexual division of labor are often "fossil free" or "even fossil proof." Deliberately focusing the attention of archaeologists on women fosters a more critical approach, restructuring assumptions about "mankind" and "man's past" (Conkey, 1991).

Brightman (1996) also explicitly questioned anthropological representations of the sexual division of "foraging labor." In particular, he criticized the lack of sound evidence or the failed logic of most evolutionary arguments adduced to explain why women do not hunt large game, namely, women lack *muscular strength and endurance*, women lack a *psychological disposition* towards aggression, female (menstrual) *odors* drive away game, *reproductive constraints* are conditions incompatible with hunting, and reproductive fitness (risks of female mortality, fetal wastage, or child mortality) is adversely affected. Thus, with respect to reproductive constraints, pregnancy and lactation would not preclude women from hunting before, after, and between reproductive events, or from eliciting the help of other mothers to care for children left behind

during hunting trips. "Child backload renders women's hunting relatively less efficient but not impossible" (Brightman 1996, p. 700). This, however, leaves open the question whether energetic constraints make hunting profitable for women. Kaplan et al. (2002) argue that for women it pays not to hunt because hunting entails a very long period of skill acquisition to make it worthwhile.

Brightman (1996, p. 691) was critical of evolutionary arguments when they reveal an "abiding confidence that the practices in place are the best possible ones,"—a Panglossian profession of faith. He argued that *versatility* or flexibility in task allocation (not necessarily predicated on gender) would be a quite successful strategy for foraging groups. However, evolutionary "narratives" have been powered by the view that foraging women are "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"... "the product at once of logistical necessity and evolutionary selection" (Brightman, 1996, p. 687). It should not simply be *assumed* that the exclusion of women from hunting rests upon "natural" physiological differences.

MODELLING FORAGING PRACTICES

Within the framework of evolutionary ecology, it is important to generate hypotheses that are testable against ethnographic and archaeological evidence. The notion of trade-offs between reproductive and *energetic* outcomes, in particular, has yielded several hypotheses and overlapping models of the sexual division of labor which remain to be fully developed (Winterhalder, 2001). Thus, male hunting could be a feature of parental investment, or of mating effort driven by sexual selection. The latter include "showing off" (hunting to trade meat for prestige, not just for sex or feeding children), a feature of male/male competition, and "costly signaling" (hunting to signal some particular valuable trait to an audience of mates, allies, and competitors, with little concern about how meat is actually distributed), often associated with female choice. While it is difficult to distinguish between these hypotheses with

⁴Challenging these assumptions, however, there exists even in art a minority of pictorial representations showing a reversal of gender stereotyping (Moser, 1993). These include portrayals of "prehistoric cave-women" defending themselves against a bear, woman as "the flintmaker in Paleolithic times" and a "pack-hunting model of hominid life" used by Binford (1984), illustrating hunting-based models of evolution without a stereotypic division of labor or well demarcated male and female roles (in Moser, 1993).

current data, both are likely to be contingent on social and ecological conditions (Geary, 2000).

The more sophisticated models incorporate life history parameters to examine how particular trade-offs vary for women of different ages, reproductive status, and social support, such as done for the Ache and Hiwi (Hurtado et al., 1992). This avoids the simplistic binary opposition of considering only males vs. females, and opens models to further empirical testing. Importantly, behavioral ecology models make different predictions for the way in which men's and women's foraging practices should differ with ecological variation. In essence, women should be guided by child welfare, while men might be guided by opportunities for mating and alliances. However, ecological circumstances matter: they impinge on the way foraging, mating, and parenting trade-offs are articulated for individual men and women.

Foraging trade-offs

Hawkes (1995) reviewed data from four contemporary foraging groups, the Ache (Paraguay forest), Hiwi (Venezuela savanna), Hadza (Tanzania), and !Kung (Botswana) in the context of the above predictions. The ethnographic data are consistent with the view that women's foraging behaviors reflect both parenting goals (child provisioning) and key ecological features. Thus, Ache mothers curtail foraging activities to spend more time in childcare because the forest area is very unsafe for children and available resources are relatively abundant. By contrast, Hiwi mothers focus on foraging because camps are safe for children and resources rather variable. The contrast between Hadza and !Kung is also drawn in terms of ecological circumstances influencing trade-offs between foraging and childcare. The Hadza hunt in teams and enlist children to be energetic foragers because the returns of such foraging strategy is profitable. The !Kung forage individually, leaving their children in camp to crack mongongo nuts to advance the tasks of food processing.

The predictions are that men should hunt and widely distribute meat in contexts where they stand to gain from forging additional alliances and mating. Such research is easily typecast into fetching

vignettes.⁵ However, the situation is undoubtedly more complex, since it would be wrong to portray men as free from any constraints related to child provisioning (Bird, 1999). Indeed, Kaplan et al. (2000, and 2002) argue that despite considerable variability in energy returns across foraging groups, men do most of the provisioning of children.

Variables shaping responses to energetic trade-offs

Ecology matters as to the ways in which trade-offs of foraging, mating, and parenting are articulated in different groups. The more sophisticated models of human behavior evaluate foraging behavior in terms of number of dependents, type of resource harvested, help enlisted by mate or kin, ability of children to provision themselves, and factors such as risk or relative environmental safety. Much attention has been given to evaluating the opportunity costs of subsistence activities, which affect the sexual division of labor (see Hurtado and Hill, 1990). Thus, Agta women may hunt because the energetic benefits outweigh reproductive costs (Hurtado et al., 1985), or because the method of hunting with the help of dogs is compatible with women's reproductive responsibilities. These lessons may be applied to past societies and archaeological material.

MALE/FEMALE LEVELS OF PHYSICAL ACTIVITY

The subsistence regimes of hunter-gatherers have also been described in terms of overall workloads, or energy expenditure expressed as physical activity levels (PAL). How have such data been used for models of human evolution? There are several issues of interest. First, how pronounced is the division of labor in terms of *overall levels*, rather than specific task allocation, among modern foragers? Second, can the activity

⁵ Ridley (1996), quick to enliven research linking hunting activities with sexual opportunities, writes: "The Hadza men are obsessive hunters and promiscuous seducers. The !Kung are intermittent hunters and largely faithful husbands" (p. 91). Similarly "Ache men are keen hunters.... and trade meat for love," while the Hiwi are monogamous and spend little time hunting. Hurtado and Hill (1992) provide the original interpretation of the data.

patterns of hominid species be estimated, using the existing profiles of modern foragers and nonhuman primates? Third, what happened to male vs. female workloads with subsistence intensification?

Overall workloads for foraging men and women

There are only three groups of foragers for whom *direct* measurements of time allocation and energy expenditure expressed as PAL⁶ are available for *both* men and women: the !Kung San, Ache, and Igloodik Eskimo (Data from Leonard and Robertson, 1992; Katmarzyk et al., 1994). PAL are customarily graded as light, moderate, or heavy (FAO/WHO/UNU, 1985). For the !Kung, PAL are light to moderate (1.71 for men, 1.51 for women). For the other two groups, by contrast, PAL are heavy (2.15 for Ache men, 1.88 for Ache women; 2.2 for Igloodik men, 1.8 for Igloodik women).

One way to evaluate the relative workload of men vs. women is to take the ratio of PAL values (Fig. 1). If the ratio exceeds 1, men are more physically active than women. This is true for all three forager groups. The use of a simple ratio circumvents the problem of relying on the absolute threshold values advocated by the FAO/WHO/UNU (1985) and James and Schofield (1990) to grade workload intensity, which may unhelpfully assign a given PAL value to different levels of physical activity according to sex. The thresholds for light, moderate, and heavy PAL are, respectively, 1.55, 1.78, and 2.1 for men, and 1.56, 1.64, and 1.82 for women.⁷ A PAL value of 1.8 would be graded, following international recommendations, as moderate for men but heavy for women, while in the Igloodik example, values of 2.2 for men and 1.8 for women are *both* graded as heavy physical activity. The choice of sex-specific PAL values to grade physical activity exists for historical reasons. The FAO/WHO/UNU

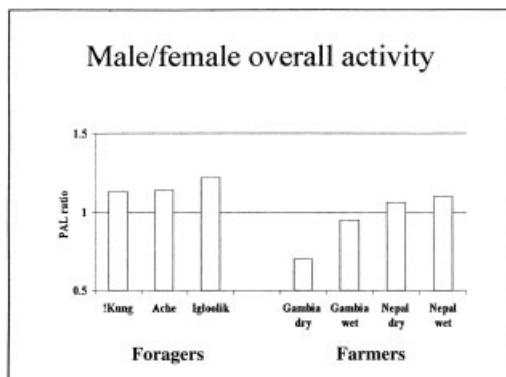


Fig. 1. Male/female overall activity (PAL ratio). Data for modern foragers are from Katmarzyk et al. (1994), while data for modern farmers, showing variation in the wet and dry seasons, are from Panter-Brick (1996).

heavily relied on data compiled by Durnin and Passmore (1967), which showed clear sex differences in the energy cost of single activities, leading to the adoption of a higher threshold value for male "heavy work" (Panter-Brick, 1996). At the time, however, there were few studies systematically comparing both men and women in Third World populations where women often assume very heavy workloads. Available data have been recently updated (e.g., Ainsworth et al., 1993; Draper et al., 1997), but the justification for sex-specific thresholds has yet to be reevaluated. At present, therefore, it is more useful to use PAL *ratios* than absolute thresholds to evaluate male/female workloads.

PAL ratios provide a way of evaluating, in terms of overall daily energy expenditure, the sexual division of labor at the level of task allocation. Among the !Kung, Ache, and Igloodik, differences in overall activity levels between males and females are quite small (Fig. 1 and 2a), which does not support common expectations that a hunter-gathering division of labor should imply marked differences in male/female energy expenditure. Among Igloodik, for instance, PAL are heavy for both men and women, with a PAL ratio of only 1.2, even though men were "hunters" and women were "housewives." Women had the job of processing animal skins, which was demanding in both time and energy. Across groups, PAL profiles also fail to support the expectation that male/female differences in energy expenditure should be greater among

⁶PAL are the ratios of total daily energy expenditure (TEE) over maintenance levels (basal or resting metabolic rates, BMR or RMR, often predicted values used interchangeably in the literature); these are corrected for body size and therefore facilitate comparisons across populations. Energetic data on other forager groups (e.g., presented by Sorensen and Leonard, 2001) have not been expressed as PAL.

⁷The recommended thresholds yield slightly different male/female PAL ratios (0.99 for light, 1.10 for moderate, and 1.15 for heavy activity), which are nonetheless close to unity.

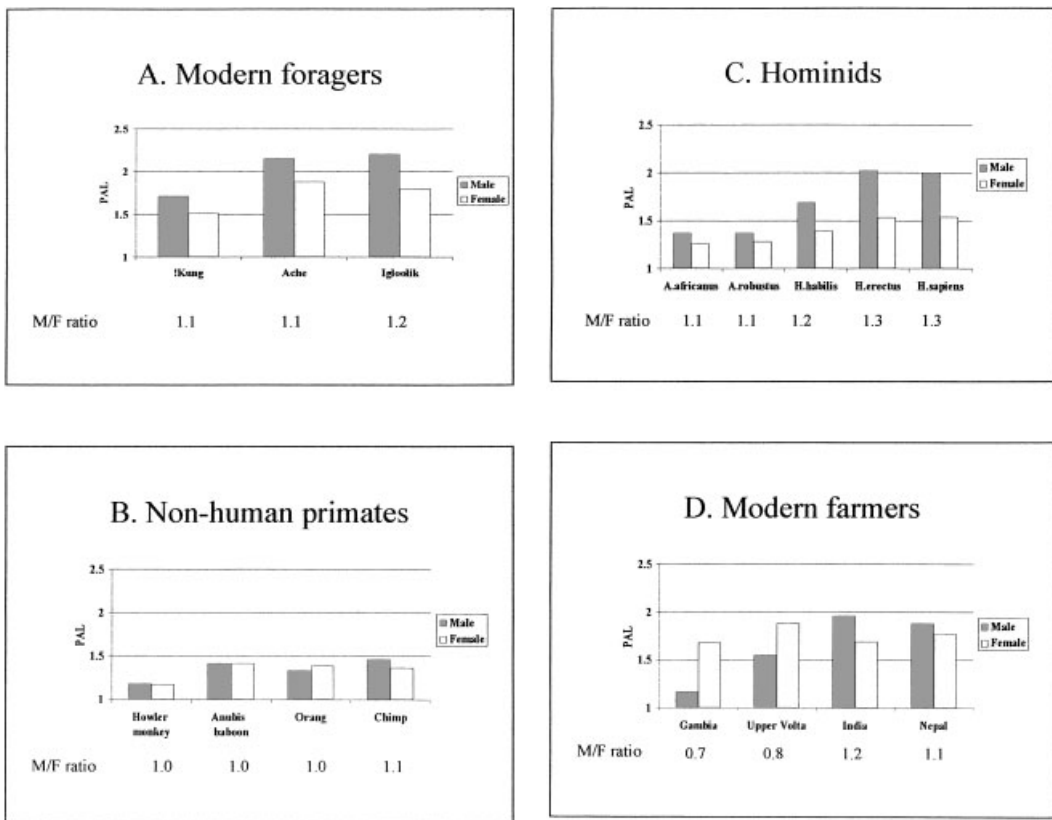


Fig. 2. Male and female physical activity levels (PAL, over and above maintenance levels). Data were derived from time allocation and energy expenditure measurements for: (a) modern foragers (Leonard and Robertson, 1992; Katzarzyk et al., 1994); (b) living primates (Leonard and Robertson, 1992); (c) hominids (from sex-specific estimates of, Leonard and Robertson, 1997); (d) modern farmers (Panter-Brick, 1996). Mean values are shown (no measure of dispersion is readily available in the literature). The M/F ratios (male/female PAL ratios) were calculated to evaluate relative workloads by sex.

the Ache than the !Kung, given that the former rely substantially more on meat (and male hunting) for subsistence, and also that Ache women bear many more children than do the !Kung and curtail gathering activity while nursing. Thus, common expectations of how dietary factors and reproductive constraints might shape task allocation do not readily extrapolate to 24-hour energy expenditure.

Hominid activity patterns

The PAL data of the !Kung and Ache have also served to build evolutionary scenarios and to estimate the activity profiles and energy requirements of hominid species. According to Jenike (2001), the !Kung

model is one of low-energy hunting and gathering, associated with less physical activity, smaller body size, and slower reproduction. The Ache, who live in a richer environment, are a model for high levels of physical activity, higher intakes, larger body size, and a much higher reproductive rate.

Leonard and Robertson (1992, 1997) compared energy data for modern human foragers with those available for living primates (Fig. 2a, b) in order to estimate those of hominid species. In one simulation, a "mixed" model was used whereby PAL for australopithecines was derived from chimpanzee data, PAL for *Homo erectus* and *sapiens* was derived after the Ache (men only), and PAL for *Homo habilis* was as-

signed intermediate values (Fig. 2c, Leonard and Robertson, 1997). Because body size increased with *Homo erectus* (especially in females), total energy expenditure (predicted from body size and activity patterns) would have increased dramatically for this hominid. Thus, following the assumptions of the "mixed" model, total energy expenditure (TEE) would have doubled for males and increased by 85% for females over levels predicted for australopithecines (Leonard and Robertson, 1997). It was suggested that a higher quality diet would have been critical to fuel the larger body size and greater physical activity of *Homo erectus*, which in turn was linked to the evolution of a hunting and gathering strategy (whereupon scenarios of food procurement, food processing, and food sharing are important). A similar evaluation of PAL and foraging efficiency for Neandertal, based on energetic data for modern foragers and nonhuman primates, is presented by Sorensen and Leonard (2001).

In a more recent context, data from modern foragers have been contrasted with the very low PAL among contemporary Western populations. While estimated PAL values are 1.8 for *Homo erectus* (a value undifferentiated by sex, Leonard and Robertson, 1992), those of Western office workers are only 1.37 or 1.18 (Cordain et al., 1998; Chen, 1999). As stated by Cordain et al. (1998, p. 331–332), the "TEE/kg/d of typical contemporary humans is about 65% that of late Paleolithic Stone Agers... For typical Americans to approximate the TEE/kg/d of recently-studied gatherer-hunters it would require adding the equivalent of a 19 km (12 mile) walk for a 70 kg man, to each day's current activity level!" Such statements, common in the sports medicine literature, highlight the health consequences of low physical activity in modern urban populations in contrast to those of our ancestors (Panter-Brick, in press).

Reconstructions of hominid activity patterns and energy requirements generally proceed on the basis of TEE or PAL data for men, rather than address male/female differences, and adopt either the !Kung or Ache model, without exploring the implications of interpopulation variability documented for contemporary foragers.

Subsistence intensification and male/female workloads

What might have happened to PAL with subsistence intensification, especially in terms of differences between men and women? Changes in overall workload and sexual division of labor with shifts of subsistence were examined by Sackett (1996), who framed his thesis in terms of whether portrayals of "original affluence" or "Hobbesian destitution" rang true for modern foragers. Using studies published before 1989, Sackett calculated average time, work intensity, and PAL from *composite* data in multiple societies (the basis for the calculations is summarized in Jenike, 2001). Sackett reported PAL for foragers (men 1.78, women 1.72), horticulturalists (men 1.87, women 1.79), agriculturalists (men 2.28, women 2.31), and industrialists (men 2.38, women 2.20), noting that the latter sample was biased in terms of heavy manual occupations (no measure of dispersion was provided). In societies where women work harder, men work harder as well (reflecting a demand for family labor); as workloads increase, however, men devote themselves to subsistence activities and women to domestic work (generating a starker division of labor). Unfortunately, composite data to portray "average" activity profiles do little to further understanding of evolutionary scenarios. More finely tuned data of working behavior, together with hypotheses as to what factors might govern behavior changes in response to local ecological conditions are needed.

Another interesting line of evidence regarding male/female workloads rests upon the comparison of prehistoric farmers with foragers, especially on the basis of bones and teeth. Larsen (1995, p. 204) noted that the shift to agriculture in the late Pleistocene led to "an increase in physiological stress, a decline in nutrition, ... and an alteration of activity types and work loads." A decrease in the sexual dimorphism of bone robusticity is usually taken to reflect the decline of male long-distance hunting and an increase in sedentism for both sexes (Larsen, 1995). In particular, Frayer (1980: p. 399) claimed that the "level of sexual dimorphism within a population is roughly proportional to the exclusivity of the division of labor by sex." Interestingly, Ruff

(1987) differentiated the consequences of overall activity level, which affect bone robusticity, from type of activity, which affect bone geometry (shape). After examining the shape of long bones in various population samples, Ruff (1987, p. 411) concluded that "hunter-gatherer populations show the greatest sexual dimorphism here, agricultural population an intermediate level, and industrial societies the least sexual dimorphism. This corresponds to a similar reduction in the sexual division of labor through these three levels of subsistence technology." This is taken to support the view that sex differences in mobility declined with the adoption of agriculture. Furthermore, because the sexual dimorphism of *Homo sapiens sapiens* and *Neandertal* resembles that of modern hunter-gatherers, the "sexual division of labor, at least with regard to relative mobility, appears to have been similar to modern hunter-gatherers at least as far back as the Middle Paleolithic" (Ruff, 1987, p. 411).

Bridges (1989) also evaluated size and strength of long bones to reconstruct changes in both level and type of activity with the shift to maize agriculture, comparing Archaic hunter-gatherers and farmers from the Mississippian period in Alabama, USA. It was concluded that maize agriculture was "more physically demanding than hunting and gathering" (Bridges, 1989, p. 392) and affected women more than men. It appears that farming led to a sexual division of labor whereby women took on a greater proportion of subsistence activities (as reflected by greater changes in long bone diaphyses relative to men). However, Bridges (1989) did not generalize the findings to all populations in farming transition.

Bridges (1992) emphasized variation in the sexual dimorphism of arthritis in prehistoric samples, such that the response to subsistence intensification with agriculture (as reflected in joint stress) is complex. It could, moreover, reflect activities other than subsistence tasks, such as warfare. For Larsen (1995), there also was no uniform biological transition with subsistence intensification. There were clear differences between males and females in dental health and activity patterns, and clear evidence for variability in health changes across geographical settings. This may well reflect local variation in gender roles, which as

Bolen (1991) argued, exhibit flexibility rather than rigidity in the transition from hunting and gathering to farming.

These various scenarios can be usefully evaluated in light of recent PAL data on modern foragers and farmers (Panter-Brick, 1996; Panter-Brick and Pollard, 1999). A comparison between modern foragers and farmers from Africa and South East Asia is shown in Figures 1 and 2. Two important points should be noted. First, PAL values overlap significantly between foragers and farmers (Fig. 2a,d). Thus, levels of physical activity or "effort" are more similar between foragers and farmers than simple readings of hunter-gatherer "original affluence" have suggested. The notions of affluence, in the sense that needs or wants are easily satisfied, among hunter-gatherers has powered many accounts of human evolution and subsistence intensification (Rowley-Conwy, 2001), but are yet another example of stereotyping activity patterns.

Second, the relative workloads of men and women show perhaps greater variability among farmers (Fig. 2d). PAL ratios show that women work harder than men in the Gambia and Upper Volta, while men work harder than women in India and Nepal. In particular, the comparison of PAL ratios show clear examples where agricultural subsistence strategies burden women more greatly (as exemplified by the Gambia, Fig. 1). The PAL data contradict a common assumption that male/female differences in overall workloads were reduced during the transition from hunting and gathering to agriculture (Ruff, 1987; Larsen, 1995), but strengthen arguments that male/female workloads show substantial variability across ecological contexts. In Fig. 1, modern foragers show similar male/female daily energy expenditure, while farmers exhibit more variability in relative workloads.

How might male/female PAL respond to seasonality? Seasonal shifts in the PAL ratio are illustrated in Figure 1 for farmers, but not for foragers, since data expressing seasonal changes of time allocation or energy expenditure in terms of PAL values for contemporary foragers are lacking. Indeed, seasonal variation for foragers is usually documented only in terms of energy intake, acquisition rates, hours spent foraging, or body weight changes (Hurtado and Hill, 1990; Jenike, 2001; Kaplan et al., 2001), rather than in terms of TEE or PAL values

(as done for farmers; Panter-Brick, 1996). However, data so far available support the conclusion that the sexual division of labor, both in terms of overall workloads and task allocation, is likely to be influenced by seasonality: it varies with ecological constraints. By implication, one must strive to explicitly incorporate behavioral plasticity in response to local ecological changes in models of human evolution.

CONCLUSIONS

Studies in the fields of behavioral ecology (or evolutionary behavior) and nutritional ecology grapple with energetic data and have recently generated new ideas for understanding the course of human evolution. These are still two separate sets of the literature, investigating the male/female "division of labor" from different angles, focusing either on task allocation or overall levels of physical activity. Yet both bear on the question of reconstructing activity patterns during hominid evolution.

In both research areas, a shift from a normative to pluralistic models of human behavior is evident. The stereotypic view of "Man the Hunter, Woman the Gatherer" has been displaced (although not dispelled) in favor of more finely tuned models of foraging behavior, exploring the extent to which potentially conflicting mating and parenting trade-offs vary with life history and local ecology. In particular, they look at how energetic trade-offs may articulate with reproductive events, social support, resource selection, and environmental safety. Better data on contemporary populations (whether foragers or farmers) have led to the exploration of human adaptability, beginning with documenting the changes in relative workloads under a range of ecological constraints. The current approach is to further understand human behavioral variability, rather than seek to categorize types of male/female behavior across subsistence regimes. The challenge, of course, is to incorporate such variability in what men and women do, contingent upon social and ecological constraints, in reconstructions of hominid evolution.

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LITERATURE CITED

- Ainsworth BE, Haskell WL, Leon AS, Jacobs DR Jr, Montoye HJ, Sallis JF, Paffenbarger R. 1993. Compendium of physical activities: classification of energy costs of human energy activities. *Exercise* 25:71-80.
- Armstrong GJ. 1998. Introduction: sex, gender and health status in prehistoric and contemporary populations. In: Grauer AL, Stuart-Macadam P, editors. *Sex and gender in paleopathological perspective*. Cambridge: Cambridge University Press. p 1-10.
- Balme J, Beck W. 1993. Archaeology and feminism—views on the origins of the division of labor. In: du Cros H, Smith L, editors. *Women in archaeology—a feminist critique*. Canberra: Australian National University. p 61-74.
- Bernaldo de Quirós F. 1987. El mundo del Arte Rupestre Paleolítico. In: *Arte Rupestre de España*. Revista de Arqueología, Extra 2. Madrid: Zugarto Ediciones. p 22-29.
- Binford LR. 1984. Faunal remains from Klasies River mouth. New York: Academic Press.
- Bird R. 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. *Evol Anthropol* 8:65-75.
- Bjorklund DF, Shackelford TK. 1999. Differences in parental investment contribute to important differences between men and women. *Curr Direct Psychol Sci* 8:86-89.
- Blurton Jones, N. 1987. Bushman birth spacing: direct tests of some simple predictions. *Ethnol Socobiol* 8:183-203.
- Bogin B. 1997. Evolutionary hypotheses for human childhood. *Yrbk Phys Anthropol* 40:63-89.
- Bogin B. 1998. Evolutionary and biological aspects of childhood. In: Panter-Brick C, editor. *Biosocial perspectives on children*. Cambridge: Cambridge University Press. p 10-44.
- Bolen 1991. Changing gender roles at the gatherer-hunter transition to farmer. In: Walde ID, Willows ND, editors. *The archaeology of gender*. Calgary: University of Calgary. p 400-405.
- Bridges PS. 1989. Changes in activities with the shift to agriculture in the southeastern United States. *Curr Anthropol* 30:385-394.
- Bridges PS. 1992. Prehistoric arthritis in the Americas. *Annu Rev Anthropol* 21:67-91.
- Brightman R. 1996. The sexual division of foraging labor: biology, taboo, and gender politics. *Soc Comp Study Soc History* 38:687-729.
- Brown J. 1970. A note on the division of labor by sex. *Am Anthropol* 72:1073-1078.
- Conkey MW. 1991. Does it make a difference? Feminist thinking and archaeologies of gender. In: Walde ID, Willows ND, editors. *The archaeology of gender*. Calgary: University of Calgary. p 24-33.
- Conkey MW, Spector JD. 1998. Archaeology and the study of gender. In: Hays-Gilpin K, Whitley DS, editors. *Reader in gender archaeology*. London: Routledge. p 11-45.
- Dahlberg F, editor. 1981. *Woman the gatherer*. New Haven: Yale University Press.
- Durnin JVGA, Passmore R. 1967. *Energy, work and leisure*. London: Heinemann.

- Draper AK, van der Pols J, Shetty PS, Durnin JVGA. 1997. Bibliography of studies of the energy cost of physical activity in humans. Human Nutrition Unit, London School of Hygiene and Tropical Medicine, London.
- Draper P, Harpending H. 1988. A sociobiological perspective on the development of human reproductive strategies. In: MacDonald KB, editors. *Sociobiological perspectives on human development*. New York; Springer-Verlag, p 340–372.
- Endicott KL. 1999. Gender relations in hunter-gatherer societies. In: Lee RB, Daly R, editors. *The Cambridge encyclopedia of hunters and gatherers*. Cambridge: Cambridge University Press. p 411–418.
- Endicott KL. 2000. Gender relations in hunter-gatherer societies. In: Lee RB, Daly R, editors. *The Cambridge encyclopedia of hunters and gatherers*. Cambridge: Cambridge University. p 411–418.
- Estioko-Griffin A, Griffin PB. 1981. Woman the hunter: The Agta. In: Dahlberg F, editor. *Woman the gatherer*, New Haven, CT: Yale University Press. p 121–151.
- Estioko-Griffin AA, Griffin PB. 1985. Women hunters: the implications for Pleistocene prehistory and contemporary ethnography. In: Goodman ML, editor. *Women in Asia and the Pacific: toward an East-West dialogue*. Honolulu: University of Hawaii Press. p 61–81.
- Falk D. 1998. Brain evolution in females: an answer to Mr. Lovejoy. In: Hays-Gipin K, Whitley DS, editors. *Reader in gender archaeology*. London: Routledge. p 115–138.
- FAO/WHO/UNU Expert Consultation 1985. Energy and protein requirements. Technical Report Series 724, World Health Organization, Geneva.
- Frayar DW. 1980. Sexual dimorphism and cultural evolution in the late Pleistocene and Holocene of Europe. *J Hum Evol* 9:399–415.
- Geary DC. 1998a. Male, female: the evolution of human sex differences. Washington, DC: American Psychological Association.
- Geary DC. 1998b. Sexual selection, the division of labor, and the evolution of sex differences. *Behav Brain Sci* 21:443–448.
- Geary DC. 2000. Evolution and proximate expression of human parental investment. *Psychol Bull* 126:55–77.
- Geary DC, Bjorklund DF. 2000. Evolutionary developmental psychology. *Child Dev* 71:57–65.
- Godin G, Shepard RJ. 1973. Activity patterns of the Canadian Eskimo. In: Edolhm OG, Gunderson EKF, editors. *Polar human biology*. London: Heinemann Medical. p 193–215.
- Grön G, Wunderlich AP, Spitzer M, Tomczak R, Riepe MW. 2000. Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nat Neurosci* 3:404–408.
- Hawkes K. 1995. Foraging differences between men and women—behavioural ecology of the sexual division of labor. In: Steele J, Shennan S, editors. *The archaeology of human ancestry—power, sex and tradition*. London: Routledge. p 283–305.
- Hawkes K, O'Connell JF, Rogers L. 1997. The behavioral ecology of modern hunter-gatherers, and human evolution. *Trends Evol* 12:1–42.
- Hays-Gilpin K, Whitley. 1998. Introduction: gendering the past. In: Hays-Gilpin K, Whitley DS, editors. *Reader in gender archaeology*. London: Routledge. p 3–10.
- Hurcombe L. 1997. A viable past in the pictorial present? In: Moore J, Scott E, editors. *Invisible people and processes: writing gender and childhood into European archaeology*. London: Leicester University Press. p 15–24.
- Hurtado AM, Hawkes K, Hill K, Kaplan H. 1985. Female subsistence strategies among the Ache hunter-gatherers of Eastern Paraguay. *Hum Ecol* 13:1–28.
- Hurtado AM, Hill KR. 1990. Seasonally in a foraging society: variation in diet, work effort, fertility, and the sexual division of labor among the Hiwi of Venezuela. *J Anthropol Res* 46:293–346.
- Hurtado AM, Hill K. 1992. Paternal effect of offspring survivorship among Ache and Hiwi hunter-gatherers: Implications for modeling pair-bond stability. In: Hewlett BS, editor. *Father-child relations: cultural and biosocial contexts*. New York: Aldine de Gruyter. p 31–55.
- Hurtado AM, Hill K, Kaplan H, Hurtado I. 1992. Tradeoffs between female acquisition and child care among Hiwi and Ache foragers. *Hum Nat* 3:185–216.
- Jackson J. 1991. Pounding acorn: women's production as social and economic focus. In: Gero J, Conkey MW, editors. *Engendering archaeology*. Oxford: Blackwell. p 301–328.
- James WPT, Schofield EC. 1990. Human energy requirements: a manual for planners and nutritionists. New York: Oxford University Press.
- Jenike M. 2001. Nutritional ecology: diet, physical activity, and body size. In: Panter-Brick C, Layton R, Rowley-Conwy PA, editors. *Hunter-gatherers—an interdisciplinary perspective*. Cambridge: Cambridge University Press. p 205–238.
- Joseph R. 2000. The evolution of sex differences in language, sexuality, and visual-spatial skills. *Arch Sex Behav* 29:35–66.
- Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet intelligence, and longevity. *Evol Anthropol* 9:156–185.
- Kaplan H, Hill K, Hurtado AM, Lancaster J (2002). The embodied capital theory of human evolution. In: Ellison P, editor. *Reproductive ecology and human evolution*. Hawthorne, NY: Aldine de Gruyter. p 293–317.
- Katzmarzyk PT, Leonard WR, Crawford MH, Sukernik RI. 1994. Resting metabolic rate and daily energy expenditure among two indigenous Siberian populations. *Am J Hum Biol* 6:719–730.
- Konner M. 1991. *Childhood*. Boston: Little, Brown and Company.
- Lancaster JB, Lancaster CS. 1983. Parental investment, the hominid adaptation. In: Ortner J, editor. *How humans adapt: a biocultural odyssey*. Washington DC: Smithsonian Institution Press. p 33–56.
- Lancaster JB, Kaplan HS, Hill K, Hurtado AM. 2000. The evolution of life history, intelligence, and diet among chimpanzee and human foragers. *Persp Ethol* 13:47–72.
- Larsen CS. 1995. Biological changes in human populations with agriculture. *Annu Rev Anthropol* 24:185–213.
- Lee RB. 1979. *The !Kung San: men, women and work in a foraging society*. Cambridge: Cambridge University Press.
- Lee Daly R (eds). 1999. *The Cambridge encyclopedia of hunters and gatherers*. Cambridge: Cambridge University Press.
- Lee RB, DeVore I, (eds). 1968. *Man the hunter*. Chicago: Aldine.
- Leonard WR, Robertson ML. 1992. Nutritional requirements and human evolution: a bioenergetics model. *Am J Hum Biol* 4:179–195.
- Leonard WR, Robertson ML. 1997. Comparative primate Energetics and hominid evolution. *Am J Phys Anthropol* 102:265–281.
- Lesick KD. 1991. Re-engendering gender: some theoretical and methodological concerns on a burgeoning

- archaeological pursuit. In: Moore J, Scott E, editors. *Invisible people and processes: writing gender and childhood into European archaeology*. London: Leicester University Press. p 31–41.
- Maguire EA, Frackowiak RSJ, Frith CD. 1997. Recalling routes around London: activation of the right hippocampus in taxi drivers. *J Neurosci* 17:7103–7110.
- Maguire EA et al. 1998. Knowing where and getting where: a human navigation network. *Science* 280:921–924.
- Moser S. 1993. Gender stereotyping in pictorial reconstructions of human origins. In: du Cros H, Smith L, editors. *Women in archaeology—a feminist critique*. Canberra: Australian National University. p 75–92.
- Murdock GP, Provost C. 1973. Factors in the division of labor by sex: A cross-cultural analysis. *Ethnology* 12:202–225.
- Narasimham K. 2000. Which way, honey? *Nat Neurosci* 3:306.
- Nelson SM. 1997. *Gender in archaeology—analyzing power and prestige*. London: Altamira Press.
- O'Connell JF, Hawkes K, Blurton Jones NG. 1999. Grandmothering and the evolution of *Homo erectus*. *Hum Evol* 36:461–485.
- Panther-Brick C. 1996. Seasonal and sex variation in physical activity levels among agro-pastoralists in Nepal. *Am J Phy Anthropol* 100:7–21.
- Panther-Brick C (in press). The anthropology of physical activity. In McKenna J and Riddoch C, editors. *Perspectives on health and exercise*. London: Palgrave Macmillan Publishers.
- Panther-Brick C, Pollard T. 1998. Work and hormonal variation in subsistence and industrial contexts. In: Panther-Brick C, Worthman CM, editors. *Hormones, health, and behavior: a socioecological and lifespan perspective*. Cambridge: Cambridge University Press. p 139–183.
- Panther-Brick C, Layton R, Rowley-Conwy PA. 2001. Lines of enquiry. In: Panther-Brick C, Layton R, Rowley-Conwy PA, editors. *Hunter-gatherers—an interdisciplinary perspective*. Cambridge: Cambridge University Press. p 1–10.
- Peacock NR. 1991. Rethinking in the sexual division of labor: reproduction and women's work among the Efe. In: Di Leonardo M, editor. *Gender at the crossroads of knowledge: feminist anthropology in the postmodern era*. Berkeley: University of California press. p 339–360.
- Ridley M. 1996. *The origins of virtue*. New York: Penguin Books.
- Romanoff S. 1983. Women as hunters among the Matsigenka of the Peruvian Amazon. *Hum Ecol* 11:339–343.
- Rowley-Conwy P. 2000. Time, change and the archaeology of hunter-gatherers: how original is the 'original affluent society'. In: Panther-Brick C, Layton R, Rowley-Conwy P, editors. *Hunter-gatherers: An interdisciplinary perspective*. Cambridge: Cambridge University Press. p 39–72.
- Ruff C. 1987. Sexual dimorphism in human lower limb bone structure: relationship to subsistence strategy and sexual division of labor. *J Hum Evol* 16: 391–416.
- Sackett RD. 1996. *Time, energy, and the indolent savage*. Doctors dissertation, University of California, Los Angeles.
- Sassaman KE. 1998. Lithic technology and the hunter-gatherer sexual division of labor. In: Hays-Gilpin K, Whitley DS, editors. *Reader in gender archaeology*. London: Routledge. p 159–172.
- Silverman I, Eals M. 1992. Sex differences in spatial abilities: evolutionary theory and data. In: Barkow JH, Cosmides L, Tooby J, editors. *The adapted mind: evolutionary psychology and the generation of culture*. Oxford: Oxford University press. p 533–553.
- Silverman I, Choi J, Mackewn A et al. 2000. Evolved mechanisms underlying wayfinding further studies on the hunter-gatherer theory of spatial differences. *Evol Hum Behav* 21:201–213.
- Sorensen MV, Leonard WR (2001). Neandertal energetics and foraging efficiency. *J Hum Evol* 40:483–495.
- Stanford CB. 1995. Chimpanzee hunting behavior and human evolution. *Am Scien* 83:256–261.
- Stanford CB. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *Am Anthropol* 98:96–113.
- Stanford CB, Bunn HT, (eds.). 2001. *Meat-eating and human evolution*. Oxford: University Press.
- Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. *Behavior* 131:1–18.
- Walde ID, Willows ND, (eds.). 1991. *The archaeology of gender*. Calgary: University of Calgary press.
- White D, Burton M, Brudner L. 1977. Entailment theory and method: a cross-cultural analysis of the sexual division of labor. *Behav Sci Res* 12:1–14.
- Willoughby PR. 1991. Human origins and the sexual division of labor: an archaeological perspective. In: Walde ID, Willows ND, editors. *The archaeology of gender*. Calgary: University of Calgary. p 284–291.
- Winterhalder B. 2001. Recent work on the behavioral ecology of hunter-gatherers. In: Panther-Brick C, Layton R, Rowley-Conwy P, editors. *Hunter-gatherers: an interdisciplinary perspective*. Cambridge: Cambridge University Press. 12–38.
- Wrangham RW, Jones JH, Laden C, Pilbeam D, Conklin-Brittain N. 1999. The raw and the stolen: cooking and the ecology of human Origins. *Curr Anthropol* 40:567–594.
- Zihlman AL. 1989. Woman the gatherer: the role of Women in early hominid evolution. In: Hays-Gilpin K, Whitley DS, editors. *Reader in gender archaeology*. London: Routledge. p 91–105.
- Zihlman AL. 1991. Did the australopithecines have a division of labor? In: Walde ID, Willows ND, editors. *The archaeology of gender*. Calgary: University of Calgary press. p 64–70.