The behavioral ecology of modern hunter-gatherers, and human evolution

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The first evidence of farming and herding is at most only 10 000 years old, much younger in most places. Since agriculture is so new in human experience, those few populations whose members still live by hunting and gathering have long seemed to offer important, potentially informative windows on our evolutionary past. But contemporary foragers are not unchanged relics of remote antiquity[1]. Modern human anatomy first appeared only in the past 100 000 years, and modern behavioral and symbolic capabilities are not reflected in the archaeological record until the past 50 000 years. Key features of recent hunter-gatherer technology and subsistence only emerge in the past 20 000 years. Every occupied continent has witnessed massive changes in the distribution of human populations following the establishment of modern climatic conditions 8000-10 000 years ago. Migration, war, trade and conquest have since been pervasive. Many contemporary hunters, in fact, have recent farming or herding ancestors. Recognizing this historical complexity, many anthropologists have begun to see modern foragers, not as a key source of information about human evolution, but as members of a world-wide, dispossessed 'rural proletariat', which is of no special interest to those studying the distant past.

Human behavioral ecologists[1,2-4], on the other hand, see an array of 'natural experiments'. If modern people who forage for a living are constrained by features of local ecology, then variation in these constraints, the behavioral trade-offs they impose, and the solutions adopted by individuals differing in age, sex and reproductive status are open to direct ethnographic observation[5]. If relationships between constraints, trade-offs and variability in behavior can be understood in general terms, then that understanding can provide a basis for hypotheses about human behavior in the past, which we cannot observe directly; hypotheses about likely patterns of behavior that extend outside the modern range. This approach, unlike conventional ethnographic analogy, can generate expectations about differences as well as similarities between the present and the past.

Which resources?

Humans always forage selectively, taking only some of the plants and animals available in any locality. Their choices vary through time and space. Since the suite of resources exploited in any given setting has implications for population size and distribution, individual and group mobility, social

Modern day hunter-gatherers are an obvious source of information about human life in the past. But can modern people really tell us anything about other hominids, those represented only in the fossil record? In a world of state governments and a global economy, can present-day foragers even tell us much about life before agriculture? Some behavioral ecologists think so. Their findings show (1) that foraging practices are closely related to the character and distribution of local resources, (2) that men, women and children react to foraging opportunities quite differently, and (3) that sex and age differences in these reactions have important social causes and consequences. Some results directly challenge long-held views about hunter-gatherer economics and social organization, and the scenarios of human evolution based on them.

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organization and other aspects of behavior, explanations for resource choice can provide important analytic leverage on other problems. In general, human foragers select food resources that maximize mean rates of nutrient acquisition. They routinely bypass resources yielding relatively low post-encounter rates when more-profitable items are common, but take a broader array of prey when those items are rare[1,6-10].

Patterns in the archaeological record of resource choice also reflect this trade-off between search and handling[11]. After the Last Glacial Maximum (18 000-20 000 years ago), many human populations began to exploit locally abundant, nutrient-rich, but previously unused resources, notably seeds and other plant foods that require extensive processing to improve digestibility or to remove toxic components. This so-called 'broad spectrum revolution' probably marks a decline in encounter rates for higher ranked prey, which is in turn the result of terminal Pleistocene climatic change, human population increase, human-induced habitat change, or a combination of these factors[6].

The use of resources that require substantial handling has implications for hypotheses about initial experiments in domestication. 'Broad spectrum' foragers spend more time processing than searching, and thus have more to gain from improvements in processing efficiency, including those gained from actively manipulating resource characteristics[12]. This makes broad spectrum diets a common, but also necessary precursor to agriculture. Not all broad spectrum plants were domesticated, and not all broad spectrum foragers moved directly to farming, probably because only a few plants and animals have the reproductive habits and genetic make-up that allow relatively rapid improvements in 'handling' efficiency.

Processing practices also have large effects on the character and distribution of the refuse they produce. An understanding of these effects allows investigators to extract more information about past foraging patterns from the archaeological record. When foragers transport food to eat at a central place, bulky, heavy, more durable and hence archaeologically more visible components, such as animal bones, mollusc shells, or the hard, inedible parts of certain plants, are often discarded at or near the place of acquisition. Relationships between actual diet and food waste left at the place of consumption (usually a residential base) are skewed accordingly. Ethnographic observation[13,14] and related modeling[15,16] indicate that differential transport and

discard are highly systematic processes, and are often consistent with the goal of maximizing the nutrient value of loads transported, given the constraints of time and transport capacity. Complex links between diet and its archaeological reflection are thus open to more accurate interpretation. Models that combine resource characteristics with transportation constraints can also be used to predict the location of residential bases and other sites[17].

Foraging goals

Despite the broad pattern of maximizing nutrient acquisition rates, hunting and gathering is not always consistent with this goal. Men often favor large animal prey, ignoring plant foods and other 'small package' resources profitable enough to increase their mean acquisition rates. Women frequently do just the opposite, taking plants and other small, more-predictable resources, but not large animals.

Two hypotheses are currently offered to account for this pattern. One attributes the pattern to the joint effect of two constraints, macro-nutrient composition of resources and the incompatibility of hunting and child care. Men may be maximizing their mean rate of nutrient gain in a currency that gives higher weight to fat and protein than to carbohydrates; women may avoid hunting because of the associated costs in child welfare[9,18].

The second hypothesis[19,20] focuses on resource predictability and defendability and their effects on patterns in foraging returns. Men favor prey that are irregularly acquired and sometimes very widely shared; women choose foods that provide a predictable daily nutrient supply. Since foragers can readily anticipate short-term variation in resource return rates and the fraction of any item acquired that they will be likely to keep, their foraging practices are affected accordingly. This line of argument makes food sharing patterns a potentially important determinant of resource choice.

Food sharing

Food sharing is far more common among humans than among other primates. Among modern hunters, sharing varies with resource characteristics: large, unpredictably acquired packages are shared more widely than smaller items taken more regularly. Most analysts see this as risk-reduction: successful hunters give some of their catch to the unsuccessful, in anticipation of a time when their respective fortunes are reversed[1,3,9,21,22]. The free-rider problem lurking here[3,23] is often veiled by the ethnographers' use of the term 'reciprocity' to describe these transfers, although the exchanges of food between pairs of individuals required for Trivers' reciprocal altruism are generally absent. In well-described cases, some individuals consistently receive food shares even when they have not provided any, while others continue to provide shares even if they are not repaid[20,23,24].

Blurton Jones[25] appealed to the economics of resource defense in suggesting that this pattern might be better described as 'tolerated theft'. When resources come in packages that are large enough, nutritional gains will decline as additional portions are consumed. If these resources are unpredictably acquired, only some foragers will make captures at any time. Those who have consumed less will value additional portions more. If the cost of contesting a portion is commensurate with its value to each contestant, then those who have less will take more. Acquirers need not necessarily have 'property rights' over the food they capture. If women forage primarily to feed themselves and their families, then the small defendable fraction of game animals, plus the higher day-to-day probability of failure associated with pursuing

them, make hunting an inferior strategy[20].

Why do men hunt?

The economics of defense create a potentially important social benefit to foragers who acquire resources that are too expensive for anyone to monopolize. Since non-acquirers can expect to benefit, they have a direct interest in monitoring and exploiting the success of acquirers who target such items. Thus, the forager attracts favorable attention by collecting resources that many can expect to consume[19,20,24,26].

This is an alternative to the long-standing hypothesis that men hunt primarily to provision their wives and offspring. Men's foraging may often represent mating, not parenting, effort[19,27]. Marked differences in the defendability of various resource types mean that foraging can serve different goals: either feeding one's 'own' or attracting positive attention from potential allies and mates. Those seeking the former should pursue defendable resources but favor companions who target items that are widely shared. Where men have more to gain from allies and additional mates than from contributing to the welfare of wife and offspring, they should pursue widely shared foods that earn them favorable social attention[24]. When potential additional mates are scarce, men's foraging patterns may be notably constrained by mate guarding[28].

Children's foraging and maternal trade-offs

Children can be surprisingly adept at foraging. The widely held idea that they are less productive among hunter-gatherers than among farmers is not supported by quantitative comparisons[29]. Mothers routinely adjust their own foraging tactics to take advantage of their children's capabilities, choosing resources that give them lower personal return rates but maximize the returns they and their children earn collectively[30]. Practices in any particular situation vary with the array of resources available and age-related variation in capabilities to procure them[31]. These variables explain both the active foraging of children in some cases[30], and the exclusion of children from food procurement in others[32].

Among non-human primates, juveniles feed themselves, thus, mothers can only exploit resources that their youngest weanling is able to acquire at a life-sustaining rate. Because human mothers supply food to their offspring, they can rely on a wider array of resources, including those that young children cannot manage. This practice expands the range of habitats that people, or food-sharing hominids generally, can occupy[27].

Mother–child food sharing has another important evolutionary implication. The more dependent children are on food supplied by their mother, the larger the impact a helper could have on mother's fertility. If someone else provides a dependable nutrient stream to the child she is about to wean, mother can divert her effort to the next baby sooner. Conventional wisdom casts her husband, the children's father, in this role; thereby establishing the nuclear family as a unit of common economic and reproductive interest. But, as reviewed above, men seek goals that are often inconsistent with provisioning offspring. Since it is the foraging strategies of women that provide the steady nutrient supply needed by young juveniles, grandmother is a better candidate. Helping the weaned children of her nursing daughter may have a significant effect on her own fitness. The argument that nominates grandmothers as essential helpers draws evolutionary links between food sharing, the use of resources that juveniles cannot handle adequately for themselves, and the long post-menopausal lifespans that distinguish human life histories from those of other primates[26,27].

Human life histories

Humans differ from other primates in the timing and rate of life-course events. Not only do we have much longer life-spans than chimpanzees, we also mature later and have generally higher levels of fertility than they do. Life history theory provides the conceptual tools to investigate the evolution of these differences, as well as the variation in patterns of development and fertility among modern humans[33].

Hunter–gatherer birth spacing was among the first topics to be addressed by human behavioral ecologists. Continuing work indicates the importance of trade-offs in parental investment in explaining patterns of fertility[29]. A small but growing number of forager demographies shows wide variation in completed family sizes. Fertilities are extremely high among some of the most mobile foragers[34], undercutting the widely held idea that mobility itself keeps fertility levels below those typical of settled agriculturalists[30]. Hunter–gatherer fertilities are lower where the character and distribution of resources, and associated age- and sex-specific foraging practices, make child rearing more expensive[35,36].

The proposition that mother–child food sharing allows older women to affect their own fitness through 'grandmothering' modifies the hypothesis commonly offered to explain the puzzle of post-menopausal lifespans. Since mutations acting after the age of last reproduction are usually assumed to have no effect on lifetime fitness, there should be no 'post-reproductive' life. The classic explanation for the evolution of menopause nominates a high value for extended maternal care. This makes marginal fitness gains for investment in existing children higher than fitness gained by continued child-bearing by aging mothers, resulting in selection for earlier termination of fertility[37,38]. Initial quantitative estimates of these trade-offs do not explain the timing of menopause[34]. The food sharing argument outlined above has stimulated a different version of the 'grandmother hypothesis'. It highlights a sharp increase in the effects that aging females can have on their daughters' fertility when young grandchildren must be provisioned. Human lifespans are much longer than those of our nearest living relatives, chimpanzees, while our fertile spans are similar to theirs. This suggests that longer lifespan, not 'early' termination of fertility, is the derived human pattern. Results and emerging arguments indicate the need for more modeling and further ethnographic assessment of grandmothering patterns.

Recent analyses of forager fertility and mortality patterns[34] are stimulated by developments in life history theory. Charnov's 'dimensionless' approach shows that a few variables capture enough empirical variation to account for characteristic life history patterns among different taxonomic groups[39]. Surprisingly, the simple growth model in this theory is sensitive enough to account for variation in age at maturity among different human populations[34]. More generally, Charnov's theory, by linking adult mortalities and growth and reproductive rates, offers a new way to compare the life history patterns of humans and other living primates. As far as the theory continues to predict successfully some life history variables on the basis of others, the fossil record may be used to test new hypotheses about hominid life histories.

Conclusion

Direct ethnographic observations in hunting and gathering communities provide an opportunity to test hypotheses about the fitness-related constraints imposed by dependence on local wild foods and simple technology. The emerging picture shows that individuals adjust their foraging behavior according to age, sex and reproductive status, relative to features of local ecology, including the age, sex and reproductive status of other members of their local group. Men often pursue resources that, once taken, draw many claimants. Women take foods they can subsequently control, their specific choices often depending on a trade-off between their own acquisition rates and those of their children.

Foraging patterns are part of reproductive strategies and interact with the timing and rate of life course events. Scenarios that invoke paternal provisioning and elemental nuclear families as keystones to human evolution are under strong challenge. Documenting connections between ecological, social and life history variables is changing our understanding of the variation within and among modern hunting and gathering communities – providing us with a new selection of hypotheses to apply to the paleontological and archaeological record.

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Stand up for parasites

In spite of *TREE*'s commendable efforts to bring parasites into the main stream of ecology[1–3], they still seem to be ignored. The recent review by Johnson *et al.*[4] is a case in point. This is not to fault the authors, because they could only review what exists, but the problem is that the perception of parasites by ecologists is too shallow. Parasites are regarded as just another travail of life, like weather, or fire, or flooding – just more obstacles to be overcome in the perpetual struggle to survive. But, just in terms of biodiversity, consider that parasites outnumber free-living organisms, as Thompson has so elegantly argued[3,5]. When ecologists deal only with free-living organisms, they are working with a minority of the species in their ecosystems. No wonder they miss the big picture!

So, what is the big picture? Parasites exert a cohesive force that holds ecosystems together[6]. That is, ecosystem stability is maintained by the pervasive, insidious actions of the ubiquitous parasites. Nature not only abhors vacuums, it also abhors monocultures. Whenever monocultures develop, something comes along to break them up, be it intensified competition with other species, or increased predation, or greater exposure to disease. This regulatory function of parasites is taken for granted as obvious, but its cohesive results on a large scale are not. Every free-living species of plant or animal has parasites and some of these parasites have several hosts and some even have parasites themselves. These intricate interrelationships among species form a very inclusive matrix that ties together the species in an ecosystem. The food web is an interconnected matrix, and parasites not only exploit it, but they extend predator–prey relationships beyond the mere cycling of nutrients. Moreover, many host–parasite relationships operate independently of food webs, for example, when free-swimming larval stages of helminths, such as the miracidia and cercariae of schistosomes, burrow into the flesh of their hosts, or when airborne eggs of nematodes are inadvertently swallowed[7]. Not all of the ecosystem effects of parasites are pathogenic. Parasites can modify the behaviors of their hosts[8–10], can act as cupids[11] or chaperones[12], and can even regulate ecological succession[13].

It is becoming more and more urgent that ecologists develop a deeper appreciation of parasites and begin incorporating them into their thinking. Parasites are an integral part of nature and deserve to be regarded as such. Equal rights for parasites is a cause that I champion[14]. Each free-living species is really an assemblage of several other species, its parasites and other symbionts. Every time a free-living species goes extinct, biodiversity suffers a multiple hit.

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Reply from K.H. Johnson *et al.*

We thank Windsor for echoing the thesis that interactions between hosts and subtending symbionts can modulate the functioning of the host species, as put forth previously by others[1–7]. In our review[8], we included discussions of symbioses between vertebrates and plants and between plants and mycorrhizal fungi as supportive examples, and we implored ecologists to study further 'the mediation of influence of species diversity on ecosystem attributes by mycorrhizae and other mechanisms' affecting the functional roles of species. Parasitic interactions certainly can be among the prominent forces shaping the functional niches of species in particular ecosystems[1,2].

The importance of animal parasites, plant pathogens and other microbial symbionts in regulating populations and contributing to species extinctions and coexistence is widely recognized[1–6]. Our article, however, focused on the hypothesized and observed roles of biodiversity (namely, species richness for vascular plants and insects) in increasing the productivity and functional stability of different ecosystems[8]. Insofar as parasites and other symbionts influence the kind of food web interactions thought to confer stability to the ecosystem, their functional roles will be subsumed by the dynamics of the community.