Received: 9 August 2017 | Revised: 20 December 2017 | Accepted: 20 December 2017

DOI: 10.1002/ajpa.23403

PERSPECTIVES

WILEY American Journal of PHYSICAL ANTHROPOLOGY The Official Journal of the American Association of Physical Anthropologists

Hunter-gatherer studies and human evolution: A very selective review

Kristen Hawkes[1] | **James O'Connell**[2] | **Nicholas Blurton Jones**[3]

[1]Department of Anthropology, University of Utah, Salt Lake City, Utah

[2]Department of Anthropology, University of Utah, Salt Lake City, Utah

[3]Department of Anthropology, University of California at Los Angeles, Los Angeles, California

Correspondence
Kristen Hawkes, Department of Anthropology, University of Utah, 270 S 1400 E Room 102, Salt Lake City, UT 84112.
Email: hawkes@anthro.utah.edu

Funding information
National Science Foundation, Grant numbers: BNS-8121209, BNS-8309834, BNS-8507859, BNS-8807436, and BCS-1534554; the National Institutes of Health, Grant number: 1 RO1 HD16221-01A2; Australian Research Council, Grant number: DP160101597.

Abstract

The century long publication of this journal overlapped major changes in the sciences it covers. We have been eyewitnesses to vast changes during the final third of the last century and beginning of this one, momentous enough to fundamentally alter our work separately and collectively. One (NBJ) from animal ethology, another from western North American archaeology (JOC), and a third (KH) from cultural anthropology came to longtime collaboration as evolutionary ecologists with shared focus on studying modern hunter-gatherers to guide hypotheses about human evolution. Our findings have radically revised hypotheses each of us took for granted when we began. Our (provisional) conclusions are not the consensus among hunter-gatherer specialists; but grateful that personal reflections are invited, we aim to explain how and why we continue to bet on them.

KEYWORDS

grandmother hypothesis, optimal foraging models, showoff hypothesis, supplying public goods, tolerated theft

1 | INTRODUCTION

Man the Hunter (Lee & DeVore, 1968) reported the proceedings of a 1966 symposium that was a benchmark in hunter-gatherer studies. It brought together ethnographers, archaeologists, and biological anthropologists interested in observations of contemporary and recent hunter-gatherers as a possible window onto the vast stretch of human experience before people depended on domesticated resources—the context in which our species evolved. Now, 60 years later, much more is known about the phylogeny of *Homo sapiens*. Genetic evidence shows how close we are to the great apes, drawing them into our hominid family with genus *Homo* and genus *Pan* closest evolutionary cousins. Chimpanzees have more recent common ancestors with us than they do with gorillas; and gorillas are closer to us than to orangutans. In addition there are more fossils assigned to our human radiation, different from us and from each other. Fossil taxa must fit between modern humans and our living evolutionary cousins; and space between continually shrinks as the more we know about their social behavior the more like us they seem.

As discussions in *Man the Hunter* show, participant opinion was complex and divided about whether any particular observations of hunter-gatherers in one time and place could do more than expand the descriptive record of human experience. In spite of the exponential increase in what we've learned about the topic over the past six decades, many of the issues under debate at that conference remain contentious today. Participants recognized the errors of previous scholars who had tried to equate particular modern human populations with those that left specific archaeological records dated to the Pleistocene. For many, the question wasn't *whether* observations of modern foragers are relevant to understanding the past, but *how to use them.*

Although the focus of the symposium was explicitly evolutionary, the conference volume did not hint at a revolution in animal behavior and ecology that was stirring at the time (Parker, 2006). George Williams' (1966) book *Adaptation and Natural Selection: A critique of some current biological thought* was a cogent call to evolutionary biologists about taking natural selection seriously and using it to develop and apply theoretical tools to explore and explain variation within and among populations and between species. Robert MacArthur and Eric Pianka's (1966) paper "On optimal use of a patchy environment" showed the power of simple economics to explain why natural selection resulted in animal foraging strategies that adjusted to local ecology. The three of us were strongly influenced by the findings and arguments in hunter-gatherer studies crystalized in the *Man the Hunter* volume and also by the developing tools in sociobiology/behavioral ecology. Common interest in the promise of those tools stimulated our collaboration and shaped the lessons we have learned over the past 40 years.

2 | BACKGROUND TO OUR COLLABORATION

We each had different research priorities when Hawkes and O'Connell accepted Blurton Jones's invitation to join him in what became the Utah/UCLA Hadza project. NBJ aimed to further evaluate and refine the backload model he had built with Richard Sibly to explain the 4-year birth intervals that Nancy Howell observed among foraging !Kung mothers at Dobe (Blurton Jones & Sibly, 1978). NBJ had started out as a student of bird behavior in Zoology at Oxford with Niko Tinbergen where David Lack's influence was pervasive. The value of observation techniques and hypothesis testing in ethology prompted him to apply the same approach to studying child development (Blurton Jones, 1972, 1975). Tinbergen (1965) had identified the fundamental error of Wynne-Edwards' (1962, 1965) influential group selection arguments that benefits to the group or population must generally override natural selection on individuals. Wynne-Edwards assumed that selection on individuals would always maximize fertility rates. Lack (1954) had previously demonstrated otherwise by accumulating evidence of the tradeoffs that birds faced between offspring quantity and quality: more hatchlings allowed less food for each; less food lowered chick survivorship. Clutch sizes that left the most descendants maximized neither number nor survivorship per hatchling. This directly contradicted Wynne-Edwards' (1965) argument that selection at the level of the group or population was required to account for "regulation" in animal numbers. The clarity of the contradiction was masterfully elaborated by Williams (1966) using Lack's work to criticize misleading talk of features evolving for the "survival of the species." Although Wynne-Edwards' view found favor among some anthropologists, including *Man the Hunter* participants, the sharpness of the contradiction for evolutionary biologists fueled the revolution in animal behavior. By explicitly focusing on competition and conflicts of interest *within* populations and modeling and measuring tradeoffs among fitness components faced by individual actors, researchers were discovering unexpected responsiveness of "simple" organisms to circumstances in ways that enhanced their own inclusive fitness (Parker, 2006; Davies, Krebs & West, 2012).

3 | BUSHMAN BIRTH SPACING

NBJ's Oxford background and a friendship with Mel Konner were instrumental in his initial work on hunter-gatherer birth intervals. Konner was part of the Harvard Kalahari Research Project interested in child development and invited NBJ to visit him in the field to explore their mutual interest in child behavior. That visit resulted in two papers (Blurton Jones & Konner, 1973, 1976) and introduced NBJ to the !Kung and the Harvard Kalahari Research Group. Subsequently Richard Lee gave him a chapter about !Kung birth spacing in which he (Lee, 1972) took up Lewis Binford's comments at the *Man the Hunter* Conference about associations between sedentism and population growth at the end of the Pleistocene. Population regulation was a topic at the conference where Wynne-Edwards' (1962) hypothesis and Alexander Carr-Saunders' (1922) model of "optimal numbers" among hunter-gatherers (which Wynne-Edwards used as foundation for his group selection hypothesis) were cited without objection. The sedentism-population growth association that Binford noted prompted Lee to consider the costs that mobility imposed on !Kung mothers.

Lee's 1972 chapter reported that foraging mothers carry their children everywhere from birth to the age of four and calculated the weight of baby mothers would have to lug each year if they gave birth at different intervals. After reading it, NBJ and Richard Sibly, a colleague and friend from Oxford, saw in Lee's data a chance to apply the explicit optimization logic that Lack employed studying birds to evaluate fitness tradeoffs between offspring number and survival for human mothers under the particular socioecological circumstances of Dobe (Lee 1968, 1979; Yellen & Lee, 1976).

The exercise predicted that, adding weight of food required to feed mother, lactating or not, and to feed her children, it was four-year birth intervals that maximized a mother's likely number of surviving offspring (Blu[illegible] Jones & Sibly, 1978, a prediction tested in Blurton Jones, 198[illegible]87, 2016a). With the backload model in hand, NBJ was eyeing chances to see whether it would explain birth spacing elsewhere, if necessary details for mothers, including foraging patterns and details of local ecology were used as parameter values. Hadza hunter-gatherers in the Eyasi region of northern Tanzania had been introduced to wider attention by James Woodburn's papers (1968a,b) in the *Man the Hunter* symposium. Hadza savanna is home to many of the same plants and animals exploited by !Kung foragers making differences between Hadza and !Kung especially interesting. Lars Smith, a student of Irven DeVore's, had begun Hadza fieldwork. NBJ sought him out and Smith agreed to introduce NBJ to his Hadza acquaintances.

4 | OPTIMAL FORAGING MODELS

In the meantime KH had been learning evolutionary biology from Eric Charnov, a remarkably patient and effective teacher. In line with most cultural anthropologists in the seventies, KH had initially been critical of "human sociobiology." But her re-education through Richard Alexander's work (e.g., as synthesized in his 1979 book), Williams' (1966) book, and most especially Charnov's extended postdoctoral tutelage, had drawn her to the explanatory possibilities of evolutionary ecology by the time JOC joined the Utah Anthropology faculty.

JOC's previous commitment to ethnoarchaeology as a guide to inferences about behavior that produced archaeological residues had led him to spend much of an Australian National University Fellowship in central Australia, observing Alyawarra foraging. His well-worn copy of MacArthur's *Geographical Ecology* (1972) had traveled with him. On arrival at Utah, common interest with KH in the utility of optimal foraging models as they had been simplified and generalized by Charnov

(1976a,b) led to their collaboration in applying them to JOC's Alyawarra data (O'Connell & Hawkes, 1981, 1984). They found the simple prey or optimal diet model especially useful. It focuses on the tradeoff between time spent searching and time spent handling particular resources. Handling includes pursuing, catching, picking, and processing a resource type, everything required for capture and consumption after encounter. The rate of gain while handling defines a resource type's profitability. Search time is excluded because search is shared over all resources. In this model a forager maximizes its overall acquisition rate by stopping search to handle resources that have higher profitabilities than the rate expected for continuing to search for something better. The initially counterintuitive consequence is that when resource types are ranked by their profitabilities, whether lower ranked types are in or out of the optimal diet is *independent of their own abundance*. Highest profitability resources are always taken by a rate-maximizing forager. Chance of encountering them determines whether lower ranked types are worth taking.

This model provided a simple answer to why Alyawarra now passed up the ubiquitous seeds that had been an important traditional resource (O'Connell & Hawkes, 1981). Implications for understanding the widespread shift archaeologists identify as the Mesolithic (Archaic) broad spectrum revolution (Flannery, 1969) after the last glacial maximum when relatively sessile, small package, ubiquitous resources that were previously ignored seem obvious: more people, lower encounter rates for higher ranking prey. Findings prompted them to reconsider the invaluable quantitative data Richard Lee (1968, 1979) had provided on !Kung foraging (Hawkes & O'Connell, 1981, 1985) and show how optimal foraging models revised the common view that a resource type's abundance or its nutrient density governs its value to foragers.

The simple searching versus handling distinction also provides perspective on questions about technological change, with possibly large implications for major subsistence transitions including domestication. Handling efficiencies make little difference if the diet is relatively narrow and much time is spent in search. "Conversely, where diet is broad and handling represents the bulk of foraging effort, improvements in handling efficiency would have large effects. If seed selection, sowing, and cultivation lead to increased handling efficiency (say, by favoring stiffer rachises, larger seeds, and thinner seed coats), they will make a much larger difference in foraging return rates when most foraging time is spent in handling" (Hawkes & O'Connell, 1992, p. 64).

5 | THE UTAH ACHÉ PROJECT

Drawn by JOC into larger questions about patterns in the broad sweep of human prehistory, KH saw the ethnographic opportunity that contemporary hunter-gatherers provide to improve hypotheses about the deeper human past. Kim Hill's entry into the Utah graduate program opened an unexpected pathway to explore how well predictions from Charnov's simple models fared in explaining the daily resource choices of people currently foraging for a living. Hill had left graduate work in molecular biology to join the Peace Corps, requesting assignment to a traditional population in Latin America. He had then lived with Aché foragers in eastern Paraguay, some of that time before the establishment of a mission agricultural settlement. Hill's knowledge, experience, and friendships, including fluency in Aché, allowed KH and Hill to follow Aché foraging parties into their traditional forest and systematically observe time allocation and return rates (Hawkes, Hill, & O'Connell, 1982; Hill & Hawkes, 1983). Subsequently Hillard Kaplan and Magdalena Hurtado entered the Utah graduate program; and Kevin Jones, a student in archaeology, joined the project, expanding the reach of our Aché data collection. Jones aimed to map and sample what remained of abandoned Aché camps (Jones, 1983, 1993). Injury in an automobile accident in Paraguay cut short his time in the field, but the Aché world remained in his memory and imagination, culminating in his recreation of that world in a novel, *The Shrinking Jungle* (Jones, 2012). The initial aim of our behavioral observations had been to see whether simple foraging models could help explain Aché resource choices, and the quantitative data we collected provided a clear demonstration that they do. Profitabilities (the post encounter return rates) of large game were by far the highest of anything taken. But if foragers took only those they would have spent so much time searching that *overall returns* would have been trivial (Hawkes et al., 1982).

The Utah Aché project collected a large data set, remarkable for the fullness of the coverage of foraging, time allocation, and consumption. An important reason for that comprehensiveness was the very high mobility of Aché foragers. Camps moved almost every day (Hill, Kaplan, Hawkes, & Hurtado, 1987) as many streams in the forest required no tether to specific water points. Clearings each afternoon were small given the brief occupation, with shelters constructed only when rain would otherwise extinguish fires. Individual activities in such close quarters were readily observable, including cooking and eating. We could record not only what foods individuals collected and how much time they spent doing it (Hill, Hawkes, Hurtado, & Kaplan, 1984; Hurtado, Hawkes, Hill, & Kaplan, 1985), but also whose stomachs those foods reached (Kaplan, Hill, Hawkes, & Hurtado, 1984; Kaplan & Hill, 1985). The quantitative observations showed that the average consumer got about three-fourths of their calories from foods acquired by someone outside their own nuclear family.

What was readily visible to us was visible to all—likely contributing to the remarkable amount of sharing. Both the extent of the sharing, and its variation among resource types were certainly notable (Kaplan et al., 1984; Kaplan & Hill, 1985). But the central lesson of these findings for KH (although not the other Aché researchers, e.g., Kaplan, Hill, Lancaster, & Hurtado, 2000) directly challenged initial expectation. Although hunting supplied a remarkably large fraction of calories consumed (Hill et al., 1984), men's prey catches *did not go differentially to their own wives and children*. The previously unexamined assumption that men hunt to subsidize mates and offspring has long been a textbook staple to explain the nuclear families always found among ethnographic hunter-gatherers (Murdock, 1949), with men usually hunting and women gathering. As elaborated at *Man the Hunter* by Sherwood Washburn and Chet Lancaster (1968, p. 301), "When males hunt and females gather, the results are shared and given to the young, and the habitual sharing between a male, a female, and their offspring becomes the basis of the human family. According to this view, the human family is the result of the reciprocity of hunting, the addition of a male to the mother-plus-young social group of the monkeys and apes" (p. 301). That hunting hypothesis is remarkably comprehensive: "In a very real sense our intellect, interests, emotions, and basic social life – all are evolutionary products of the hunting adaptation" (Washburn & Lancaster, 1968, p. 293).

Food sharing's fundamental importance in human societies has long been recognized in all the intellectual traditions of anthropology. As summarized by cultural anthropologist Morton Fried (1967, p. 106), sharing was "the paramount invention that led to human society . . . because it underlay the division of labor that probably increased early human productivity" and provided the "solution to maintenance problems as the human species radiated over the globe." At the *Man the Hunter* symposium, Glynn Isaac (1968) proposed that features of early archaeological sites identified them as home bases where ancestral hunters brought their prey to share with mates and offspring, making archaeology a key line of evidence supporting Washburn's scenario. Paternal provisioning by ancestral hunters was seen to be the basis for human pair bonds and nuclear families. Isaac's (1978) version of this home base argument continues to be influential in paleoanthropology and to be widely cited in the social sciences.

The Aché evidence was a quantitative account of food sharing's importance among modern hunter-gatherers. But at the same time it was clear and stunning evidence of men preferentially spending their time targeting resources that went mostly outside their own nuclear families (Kaplan et al., 1984; Kaplan & Hill, 1985). Aché men spent much more time foraging than !Kung men did, resulting in a great deal more food for Aché than for !Kung consumers (Hawkes, O'Connell, Hill & Charnov, 1985; Hawkes, 1987). The Aché project had demonstrated the utility of the foraging models we had aimed to assess. The unexpected question that arose directly from the quantitative data was why Aché men prioritize resources that they frequently fail to get, and when they do, go mostly to others. Moreover, was there a way to account for the longer hours Aché men worked to acquire more food than documented for the !Kung?

6 | SHOWOFF MODELING

While Charnov's work in optimal foraging theory was a strong Utah influence, another of his areas of specialty was sex differences. His 1982 book *Sex Allocation* synthesized theory that followed from RA Fisher's (1930) recognition of enormous implications for variation in physiology, anatomy, and behavior that follow simply from sexual reproduction. Charnov (1982) also reviewed the empirical record including work with his own students demonstrating the explanatory power of that theory. This work was part of the foundation for skepticism about 'division of labor' arguments, including the hunting hypothesis that assumed parents form social units of common interest. The higher hunting success rates and greater effort for Aché compared to !Kung men suggested Aché men had more to gain from spending time prioritizing big package, high variance resources (Hawkes, O'Connell, Hill & Charnov, 1985; Hawkes, 1987). This and other differences between the cases warranted more serious attention to sex differences, reasons to expect that strategies serving the fitness interest of women differ from those that payoff for men. Whereas women, like female mammals generally may have more fitness interest in managing offspring quality–quantity tradeoffs; men may have more to gain by competing with other men for mating benefits. This perspective was the foundation for a showoff-provisioner game that considered conflicting interests between and within the sexes (Hawkes, 1990). Women were assumed to favor a provisioning husband, but men could sometimes gain more by specializing in bonanzas that went to all. Using Aché data to assign values to parameters in the game, showing off was the winning strategy for men. Parameter values more !Kung-like led to more provisioning (Hawkes, 1990).

Further analyses of Aché data from this perspective (Hawkes, 1991) used our evidence that Aché men, like !Kung men, although not as often, also spent time on resource types that were usually acquired by women. For the subset of resources taken by both, sex of acquirer was irrelevant to how much a resource was shared. Instead, some resource types were always shared more widely than others. Something about the resource type itself, not sex of acquirer, accounted for differential sharing (Hawkes, 1991, fig. 7). That something, as had been shown by Kaplan and Hill (1985), was package size and predictability (Hawkes, 1991, figs. 1, 2, 4, and 5). Aché men, whether or not their own families were in the group, preferentially targeted the foods that went most widely around (Hawkes, 1991, figs. 3 and 6).

For KH, the combination of high foraging effort that Aché men spent on resources that would be widely distributed posed a crucial question that the showoff hypothesis aimed to answer. What, in terms of their own individual fitness related benefits, did hunters gain by prioritizing foods that went mostly to others instead of their own households? The question made NBJ's invitation to join him to study Hadza especially enticing. Hadza country, adjacent to the Serengeti, is home to many much bigger animals than those that inhabit the Aché forest. The largest animals regularly taken by Aché hunters, white-lipped peccaries, are similar to the smallest of the big game taken by Hadza. Bones of animals in larger size classes contributed to the earliest archaeology and directly to interpretation of those assemblages as support for the hunting hypothesis in which paternal provisioning is foundation for the evolution of our own lineage.

7 | ETHNOARCHAEOLOGY AND THE EARLY EAST AFRICAN SITES

JOC's perspective had drawn KH to questions posed by the deeper temporal record of subsistence changes in the history of our lineage. He had been a graduate student at Berkeley when Glynn Isaac joined that faculty. Isaac's arrival added to the eminence of the Berkeley program as arguably the best in human evolution at that time anywhere in the world. In addition to face-to-face acquaintance with the issues under investigation there, JOC had subsequently hosted Lewis Binford (Binford & O'Connell, 1984; O'Connell, 2011) on a visit to his Alyawarra study site. Questions about archaeological site formation processes that Binford wrote about (e.g., 1977) had long interested JOC as well. The

FIGURE 1 Hadza scavenging a giraffe. (Late dry season, 1988) Copyright JF O'Connell

debate between Isaac (1968, 1978) and Binford (1981) about the home base interpretation of early East African archaeological sites highlighted the need for systematic ethnoarchaeological observations. JOC's perspective and experience suited him to see how the Hadza project could provide them (Hawkes, 2016). While modern people differ from populations that left the earliest record, we can also be the best living models for them. Hadza are bipedal hunters who depend on foot transport and use blade technology to dispatch and dismember large carcasses in an environment where competing carnivores use teeth and jaws to kill, crush and drag their prey—a dimension of the ancient foraging context especially emphasized by Binford (1981). Investigating the formation of archaeological residues and how they vary with circumstances could shed empirical light on debates about early scavenging versus hunting, about the kind and location of archaeological sites, and about the meaning of body part composition and damage characteristics of faunal assemblages. Near the Serengeti, Hadza country is even closer to Olduvai Gorge and the Laetoli footprint locality, demonstrating deep ancestral occupation of this region. Its landscape and inhabitants made NBJ's invitation an obvious opportunity for JOC to supply relevant quantitative observations to debates about archaeological method, theory and interpretations of early sites (O'Connell 1987, O'Connell, Hawkes & Blurton Jones 1988a, O'Connell, Hawkes & Blurton Jones O'Connell 1990, O'Connell, Hawkes & Blurton Jones 1992).

8 | INITIAL HADZA FINDINGS

As our Hadza project began in the early eighties, some archaeologists assumed that ancestral populations, lacking projectile tools, would only have access to the meat of big game by scavenging from carnivore kills. If so, did the early sites represent tool users claiming what remained when the kill was abandoned, or did the tool users get more from carcasses by driving off the primary predators? JOC, attending especially to Hadza interactions with big game carcasses, first tallied acquisitions by hunting and scavenging (O'Connell, Hawkes, & Blurton Jones, 1988b). Of the big carcasses taken by people we were with, 20% were acquired by aggressive scavenging. As the primary predators had usually eaten some by the time Hadza took control, that was about 15% of the meat. Perhaps not surprisingly, success by both means correlated over time, but seasonal variance was enormous (O'Connell, Hawkes, & Blurton Jones, 1988b). The especially headline-worthy findings were about the possible scavenging contribution to early human diets (see Figure 1).

Woodburn had mentioned the importance of Hadza scavenging at the *Man the Hunter* conference (Discussions, Part VII, Lee & DeVore (Eds.) 1968, p. 342) noting that big carcasses are pinpointed from miles away by circling vultures. At those signals or on hearing carnivore calls, Hadza drop other activities and hurry to the kill. Armed with powerful bow-and-arrow technology, Hadza hunters are always successful at driving off the primary predators. In JOC's initial sample, 85% of the scavenged meat was taken from lions still on the kill. Since Hadza successfully pursue every opportunity with technology no older than the Upper Paleolithic, the straightforward inference is that Hadza success rates represent an upper bound to what might be possible for earlier tool-using competitive scavengers in similar environments. Even at that upper bound, "the total amount of scavenged animal tissue available to the Hadza would have been small indeed" (O'Connell, et al., 1988b, p. 361). The relationship between rainfall and herbivore biomass allowed estimates of likely scavenging opportunities in the deeper past, underlining how low they generally would have been (further exploration in Blurton Jones, 2016a).

9 | TOLERATED THEFT

The focus in the 1988 report was scavenging, but the larger implications of big carcass acquisition rates began slowly to come into focus in light of the simple sharing model that NBJ had developed from his habit of considering individual fitness tradeoffs (Blurton Jones, 1984, 1987). The label "reciprocity" has a long history of use in cultural anthropology. Marshall Sahlins (an influential participant in the *Man the Hunter* symposium, and a famously fierce opponent of human sociobiology) had published a broad historical and ethnological synthesis (first in 1965, then reprinted as chapter five of *Stone Age Economics*, 1972) demonstrating that as widely used by anthropologists, "reciprocity" did not mean literal exchange. Sahlins showed that transfers were best predicted by social relationships. Instead of sequences of back-and-forth exchanges over time between close kin and neighbors, transfers were most often "one-way flows." Sahlins fit the ethnographic reports into a "spectrum of reciprocities," and distinguished transfers in non-state societies from those of market exchange (some elaboration of this history in Hawkes, 1992a).

Robert Trivers (1971) used the label 'reciprocity' in the literal way in the first of his notable contributions to the revolution in animal behavior (Parker, 2006). Trivers later allowed that his formal exchange model was flawed and the non-human examples did not fit the verbal story (Trivers, 2002, chapter 1). Animal behaviorists have subsequently found that most examples initially hypothesized to be individuals paying each other back are better explained in other ways (West, El Mouden, & Gardner, 2011; Davies, Krebs, & West, 2012). But Trivers' (1971) rehearsal of human psychological predispositions was compelling enough to assure its influence in evolutionary psychology. Human behavioral ecologists have also favored it as a way to explain human food sharing (e.g., Kaplan & Hill, 1985; Gurven, 2004; Gurven & Hill, 2009—whose analyses are disputed in Hawkes, O'Connell, & Coxworth, 2010). As noted above, recognition that food sharing is a hallmark of human social life has a deep history in anthropology (Sahlins, 1965), with risk reduction benefits of resource pooling an attractive explanation (e.g., Fried, 1967); but benefits to the group are not satisfactory answers to behavioral ecologists (Winterhalder, 1996).

Considering sharing as a strategy for reducing shortfall risks, NBJ (Blurton Jones, 1984, 1987) had noted that those benefits were associated with particular ecological circumstances that contrasted with situations that might favor storing surplus instead. But, he pointed out, even when sharing has risk reduction consequences, those benefits cannot explain the origin (or even the persistence) of the practice if individuals can continue to take shares from others' acquisitions independent of past or future "payments." Instead of assuming exchange, he built a simple resource defense model. Resources like large carcasses might be shared widely simply because the net benefits of additional bits could be higher to those who had less. No exchange, no repayment of meat "stored in neighbors' bellies" was required. Instead, the wide distribution of large, divisible, and unpredictably acquired resources might simply reflect individual differences in the immediate benefit for claiming an additional unit. His memorable label 'tolerated theft,' suggested to some that ownership rights were implied. But the simple model actually shows that the ownership assumptions easily made by those used to well-defined property rights may be in error. Something as simple as the cost of *not* sharing could be enough to explain the wide distribution of food acquired unpredictably in large packages.

NBJ's 1987 paper also included a simple 'forager-scrounger game' in which a player's goal was to maximize its own consumption. Anything acquired was shared equally by all waiting. The game imposes a cost on foraging; but whether an individual did better to take that cost and forage anyway depended on how many others were foraging. The frequency-dependent equilibrium—when no one could do better by switching—was a mix of both strategies. Yet, scroungers consumed more than foragers at any combination.

The game aimed to see whether foraging would persist even if scroungers did better. Not considering varying resource characteristics, it assumed all foragers acquired the same thing. But the basic tolerated theft framework shows the importance of a particular resource feature for both foragers and scroungers. The cost of *not sharing* only results in wide distribution for foods that come unpredictably in large divisible packages, unsyncronized among foragers. This aspect of resource acquisition is not addressed in the simple prey choice or optimal diet model where foragers maximize their overall acquisition rates by trading off time spent searching and handling. NBJ's game underlined how substantial the difference between acquisition and consumption could be among social foragers.

10 | COMMON GOODS AND COLLECTIVE ACTION PROBLEMS

NBJ did not use the framework of common pool or public goods. But his simple model highlighted its relevance for explaining patterns of both resource acquisition and distribution among hunter-gatherers. Big package resources, that are acquired with high day-to-day unpredictability, like large animal carcasses, are more like public than like private goods. When supplied by anyone they can be consumed by all (Hawkes, O'Connell, & Blurton Jones, 1991, 2001a,b; Hawkes 1992a,b, 1993a,b, 2000, 2001). Among self-interested actors this poses a problem long recognized in economics as the "undersupply of public goods" (e.g., Samuelson, 1954), and identified in social science generally as the problem of collective action (Olson, 1965). Mancur Olson influentially identified reasons that groups so often fail to achieve collective goals. At the time, explanations for patterns of behavior in social science generally (including anthropology) hypothesized effects on group persistence. This paralleled the 'good of the species' talk that was rife in biology and criticized by Williams (1966). But such group level functionalism mistakes groups for individual actors and ignores pervasive conflicts of interest. Some good or service might indeed benefit a group, but the limited means of individuals pose unavoidable tradeoffs in time and resources. As in NBJ's forager-scrounger game, each may do better not to contribute even though all do better the more *others* do.

Olson's research showed that nevertheless sometimes people do contribute to collective goods, most often when suppliers also get something *in addition to consumption of the collective good* itself. He called benefits available only to suppliers 'selective incentives,' showing those could draw individual contributions. This suggested another way to frame the showoff model for why Aché men hunt (Hawkes, 1990, 1991). The general pattern captured by "tolerated theft" helped explain why big package, unpredictably acquired foods are much more widely shared. If that explained the sharing, the question for self-interested actors became, why prioritize resources that will be widely appropriated? Selective incentives might make it worthwhile.

11 | THE SMALL GAME HUNTING EXPERIMENT

That framework suggested a simple model supposing alternative goals. On one hand, foragers could prioritize feeding their own households by focusing on resources that came predictably in small packages they could likely control. On the other hand, they could prioritize social benefits by going for large package resources, which, if captured, would attract many claimants. Potential consumption benefits for those claimants would make them especially interested in hunters' success rates. We consider application to hunting versus gathering below. But macronutrient differences between plants and animals complicate that comparison (Hill et al., 1987; Hill, 1988). To circumvent that problem, and because men's foraging goals were of special interest, we could compare hunting for small versus large animals—both made of meat. Small animals are always more abundant than large, so could likely be acquired at lower daily failure risk. Small packages would also be less subject to appropriation by tolerated theft.

JOC's initial tally of big carcasses, camp compositions, and observation days allowed calculation of mean failure rates and acquisition rates per hunter-day. However, "men did not often take small game" (O'Connell, et al., 1988, p. 357). We needed an experiment to determine the acquisition rate Hadza hunters *could* earn if, instead of usually passing up small game, they pursued them on encounter. So we asked men to take as many small animals as possible in return for daily food and a wage (Hawkes, O'Connell, & Blurton Jones, 1991).

Results from that experiment and a modified prey model allowed a simple representation of the choice. The modification of the prey model converted acquisition rates into expected household income rates because the apparent choice of men not to prioritize provisioning their own household was of central interest. As NBJ's forager-scrounger game showed, a player could (sometimes) increase its own consumption by acquiring foods that would be mostly appropriated by others. This is the case with public goods: More is more for all. But what of the opportunity cost? We needed to evaluate the household income rate expected from targeting small prey, assuming they would mostly go to the household, to compare that to the expectation for big game, subtracting the portion of the take that went elsewhere. All Hadza grow up with the local acquisition and sharing patterns, knowing that when a large carcass is down, many—even from neighboring camps—come to help eat "the peoples' meat" (Woodburn, 1998). As to small animals, Woodburn (1968, p. 51) had reported at the *Man the Hunter* conference that a Hadza hunter "will normally light a fire, cook, and eat on the spot any small animal he kills." If he did bring home a small package, it need not attract much attention.

The small game hunting experiment aimed to get an estimate of what hunters could expect to earn for their own household by targeting small prey so that we could compare it with expected daily rates from passing them by to continue targeting big game instead (Hawkes, et al., 1991, 2001a,b; Hawkes, 1992a,b, 1993a,b). Expected rates are averages that do not take account of the risk of failure. But all those failures had to be included to calculate the average. That daily rates for big game are low should not be a surprise. Lee (1979, p. 242) had already reported for !Kung hunters around Dobe that "over the long run a hunter averages only two or three large antelope a year." Still the overall daily rate of big carcass acquisitions in our observations was notable: 0.034 per hunter-day. That is, on any day, the average hunter was all but sure to score no big animal; yet every day they passed up other opportunities to continue seeking them anyway. Expected success rates varied by season and between daytime encounter and dry season ambush hunting at night (O'Connell et al., 1988b, Hawkes et al., 1991, 2001a). Considering only daytime encounter hunting and scavenging, the rate was 0.022 carcasses per hunter-day, one every month-and-a-half of trying; and most of that went to others.

The assumption motivated by tolerated theft and our casual observations was that shares from big carcasses went about equally to all men's households—later found to be consistent with analysis of the household shares we weighed (Hawkes, O'Connell, & Blurton Jones, 2001b). We initially assumed equal distribution to evaluate whether—ignoring the whopping failure rate—a man got more on long term average for his own household by focusing on big carcasses or by stopping to pursue small animals he encountered. Our time allocation data, daily success rates, and big game carcass size gave an average daytime rate of 0.71 kg/hr. If a carcass went around to the households of six men, a hunter could expect to keep 0.12 kg/hr for his own household. For small game, profitabilities were 0.42 kg/hr or more. Even if a hunter expected to keep less than half for his own household, each encounter with small prey was a chance to get more than continued search for big game. Yet they mostly ignored small game. The averages made the collective action problem starkly apparent. Since most of a big animal carcass went to others, the more men who focused on them, the more meat for all. But, again even ignoring the huge daily failure rate, each man would get more for his own household by taking shares from big animals when captured by others while exploiting each encounter with small game himself (Hawkes et al., 1991).

Note that the portion of big game claimed by others *could* be part of the hunter's household income as well. Since everyone knows and talks about who it was that killed the animal, often referring to it by the hunter's name, claims made on the meat might be counted as recognized debts the claimant now owes the hunter. If so, that *would* fit some assumptions of risk reduction reciprocity with hunters "storing meat in the neighbors' bellies." Woodburn (1998) claimed otherwise for the Hadza and the household shares we measured and subsequently analyzed showed none of the quid-pro-quo required to fit that exchange model (Hawkes et al., 2001b). As in other ethnographic accounts (including Aché: Kaplan & Hill, 1985) some hunters continue to be much more successful than others, even spending more time hunting. As with the Aché, even those who were never successful continued to get shares. And, as with the Aché (Kaplan, Hill, & Hurtado, 1990) successful hunters do not even distribute the meat from their kills. Nevertheless, hunting reputations are widely recognized to affect men's social standing (e.g., Wiessner & Schiefenhovel, 1996; Sahlins, 1972). Reputation benefits for better hunters could serve as "selective incentives" because, unlike the meat, those benefits go only to suppliers.

12 | MEN'S AND WOMEN'S FORAGING GOALS

These Hadza observations resonated with the showoff model initially built to explain the greater time investment in hunting, and higher total acquisition rates of Aché compared to !Kung hunters (Hawkes, 1990). NBJ considered how parameters in the showoff model might help explain Hadza and !Kung differences, including the greater number of unmarried Hadza women between the ages of 20 and 45 (Blurton Jones, Hawkes, & O'Connell, 1996) !Kung men's use of traps, their attention to small game, and their mong[illegible] nut gathering contribute to household provisioning, which indicat[illegible]erests "closer to those of their womenfolk. . ..[When Hadza/!Kung contrasts are drawn this way] it is a small step . . . to the description Woodburn gives of a degree of separateness and almost opposition between the sexes in Hadza society. . . [in contrast to] the equality and relatedness of men and women in !Kung society" (Blurton Jones, et al., 1996, p. 177). In the showoff-provisioner game, more allocation to household provisioning paid off when hunting bonanzas were too rare. Hadz[illegible]cess rates of about one large carcass per hunter per month were [illegible] six-fold higher than the !Kung hunter success rates reported by Lee (1979, p. 242). "During the 83 hunter-days covered by his 1964 !Kung work diaries, no large antelope were taken. Only four of the 18 prey captured during that period weighed more than 10 kg (p. 266), and those were warthogs taken by the best hunter using his "excellent dogs"" (Hawkes et al., 2001b, p. 687).

Both the showoff model and the small-big game Hadza comparison highlighted the contribution men make to public consumption. Men forgo alternatives that would provide more to their own household. But women don't. Our observations of Hadza women's gathering (like similar data on foragers elsewhere) found women almost never scored bonanzas comparable to a big animal carcass. As Woodburn had suggested at the *Man the Hunter* conference, we also saw that women never fail to acquire plant foods when they look for them. If women are especially concerned to feed children every day, but sometimes men have more to gain or lose from their reputations as desirable allies and dangerous co[illegible]itors, different foraging goals follow (Hawkes, 1992a,b, 1993a,19[illegible]Bliege Bird, 1999).

The showoff model is *not* a challenge to the importance of hunting, of meat, or of men's work among hunter-gatherers. Men make substantial contributions to consumption by women, children, and each other. This is a sharp contrast with most other primates, including our closest cousins, chimpanzees, the other hunting ape (Stanford, 1999). Showoff or costly signaling models initially proposed by Amotz Zahavi (1975, 1977, 1995; Grafen, 1990) do not dispute that. "The hypothesis that men's work evolved and often continues to be shaped by showing off does not imply that men contribute little to subsistence. On the contrary, the showoff hypothesis and costly signaling can help explain how individuals seeking competitive advantages can increase their own standing and so earn preferential treatment by acting in ways that supply highly valued benefits to others" (Hawkes & Bliege Bird, 2002, p. 65). No "exchange" is assumed. Showoffs and audience are responding to each other, but information in the signal (as well as the meat) is "public," available to all. The importance of men's economic contributions among modern hunter-gatherers is clear to local folks and ethnographers alike. However, these data and analyses explicitly counter contentions that men's big animal hunting and scavenging is paternal effort. Effort is paternal if the fitness benefit for it is improved welfare of the hunter's offspring, not the whole group including other men's children. Showoff (and costly signaling) hypotheses are mutually exclusive alternatives to "sexual division of labor" views of nuclear families as units of common economic and reproductive interest.

Conflicts of interest both between and within the sexes are the basis for Darwin's theory of sexual selection, which explains why mating competition can result in costly "ornaments and armaments," and why such traits usually evolve in males. With a simple framework from economics KH with Alan Rogers and Eric Charnov modeled the problem that mating competition poses for males. Model males could allocate effort in three mutually exclusive ways, competing for additional mates, mate guarding, or caring for mate's offspring. The modeling showed "that mating competition has a different and much stronger effect on the optimal allocation of a male's reproductive effort than does the impact he can have on the survival of infants" (Hawkes, Rogers, & Charnov, 1995a, p. 662ff). The models showed that, "the problem of allocating effort between the struggle for paternity and caring for babies [is] another version of familiar sex allocation problems (Charnov, 1982). . . the pay-off to one of the alternatives (sons or male function) is frequency dependent in a way the other (daughters or female function) is not" (Hawkes et al. 1995a, p. 671 ff). Given these tradeoffs, males allocate less to dependents *and* less to competing for additional mates as the number of competitors increases. In these models mate guarding proved to be the fitness maximizing strategy under a very wide array of parameter conditions.

In the hunting hypothesis the central importance of father effects is proposed to override mating competition in the evolution of our lineage. NBJ explored whether the size of the effect fathers have on the survival of their offspring could explain the varying stability of pair bonds across four hunter-gatherer cases, Aché, Hiwi, Hadza, and !Kung, using parameter calculations that Hurtado and Hill (1992) had developed for the Aché and Hiwi. The analysis (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000) showed that father effects did not explain pair bond stability. Whether marriages persisted depended not on their expected effect on their children's survival but on an index of the operational sex ratio (OSR), the ratio of males to females currently capable of a conception. The lower the OSR, the more paternity opportunities per man there were in each population, the higher the

FIGURE 2 Hadza youngster too small to be effective at digging deeply buried under ground storage organs, but trying. (Late dry season, 1988) Copyright JF O'Connell

divorce rate (Blurton Jones et al., 2000; Blurton Jones, 2016a shows that improved measurement of the endurance of Hadza marriages conforms to that conclusion). Placing these findings about conflicts of interest between the sexes in the context of primates more generally (Hawkes, 2004) raised further questions about sexual division of labor explanations for why men hunt and women gather.

Nevertheless, as noted above, other hunter-gatherer researchers have continued to prefer division of labor, paternal provisioning explanations (e.g., Kaplan et al., 2000, Gurven & Hill, 2009), discounting our own analyses contradicting theirs (e.g., Hawkes, O'Connell & Coxworth 2010). Other Hadza researchers have reported their observations to be inconsistent with our observations as well (Wood & Marlowe, 2013). Our reanalysis of their observations show that although hunting success rates they report are mostly lower, their data are otherwise quite consistent with our earlier observations and analyses (Hawkes, O'Connell, & Blurton Jones, 2014). We return to male strategies below; but before that, some other Hadza findings.

13 | ACTIVELY FORAGING CHILDREN

When first visiting the Hadza, NBJ encountered children who were eager foragers at very young ages. In the 5–10 year age class they could sometimes earn about half of their daily caloric requirements (Blurton Jones, Hawkes, & O'Connell, 1989). This finding was inconsistent with usual anthropological assumptions that children become economically productive only when people are exploiting domesticated resources (e.g., Barry, Child, & Bacon, 1959). It also contrasted with NBJ's own observations at Dobe, where dependence of children on their mothers was part of the backload model that explained the long !Kung birth spacing. Hadza observations were surprising. The contrast made the question why !Kung children *don't* forage as well as why Hadza children *do* irresistible explanatory challenges for an evolutionary ecology of hunter-gatherers. Addressing them required understanding differences between the two ecological settings, their consequences for foraging strategies, opportunities for children, and resulting fitness interests of mothers in each. Taking on those challenges NBJ did several things. He highlighted wide variation in hunter-gatherer parenting strategies, demonstrated the value of an approach focused on individual fitness for explaining that variation, and drew to the center of attention inevitable conflicts of interest between parents and children (Blurton Jones, 1993, 1989, 2016; Blurton Jones, Hawkes, & Draper, 1994a,b; Blurton Jones et al., 1989, 1996, 1997).

The marked difference between the extreme indulgence of !Kung parents and the much less attentive, sometimes demanding Hadza parenting tactics contradicted notions that our long childhoods and delayed maturity evolved because hunter-gatherer children need more time to learn the skills for successful adulthood. Hadza children begin trying to collect foods while they are still very small (see Figure 2) but !Kung children don't. At the *Man the Hunter* conference Richard Lee had reported that, "young people are not expected to provide food regularly until they are married. … it is not unusual to find healthy, active teenagers visiting from camp to camp while their older relatives provide food for them" (1968, p. 36). Pat Draper (Draper, 1976; Draper & Cashdan, 1988), quantifying the time that bush-living !Kung children spent foraging, found it to be very little indeed.

Much had been detailed about the Dobe environment. !Kung camps are tied to a few permanent water holes in the dry season while more surface water in Hadza country allows camps to move more often. Seeking more information to address the possible consequences, NBJ and KH took advantage of Draper's invitation to visit her in the field (Blurton Jones et al., 1994a,b). Interviews about children's foraging converged on a few themes. One was that children were instructed not to leave camp unsupervised because they might get lost. Unlike the high relief of Rift Valley Hadza country, the flatness and scrub cover around Dobe offer no landmarks. Anecdotes about lost children demonstrated the shared worry. Another theme was that taking children on foraging trips "spoiled the work" because they complained of getting tired and slowed down travel. We invited people to participate in an experiment in which we used a truck to take them different distances from Dobe where they foraged for a measured amount of time, then identified and weighed their acquisition. Adult acquisition rates only reached rates earned by Hadza children foraging near camp at distances greater than ten kilometers round trip. The nearby foraging opportunities always available to Hadza children were missing, at least in the dry season at Dobe.

Another aspect of subsistence around Dobe is relevant here. At *Man the Hunter*, Lee reported that subsistence requirements were easily met by !Kung foragers: "the adults of the Dobe camp worked about two and a half days a week. Since the average working day was about 6 hr long, the fact emerges that !Kung Bushmen of Dobe. . .devote 12–19 hr a week to getting food" (p. 37). This was among symposium reports that prompted Sahlins' characterization of what he called "original affluence" (1968, p. 85ff). Further elaborated in *Stone Age Economics* (1972), Sahlins hypothesized inevitable fitness tradeoffs that mobile hunter-gatherers face and used those to explain low work effort, lack of concern about possessions, or future hardships, and consequent "underproduction." Although a critic of explicit cost/benefit analyses, his informal optimization logic is very persuasive (Hawkes, 1992b).

Lee (1968) had used a workweek tabulation to make comparison easier with our familiar 40-hr workweek, which famously does not include "housework." He counted only time out of camp as subsistence work. The short workweek he attributed to the abundance and nutritional value of mongongo nuts, "by far the most important food" (1968, p. 33). Subsequently, tally of the enormous amounts of time required to process those nuts (Lee, 1979) had allowed KH and JOC (Hawkes & O'Connell, 1981, 1985) to reconsider the ease of subsistence from the perspective of the optimal diet model. As mentioned above, that model explains why and when foragers maximize their acquisition rates by including foods that may be quite abundant but were previously ignored. The post-encounter return rate that characterizes a resource type in that model includes not just time spent pursuing, catching, picking it, but also time required for processing.

The substantial processing time mongongo nuts require was an obvious reason that women didn't collect them every day. It took at least three times as long to crack a backload of nuts as it took to collect it in the first place (Lee, 1979, p. 198). This high processing cost is directly relevant to the question of !Kung children's subsistence contribution. Lee (1979, pp. 277–278) reported that "children over eight and all adults of both sexes do most of their own cracking. Children aged 4–7 eat smaller quantities of nuts and these are cracked for them by their parents and older siblings." With the importance of nut cracking in mind, our Dobe experiments included cracking trials for people of varying ages (Blurton Jones et al., 1994b). Results allowed calculation of the "team rates" that mothers and older children could earn by either both traveling to the nut groves and both cracking nuts or by the child staying home to just crack nuts. Even though children got better at cracking as well as carrying larger loads as they got bigger, the robust result was always a higher consumption rate for the team if mothers left children at home to crack nuts while adults traveled to the nut groves.

The likely importance of team rates also explained why Hadza mothers *did not* leave their children at home when they traveled to distant berry patches. In berry seasons Hadza mothers forgo the return rates they could earn nearer camp by digging deeply-buried tubers. That digging requires substantial strength and endurance. Although small children often tried to do it, the rates they earned were low compared to those of adult women (Hawkes, O'Connell, & Blurton Jones, 1995b). Berries on the other hand are easy to pick and give children relatively high rates (Hawkes et al., 1995b). Although women's own overall rates would be higher if they chose the nearer tubers and did not spend so much time in travel, they nevertheless took their children on long trips to the berries instead (Hawkes et al., 1995b). The berry trips maximized the team rates of mother and children combined. Mothers made more food available to their children, enhancing their own fitness by taking those trips with children in tow (Hawkes et al., 1995b).

Just as !Kung children's nut-cracking rates and potential load-carrying capacity increase with age lurton (Blurton et al., 1994b), foraging return rates of Hadza children increase with age as well (Blurton Jones et al., 1989, 1997; Hawkes et al., 1995b). The increases might be attributed to improved skill with more practice. NBJ and Frank Marlowe (Blurton Jones & Marlowe, 2002) investigated that by measuring Hadza return rates while recording both weight and age. Body size turned out to be a fine predictor of rate. NBJ and Marlowe took advantage of a natural experiment to separate the effects of size from practice. Because some Hadza children had been sent to boarding school, they missed the chance to practice foraging during those years. The "forager Olympics" showed no deficit in the rate earned by those who had missed years of practice (Blurton Jones & Marlowe, 2002). This result underlined the particular importance of size and strength, which had come to seem especially important as we began to recognize the likely consequence of another set of observations we had not anticipated.

14 | VERY PRODUCTIVE OLD LADIES

In addition to the active foraging of Hadza children, we were surprised to find long hours spent foraging and high return rates for women long past their childbearing years (Hawkes, O'Connell, & Blurton Jones, 1989). Perhaps we shouldn't have been. In *Man the Hunter* Lee (1968, p. 35) summarized the widespread view that "hunting and gathering is so rigorous that [foragers] are rapidly worn out and meet an early death." He then reported, "the !Kung Bushmen of the Dobe area flatly contradict this view. In a total population of 466, no fewer than 46 individuals (17 men and 29 women) were determined to be over 60 years of age, a proportion that compares favorably to the percentage in industrialized

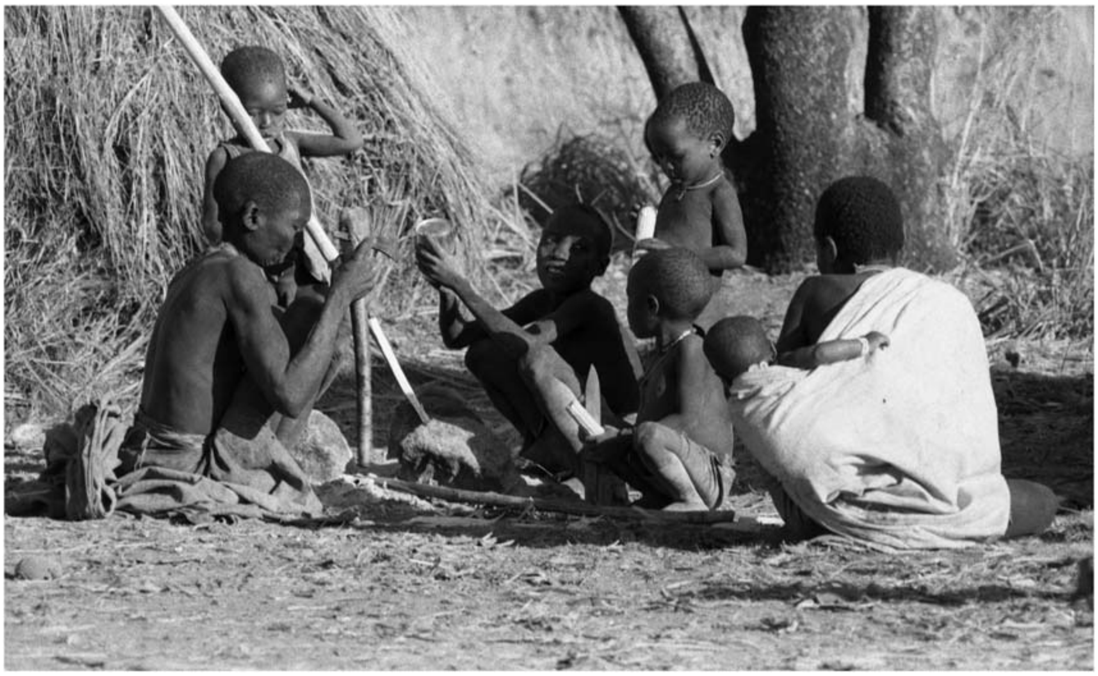

FIGURE 3 Hadza grandmother sharpens her digging stick surrounded by grandchildren while her daughter with new baby watches. (Late dry season, 1986) Copyright JF O'Connell

populations" (p. 36). Lee went on to surmise that it was "people in the age group 20–60" that supported the younger and older ones.

Perhaps because we were all thinking of other puzzles we did not anticipate the economic productivity of old Hadza women. Women's foraging time and the resources they took varied by season and also by age. In our initial report (Hawkes, et al., 1989), the overall average time spent foraging by maturing girls yet to have a pregnancy was not quite 3 hr a day; childbearing aged women spent 50% more, about 4.5 hr a day; while women past their childbearing years averaged more than *7 hr a day*. Moreover, the extra time the old women spent was doing the most energetically expensive work, digging the deeply buried tubers of *Vigna frutescens* (Hawkes, et al., 1989) (see Figure 3).

Anne Vincent, a student of Glynn Isaac's, had previously quantified the distribution, abundance, and return rates of tubers exploited by Hadza women, reporting that, "unlike many other food plants, tubers are available and edible with minimal processing throughout the year" (Vincent, 1985, p. 144). One species in particular, *Vigna frutescens*, is "the favorite of the Hadza because it is recognized as filling one up properly. It is also . . . considered to be one of the hardest to dig, occurring as it does down to a depth of 1.5 m" (Vincent, 1985, p. 138).

Our observations showed that acquisition rates earned by the old women (later determined to be well into their 60s) were not lower than the rates earned by younger ones. Yet the senior women spent much more time doing the hardest work. To explain that, we considered some hypotheses that assumed women traded plant food for meat from hunters, with older women charged "higher prices" (Hawkes, et al., 1989), an assumption that seems indefensible in retrospect. (Although the tolerated theft model should have been enough for skepticism about that, recognizing the public good-like features of big carcasses was yet to come.) More usefully we drew on life history theory to suggest a division of labor between women in their childbearing years and those beyond them. "Humans are distinguished from other primates by their capacity to extract resources with enough efficiency to regularly feed others as well as themselves. If female investments in resource acquisition compete with investments in fertility, older females may gain greater fitness by helping their adult daughters than by carrying additional, riskier pregnancies themselves" (1989, p. 341). NBJ subsequently investigated whether older Hadza women were living where their help would matter most (Blurton Jones, Hawkes, & O'Connell, 2005a,b) and found that, indeed, they tended to be where their help most likely enhanced their own inclusive fitness.

15 | MENOPAUSE

Considering menopause in 1989 we noted that, "Some have argued that it is... an artifact of increased longevity in post-industrial societies (see, for example, Weiss, 1981). But life expectancy at reproductive age for hunting and gathering and horticultural societies allows most mothers to live past their middle forties (Howell, 1979; Lancaster & King, 1985). It is likely that long before the industrial revolution most women who lived to reproductive age also went through menopause" (Hawkes, et al., 1989, p. 353). We identified some likely life history tradeoffs: "Growth, maintenance, bearing offspring, and aiding the survival and reproduction of close kin are to a large extent competing expenses... The fitness costs and benefits of alternative investment schedules depend on the present and probable future characteristics of the individual itself, of potential competitors, mates, and kin, and on other features of the environment including the food resources available and the costs and benefits of acquiring them. . .” (Hawkes, et al., 1989, p. 353–354).

At the time we followed without objection the influential hypothesis that human menopause evolved as “stopping early” proposed by Williams (1957) in his field-defining paper on the evolution of senescence. Williams was developing theory to explain why aging rates vary among living things as a consequence of natural selection. This included recognizing that selection will not favor post-reproductive life. He took on the apparent exception of humans by proposing that menopause evolved in our lineage as births became riskier and offspring more dependent. Then women who stopped childbearing early and invested maternal effort into previously born children would leave more descendants. Now we know that female fertility ends at about the same age in all the living hominids. However, unlike humans, great apes experience geriatric symptoms that make them vulnerable to mortality while still in the fertile years and they rarely outlive them (Goodall, 1986; Emery Thompson et al., 2007). Rather than women stopping early, the broader evidence is consistent with the hypothesis that an ancestral end of female fertility persisted while slower aging and greater longevity evolved in our own lineage (Hawkes, 2003; Hawkes & Smith, 2010; Hawkes & Coxworth, 2013).

16 | THE IMPORTANCE OF LONGEVITY

Nancy Howell published *Demography of the Dobe !Kung* in 1979, 10 years before we described hardworking Hadza grandmothers. Howell had been trained as a sociological demographer, well acquainted with the use of stable population theory and model life tables. Coale and Demeny’s (second edition 1983) widely used models were built from national samples, largely from European countries, the narrow source pool justified by the surmise that patterns of mortality elsewhere are “essentially unresolvable, because there exists no way to determine the exact age of an illiterate person who does not know it himself” (Coale & Demeny, 1983, p. 25). Howell understood the problem, “The models, after all, have been constructed by summarizing the experience of well-studied populations of agricultural and industrialized societies, people who live under different conditions than those of hunter-gatherers” (1979, p. 79). That made resolving the problem of estimating the age-specific survival patterns of the !Kung central questions of her study. “If the !Kung experience fits the model life tables, we can tentatively conclude that the model life tables express general features of human biological processes that are sensitive to environmental fluctuations in level but not in age patterns of mortality” (Howell, 1979, pp. 79–80). Several estimation procedures and a series of simulations led her to conclude that !Kung age patterns did fit those models. Elsewhere she explained the “uniformitarian assumption” that her analyses supported this way: “the human animal has not basically changed in its direct biological response to the environment in processes of ovulation, spermatogenesis, length of pregnancy, degree of helplessness of the young and rates of maturation and senility over time” (Howell, 1976, p. 25). In the model that best fit her data, a third of the adult women are past their childbearing years. Although many were skeptical of Howell’s conclusions (review in Hawkes & Blurton Jones, 2005), careful demographies of both Aché (Hill & Hurtado, 1996) and Hadza (Blurton Jones, Hawkes, & O’Connell, 2002; Blurton Jones, 2016a) show large fractions of female-years-lived are past the childbearing ages.

An obvious question then is what accounts for the evolution of increased longevity in our lineage? As we analyzed more of our Hadza observations, Charnov then still at Utah was talking about life history evolution. Mammal life tables had been accumulating that documented wide variation in age-specific fertility and mortality across the class. The variation showed a robust “fast-slow” regularity that was initially surprising (Promislow & Harvey, 1990). Although life history features correlated generally with adult body size, the life history features also correlated with each other even when body size was statistically removed (see review in Hawkes, 2006). Charnov (1991) built a model to explain some of those regularities. By using a separate production coefficient to capture the variation in growth rates across the mammalian radiations, his model retained an important role for body size but made it a consequence of age at maturity. In taxa with low production coefficients, juveniles grow slowly and adults are smaller for a given age at maturity. In his mammal model, optimal age at maturity is set by adult mortality; if adult mortality goes down, it costs less to wait longer and grow bigger before maturing. He identified and built theory to explain the near “invariance” of the product of age at maturity (α) and average adult mortality (M) across the wide range in values of the individual parameters. A second invariant he highlighted is age at maturity (α) times the rate of baby production (b). Those products, αM and αb remain approximately the same across the body size differences from mice to elephants. Primates have generally low production functions compared to non-primate mammals. Members of our order are relatively small at a given age at maturity, and have relatively few babies for a given adult size (Charnov & Berrigan, 1993). The mammal model that explained so much of this variation made adult mortality or average adult lifespans the driver of other life history variables. As does much of life history theory and demography, Charnov’s mammal model focused on females because it is the age-specific fertility and mortality of females that determines population growth rates. It seems curious in retrospect that it took so long to see how this pointed to the evolutionary relevance of grandmothers.

In his 1993 book, Charnov included a figure plotting average adult lifespans (the inverse of adult mortality, M) and ages at maturity (α) for females in 15 primate subfamilies. At the time great apes were classed as pongids with modern humans the only hominid. Pongids, the longest-lived, latest-maturing non-human primates, were notably high on both parameters. But, of course, the highest point on both was the point for humans. Anything but an outlier, humans represented the “invariance” of the relationship between these parameter values especially well. Unremarked at the time, the fit should have been perplexing. In most mammals including other primates, females spend adulthood continually producing offspring. In building his mammal model, Charnov assumed all of adulthood was devoted to repeatedly giving birth. But that is not so in humans. A substantial fraction of the female-adult-years lived in human populations are post-fertile.

17 | A GRANDMOTHER HYPOTHESIS

The active and productive foraging of Hadza compared to !Kung children was initially of special interest (Blurton Jones, et al., 1989, 1997; Hawkes et al., 1995b). But even on the occasions when Hadza children in the 5–10-year-old age class can supply half their own nutritional requirements, that leaves the rest to be met. Hadza youngsters try to handle the deeply buried tubers that are a year-round staple of the diet, but they are too small to do it effectively (Blurton Jones & Marlowe, 2002). As we tabulated time allocation and body weights (Hawkes, et al., 1997), a relationship previously suggested in only the most general terms (Hawkes, O'Connell, & Blurton Jones, 1989) came into sharp focus. Since children can't supply all they need, they continue to depend on their mothers for food long past weaning. But when mothers have newborns they forage less. For those mothers the relationship between their own foraging and their weaned children's weight gains disappeared. Then the correlation was with the work of their grandmothers (Hawkes et al., 1997, more data and analysis in Blurton Jones, 2016a).

Of course Hadza are modern people not ancestral survivals. But as Lack's classic work on birds had shown, maternal tradeoffs between numbers of offspring versus their survival are not even restricted to mammals. If others subsidize dependent juveniles, then this changes the quality/quantity tradeoff for mothers who leave more surviving offspring by bearing more. If grandmothers subsidize those dependents, the grandmothers leave more descendants. Longer-lived grandmothers would leave even more. Here is an answer to what would have favored increased longevity in our lineage.

In an ancestral population with a life history like the living great apes, most females would be growing old and dying before the end of their fertility. As forests were retreating and savannas spreading with changing climate, some mothers might follow the retreating forest where their weanlings could feed themselves. If instead they took advantage of new resources in the spreading grasslands, they would have to subsidize their weanlings. But others could also do it. Continued food production by females aging slightly more slowly as their fertility declined would allow their fertile daughters to bear more offspring without unsustainable costs in offspring survivorship. As slightly longer-lived grandmothers helped more, they would leave more descendants, increasing longevity in subsequent generations. The productivity of older females subsidizing their still dependent grandchildren allows mothers in the childbearing ages to stack multiple dependents rather than managing only one at a time (Robson, van Schaik, & Hawkes, 2006).

Distinctive features of human life history include our notable longevity with a post-menopausal stage, long juvenile dependency, late maturity, and early weaning (Smith & Tomkins, 1995). The scenario above could explain them all (Hawkes, O'Connell, & Blurton Jones, 2003). Since the whole adult lifespan, both fertile and post-fertile years, are spent producing descendants, increasing longevity would favor later maturity by the pathways in Charnov's mammal model. If new offspring are produced only during the fertile years with subsidies from grandmothers, the rate of baby production during those fertile years would be higher than expected for a non-grandmothering mammal. Using data from modern hunter-gatherers and those available for chimpanzees, gorillas, and orangutans, that is what we found (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998). Charnov's αM invariant, age at maturity times average adult mortality, is very similar in all the living hominids. But the αb invariant, age at maturity times babies per year, is more than twice as large in humans (Hawkes, et al., 1998). Our postmenopausal longevity, long juvenile dependency, late age at maturity, and short birth intervals could all be the evolutionary legacy of ancestral grandmothers.

17.1 | Homo erectus

In the paper first detailing that hypothesis (Hawkes, et al., 1998), we canvassed three possibilities for the timing of the life history shift, one was the evolution of the first members of our genus that expanded from Africa and quickly colonized new habitats in the temperate Old World. This was an especially attractive possibility because release from habitats where weanlings can feed themselves would be an important consequence of grandmothering. Two other possibilities mentioned were the divergence of our lineage from a shared ancestor with Neanderthals or the expansion of modern people out of Africa about 50,000 years ago. The first of the three seemed much more promising.

Elaborating that possibility, JOC "then assessed it in light of the available data on *H. erectus* life history and anatomy, Plio-Pleistocene environment, the economics of tuber exploitation, and Lower Paleolithic archaeology," finding the evidence "consistent with the proposition that grandmothering played a central role in the evolution and spread of this long successful taxon" (O'Connell, Hawkes, & Blurton Jones, 1999, p. 479). An association between larger body sizes—as expected with delayed maturity—and larger group sizes followed from "heavy reliance on resources like tubers that occur at high densities, with returns limited primarily by handling requirements, should have favored larger group sizes. The associated predator defense advantages should have reinforced the pattern, especially in more open habitats." (p. 468). Another mutualistic advantage, which we return to below, is that "cooking typically improves the nutritional yield of even the simplest starches" (O'Connell, et al., 1999, p. 474). If ancestral foragers were cooking tubers, economies of scale would flow from using the same fire after a digging bout as do Hadza women.

Perhaps especially important for the archaeological record, larger body size and larger group size would have increased success at aggressive scavenging discussed above. "Repeated confrontations at the same spot, perhaps a dry season water source in a stream channel, would create archaeological sites very like those often identified as characteristic of the Lower Pleistocene record, particularly in East Africa. . . . sites so created need not indicate that large animal prey were either commonly acquired or an important part of *H. erectus* diets. On the contrary, their appearance might simply reflect changes in hominid group and body size stimulated largely if not entirely by prior changes in female foraging, food sharing, and life history" (O'Connell, et al., 1999, p. 478).

Addressing male strategies directly, JOC subsequently rehearsed ethnographic inconsistencies with the widespread assumption that men hunt to provision their mates and offspring, then considered the depositional context and numbers of prey taxa indicated at nineteen Early Pleistocene archaeological sites in East Africa and body parts represented at a dozen of them (O'Connell, Hawkes, Lupo, & Blurton Jones, 2002). Karen Lupo (1993) had analyzed a small surface sample of bones we collected near a stream channel regularly used as an ambush location by both carnivores and Hadza hunters. The near-water context of the Hadza hunting blind, the multiple taxa, and the body parts represented were strikingly similar to the early sites. The recurrent aridity that accompanied Early Pleistocene climate change would have increased the regular use of persistent wet spots by herbivores, consequently their predators, localizing scavenging opportunities for ancestral hominins. An archaeological record would thus become "more prominent, *even in the absence of any real change in degree of reliance on meat*" (O'Connell et al., 2002, p. 861).

Thorough review of ethnographic challenges to the hunting hypothesis, the grandmother hypothesis, and the relevant paleoclimatic and archaeological record built "a theoretically and empirically well-supported case" for the following: "Changes in the early archaeological record of carnivory tell us not about the development of paternal provisioning and nuclear families in early *Homo*, but instead reflect the operation of two related processes: (1) a climate-driven change in environment that made the archaeological record of meat-eating more visible and (2) an increase in body size, also climate-driven, that enabled early humans to capture a broader range of prey, mainly via competitive scavenging. The important implication: increased archaeological evidence of meat eating in the Plio-Pleistocene is a consequence of the evolution of *H. ergaster*, not an index of its cause." (O'Connell et al., 2002, p. 862; subsequent archaeological findings have provided further support, Hawkes, 2016).

18 | HADZA DEMOGRAPHY

NBJ's initial report of Hadza demography (Blurton Jones et al., 1992) established that "Hadza have a higher population density, higher fertility, and a faster population growth rate than do the !Kung. These demographic differences are consistent with our expectations, which were based on differences in the costs and benefits of foraging in the two regions" (p. 159). Joseph Birdsell's contribution to the *Man the Hunter* Symposium had emphasized the link between human populations and the richness and distribution of resources. But Birdsell's notion of "local group equilibrium systems" was based on the claim that "most terrestrial vertebrates have evolved patterns of behavior which result in their efficient distribution in space to maximize population survival probabilities" (Birdsell, 1968, p. 234). The notion that behavior evolves to maximize population survival parallels Wynne-Edwards' arguments (1962, 1965), which had been so effectively countered by Lack's work on birds, and more generally by Williams (1966). We share Birdsell's view that patterns found in other species are relevant to understanding human patterns, but instead of "group equilibrium systems" we expect population consequences to flow from fitness tradeoffs faced by individuals (Blurton Jones & Sibly, 1978; Blurton Jones, 1986, 1987, 1989).

As NBJ continued accumulating Hadza censuses to improve estimates of age-specific fertility and mortality rates, he addressed the question of how much those rates were affected by changes in the Eyasi region over the last several decades. Stable population models are the fundamental tools of both demography and evolutionary life history theory. They are based on the Euler-Lotka truism that when fertility and mortality remain the same over a few generations (and migration is negligible) populations reach a stable age structure. Each age class grows (or declines) at the same rate. How much had the Hadza changed with the global, national, regional changes of the 20th century? Accounts written by European visitors as early as the 19th century (Marlowe, 2010, table 2.1) suggested surprisingly little (Blurton Jones, et al., 1996; Blurton Jones, 2016a,b).

In 2002 NBJ pursued a particular question about secular changes that inevitably arises in response to the grandmother hypothesis (Blurton Jones et al., 2002). Is the population age structure with its notable fraction of post-fertile women a consequence of "outside" influences on Hadza life including our own visits? Evaluating possible effects showed them to be negligible (Blurton Jones et al., 2002). Hadza women who reached age 45 had on average more than two decades additional survival. Comparing Hadza to !Kung (Howell, 1979) and Aché (Hill & Hurtado, 1996) showed "very similar adult mortality… Each population also shows the usual Gompertz-like increase in probability of death in the late 60s and 70s. … compatible with Hamilton's (1966) picture of the evolution of senescence, but only if we assume that individuals age 45–65 have reproductive value" (Blurton Jones et al., 2002, p. 201; similarities with historical European populations in Hawkes, 2003; replicated on a larger sample by Gurven & Kaplan, 2007).

Hamilton's (1966) model was built to mathematically explore Williams' (1957) verbal arguments about the evolution of senescence. By Hamilton's calculations, survivorship and fertility should asymptote near zero at the same age, confirming Williams' (1957) assessment that selection would not favor "post-reproductive" life. One empirical example Hamilton used to evaluate those predictions came from our own species: life table data from a high mortality farming population. As had Williams, Hamilton confronted an apparent mismatch. Age-specific fertility and age-specific survival do not approach zero at the same age in women. Hamilton pointed out that the notably high rate of women's post-fertile survival "inevitably suggests the special value of the old woman as mother or grandmother during a long ancestral period (Hamilton, 1966, p. 37). We interpret his surmise as prelude to our grandmother hypothesis. Data unavailable when Hamilton—or Williams before him—was writing now points to the specific form and particular ecological context of that "special value."

19 | DEMOGRAPHIC DATA AND HYPOTHESES ABOUT HADZA FITNESS TRADEOFFS

In 2016 NBJ's long awaited Hadza demography was published (Blurton Jones, 2016a). In it he covers the geography and ecology of the Eyasi Basin, the history of the Hadza, and the age-specific fertilities and mortalities of the population with detailed explanation and exploration of methods including those of age estimation needed to calculate them. Then he considers a version of the question that Birdsell's (1968) "local group equilibrium systems" did not answer. What is the rate of Hadza population growth? And what is the possible magnitude of each of the variables likely to affect it? The growth rate is clearly unsustainable, just as Hill and Hurtado (1996) had noted for Aché. Dubbing this the "forager population paradox" NBJ explores Hill and Hurtado's suggestion that hunter-gatherer populations may usually be increasing but with periodic crashes.

The second half of the book is an evaluation of the actual demographic effects of living grandmothers, older siblings, continued search for any demographic effects of fathers, and measurements of the association between hunting reputations, offspring numbers and offspring survival. The effect of living grandmothers on Hadza child survival is strong. Even after control for family vigor, possibility of epidemics taking away very young and very old, and the smaller size of orphaned mothers, the effect is large with odds ratio 1.6–2.0. The chance of children with a grandmother living to 15 is 0.63 while it is 0.45 for those with no grandmother. Paternal grandmothers (previously shown to live with their son if his wife had no mother) are also effective (chapter 18).

For Aché, Hill and Hurtado (1996) had found that a man's hunting reputation had a much stronger effect on his number of offspring than on their survival. For Hadza NBJ (2016a) found a man's hunting reputation also had a strong effect on his number of offspring, mainly as a result of marrying a younger woman in mid-life and raising a second family, as also reported by Marlowe (2010). But survival of children was actually lower for good hunters than for "average Joes." Among the latter, father's presence in the family showed a marginally significant positive effect on child survival. This suggests that the comparisons between !Kung and Aché discussed above may apply within populations as well as between them, underlining the possible explanatory payoffs for attending to specifics of the variation (as urged in Hawkes et al., 2010). Investigating whether women gain fitness benefits from marriage, NBJ (2016a) finds, counter to usual expectations, that it is men not women who benefit. While some Hadza women, even in their childbearing years, spend substantial amounts of time unmarried, most are married most of the time. This could be entirely a consequence of advantages to men for mate guarding. But women are angry on learning of a husbands' interest in other women. Investigations continue with an eye to social situations of women in relation to marriage and their husbands' reputations. The many analyses and the questions arising are a blueprint for posing and testing hypotheses about fitness effects with demographic data.

20 | MATHEMATICAL MODELING OF LIFE HISTORY EVOLUTION

The grandmother hypothesis we have been pursuing is about a life history transition in the past. All modern human populations are on this side of it. Evidence about that past comes from the fossil and archaeological records, but they cannot speak for themselves. As reviewed above, most can be wrung from those records with the guidance of well-warranted hypotheses (O'Connell, 1995). Mathematical modeling can be especially useful because it can show whether (given model assumptions) proposed causes actually can have proposed effects. Peter Kim built an agent-based model of the grandmother hypothesis (Kim et al., 2012, 2014) parameterized for hominids where the age female fertility ends remains essentially unchanged across the radiation. The model investigates whether grandmothering subsidies would be enough to propel the evolution of longevity and drive a great ape-like life history into a human-like one. The model only allows females to grandmother at the end of their fertility so in the ancestral condition, the initial great ape-like equilibrium, there are very few potential grandmothers. But the simulations show that indeed, with grandmothering subsidies and the end of female fertility fixed, great ape-like longevities evolve to human hunter-gatherer longevities with age structures containing a human-like fraction of post-fertile females.

This is a two-sex model in which longevity is allowed to vary with different costs and benefits, different tradeoffs for varying longevity in each sex. Female tradeoffs are those assumed in Charnov's mammal model (1991, 1993): The benefit of greater longevity is higher survival but this imposes the costs (in terms of likely number of descendants) of waiting longer to mature and then producing offspring that are dependent longer. For males, the benefit of increased longevity is more opportunities to compete for paternities, but greater longevity carries a cost. Following Williams' (1957, p. 410) deduction that "successful selection for increased longevity should result in decreased vigor in youth," males with greater longevity are assumed less successful in the paternity competition. A hint that sexual conflict is important emerged from modeling results because the equilibrium longevity for females alone (the one that maximizes population growth rate) is less than the population longevity reached when males are included. In 7 out of 50 simulations without grandmothering, populations are pushed to unsustainable longevities by advantages for higher longevity gained in males (more paternity opportunities). Those populations go extinct as the longevity costs to females without grandmothering drive the growth rate below zero (Kim et al., 2014; fig. 4).

21 | MALE STRATEGIES WITH A GRANDMOTHERING LIFE HISTORY

Until this modeling, investigation of grandmothering on one hand and male strategies on the other had intersected in connection with the likely effects of larger body size on male competitive scavenging success. We had also noted (Hawkes, O'Connell, Blurton Jones, Alvarez & Charnov, 2000, p. 252) that, "With long postmenopausal lifespans, the age profile of fertility no longer coincides with aging in most aspects of female adaptive performance. General health and competence become poor fecundity cues. Male preference for young partners, which sharply distinguishes men (Jones, 1996) from chimpanzees (Morin, 1993), could be favored as a consequence." (Male chimpanzee preferences for older females are now further documented in Muller, Emery Thompson, and Wrangham, 2006). But the sexual conflict around longevity suggested in the simulations drew attention to the "other side of post-menopausal longevity" that was hiding in plain sight.

As longer-lived grandmothers have longer-lived daughters and longer-lived sons, longer-lived granddaughters and longer-lived grandsons, the older fraction of the population increases. While the age at which fertility ends remained little changed in females, fertility continued in older males. In all mammals, including humans, females build their stock of oocytes in early development. That stock then depletes continuously by atresia. Males however continue spermatogenesis throughout adulthood. Even though mortality is higher in males than in females at all ages, the survival of all those old men turns the sex ratio in the fertile ages from a female to a male bias.

In other animals the sex ratio in the fertile ages is called the adult sex ratio (ASR) since adulthood is spent producing offspring. But that is not the case in humans where a substantial fraction of female adulthood is post-fertile. The increasing number of older fertile males pushes the sex ratio in the fertile ages from the female bias that is typical of mammals generally, to a male bias. Both the ASR and the operational sex ratio (OSR), which includes only those in the fertile ages currently capable of a conception, affect payoffs for alternative mating strategies. The less male-biased these ratios are, the more mating opportunities per male; the more biased toward males, the greater the paternity competition. More competitors lower the expected benefits for each male. When the pool of competitors is large, guarding a current mate may give higher fitness benefits than joining that pool to compete for another one.

OSRs are generally quite male-biased in mammals as females are committed to gestation and lactation and unavailable for a conception during those commitments. As noted above, an index of the OSR for four hunter-gatherer populations (Blurton Jones et al., 2000) found the less male-biased the OSR (the more paternity opportunities per male) the more fragile the pair bonds.

Recent general interest in the role of ASRs (e.g., Kokko & Jennions, 2008) in explaining variation in mating strategies turns partly on the broad contrast between mammals and birds. ASRs are generally female-biased in mammals, including most non-human primates where pair bonding is rare. ASRs are generally male biased in birds where pair bonds are common. Lack's classic hypothesis about monogamy in birds (1968) was that paternal provisioning increased numbers of offspring fledged. But as conflicts of interest between the sexes came more clearly in to view, so did mating competition. Nick Davies' 1991 review concluded that, "the predominance of monogamy in many birds arises not, as Lack proposed, because each sex has greatest success with monogamy… Strong competition among males makes it difficult for a male to gain another female" (Davies, 1991, p. 283).

We have noted that anthropologists "with diverse theoretical orientations have emphasized the mate-guarding aspects of marriage (Goodenough, 1970; Broude & Greene, 1980; Flinn, 1988; Wilson & Daly, 1992). In humans, however, this has been attributed to an assumed species habit of high paternal investment, with mate guarding a consequent strategy to improve the chance that the effort is not misdirected (Daly, Wilson, & Weghorst, 1982; Daly & Wilson, 1987; Wilson & Daly, 1992). No such habit need be implied (Hawkes et al., 1995a). Widespread evidence that males display jealousy in species where they make little or no parental effort shows that male competition for paternity by itself is enough to favor male jealousy and coercion (de Waal, 1982; Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995)" (Hawkes, et al., 2001, [illegible] 593).

JE Coxworth, Kim, McQueen, and Hawkes, (2015) highlighted the mating sex ratio change associated with the evolution of our own lineage by running simulations of Kim's agent-based grandmothering model (Kim et al., 2014) and plotting the sex ratio in the fertile ages rather than longevity. As grandmothering subsidies propel simulated hominid populations toward a human-like life history, the ASR moves from an ancestral great ape-like average of 0.77 males/female in the fertile ages, to an average of 1.56 males/female at the human-like equilibrium. Life tables for chimpanzees and four hunter-gatherer cases provided a reality check. Chimpanzee average ASR was 0.55; hunter-gatherer average 1.64, fair correspondence with the model.

Coxworth and colleagues (2015) reviewed some history of behavioral ecologists' attention to mating sex ratios and the convergence in modeling, observation and experimental studies on male mating strategies. Male-biased sex ratios favor mate guarding. These findings across a range of species suggest "that human pair bonds evolved with increasing payoffs for mate guarding, which resulted from the evolution of our grandmothering life history" (Coxworth et al., 2015, p. 11810). As mentioned above, others had previously noted mate-guarding aspects of human pair bonds. Connecting payoffs for mate guarding with mating sex ratios, and those with the male bias that accompanies evolution of our grandmothering life history now seems obvious. But the connection raises challenges for future work as shown by Chan, Hawkes, and Kim (2016).

Matthew Chan and colleagues (Chan et al., 2016) explored the ground laid by Kim et al. (2014) with partial differential equations, which are more economical than agent-based models for exploring the effects of parameter values. Chan also used more realistic mortality assumptions, restricted grandmothers to subsidizing offspring of fertile daughters, and allowed age at last birth as well as longevity to evolve. As in Kim et al. (2012, 2014) the model resulted in (only) two equilibria—a great ape-like and a human-like one. "[G]randmothering enables the transition between these two equilibria, without extending the end of fertility. Moreover, sensitivity analyses of the model show that male competition, arising from a skew in the mating sex ratio toward males, plays a significant role in determining whether the transition from great ape-like longevities to higher longevities is possible and the equilibrium value of the average adult lifespan" (Chan et al., 2016, p. 145).

Since optimal male strategies change with mating sex ratios (Coxworth et al., 2015), what would happen in grandmothering models if male strategies were allowed to evolve? Focusing only on male mating strategies, Schacht and Bell (2016), Loo, Chan, Hawkes, and Kim (2017a), Loo, Hawkes & Kim (2017b) have modeled the effects of varying mating sex ratios on the relative success of three male strategies, multiple mating, dependent care, and mate guarding. Models converge on a poor showing for dependent care, dominance of multiple mating when sex ratios are female biased, and takeover by mate guarding when the bias is toward males—although how male-biased depends on the effectiveness of guarding (Loo, et al., 2017b). All this modeling points to a switch from multiple mating to mate guarding as a great ape-like life history evolves into a human-like one. The grandmothering models (Kim et al., 2012, 2014; Chan et al., 2016, 2017) do not include evolution of male strategies. Incorporating that might give something other than the two equilibria that is a robust result so far.

22 | FIRE, COOKING, TOLERATED THEFT

We initially found tolerated theft a crucial tool for understanding why big animals are so widely shared. Now it also helps highlight an important consequence of ancestral cooking. Initially we reported cooking as part of Hadza women's tuber handling this way. "Women usually dug to just past midday, when they gathered to cook the tubers on a common high flame fire. If the party was large, more than one fire was kindled. . . . After appetites were satisfied, or the tubers all eaten, a second bout of digging began and continued through the afternoon, followed by more cooking and eating. Women then loaded the remaining cooked tubers into their carrying cloaks and returned home" (Hawkes, et al., 1989, p. 344). JOC noted implications for the early archaeological and fossil record (O'Connell, et al., 1999, p. 474ff). "[L]arge fires [are] kindled on unprepared ground surfaces. Even where cooking sites are used repeatedly, archaeological evidence of this practice is likely to be ephemeral." However the fossil record is more than suggestive. The morphology and especially reduced chewing architecture of *H. erectus* suggests more "pre-consumption processing" of which "tuber cooking is a good example."

Nevertheless archaeologists have continued to expect that whenever cooking was important in the human past, it would leave more than ephemeral traces; and many remain skeptical that *H. erectus* was a regular fire user. The result is what Richard Wrangham (2007:313) has called "the cooking enigma." "On the one hand, cooking is absent among animals, universal in humans, and rich in biological consequences. It is therefore expected to have a strong impact on evolutionary biology. On the other hand, archaeological data place the acquisition of cooking at [a quite recent date] when nothing dramatic was happening in human evolution." Marshaling and elaborating many other lines of evidence, Wrangham and his collaborators have provided compelling reasons to see cooking as obligatory for humans, and identified features of *H. erectus* that are consistent with the deep antiquity of that reliance (e.g., Wrangham & Conklin-Brittian, 2003; Wrangham, 2009; Wrangham & Carmody, 2010). Agreeing the case is persuasive, we suggest amendments on two counts.

First, Wrangham, Jones, Laden, Pilbeam, and Conklin-Brittai (1999) and Wrangham (2009) have argued that cooking increases the vulnerability of resources to appropriation. We concur, finding this to be a place where tolerated theft usefully applies. The cost of not sharing large divisible food piles is not worth paying. "Cooks gain notable economies of scale as items are accumulated, fuel gathered, and the nutritional utility of the meal increased with processing. These steps concentrate feeding into long handling stages followed by bursts of highly efficient consumption. The size and nutritional richness of meals make them attractive opportunities for potential consumers other than the processor" (Hawkes & Coxworth, 2013, p. 299). But Wrangham and colleagues (1999) and Wrangham (2009) propose that vulnerability causes cooks to take a mate who acts as guard, and see this as the foundation for pair bonds. Unlikely from our perspective, this obscures the more immediate issue. "Youngsters are especially likely appropriators. Some food sharing between mothers and offspring is widespread among primates and more likely with foods that are difficult for infants and juveniles to handle on their own... Wrangham's enumeration of the anatomical characteristics of *Homo erectus* that indicate dependence on cooked food identifies evidence of reliance on processing that young juveniles cannot manage. This directly implicates helpful grandmothers in the evolution of our genus" (Hawkes & Coxworth, 2013, p. 299).

A second amendment is to notions about how human dependence on cooking evolved. Other animals don't cook (although Wrangham and colleagues have shown that chimpanzees and many other animals prefer cooked food). Noting the many origin stories about human cooking, Wrangham (2009) attributes it to a lucky accident. More than chance likely underlies this important chimpanzee-human difference. "Though chimpanzees can make simple tools that might be suitable for collecting deeply buried tubers, and in some circumstances are even able to maintain fire (e.g., in connection with cigarette smoking [Brink, 1957]), they apparently never use either skill to take deeply buried tubers in the wild, probably because other resources, easily taken by juveniles, are readily available in the habitats they occupy" (O'Connell, et al., 1999, p. 472). Ecological context is likely key to how we become the pyrophilic primate (Parker, Keefe, Herzog, O'Connell, & Hawkes, 2016). In savannah environments fire is a part of the experience of many animals. This includes other savannah dwelling primates who respond to the effects burns have on foraging opportunities (Herzog et al., 2014; Herzog, Keefe, Parker & Hawkes, 2015; Pruetz & LaDuke, 2010; Pruetz & Herzog, 2017).

Ancestral populations in our own lineage faced drier, more seasonal climates, retreating forests, and spreading grasslands with more frequent landscape fires in Pliocene tropical Africa. The same changes that increased fire frequency favored proliferation of savannah plants like the deeply buried tubers important to Hadza foragers. As noted above, the optimal diet model directs attention to two main components of foraging time, searching and handling. Fire could have affected both, reducing search costs and raising profitabilities of some resources. Control of fire could begin by simply moving burning grass or sticks across natural firebreaks to extend burns and magnify these effects just as some birds are reported to do today. The crucial step was recognizing the improved profitabilities of resources when processing extended to cooking them (Parker et al., 2016). Cooking increases ease of mastication and digestive access to nutrients. It thus shifts the shape of gain curves, increasing benefit for that additional processing and raising the mutualistic benefits for gregarious foraging noted above. All can benefit from continued productivity of the elder females as both adults and children net fitness gains when the youngsters appropriate shares for themselves.

23 | HUMAN SOCIALITY

Attention to our primate cousins and phylogenetic relationships contributes to developing reasonable hypotheses about morphological and behavioral changes and their likely order in the evolution of our lineage. Modern people differ from ancestral ones. We want to understand what happened in a different past, populated by taxa known only (if at all) from paleoanthropology. Whether some of those fossil taxa identified as hominins were ancestors or cousins remains contested. But if they were hominids they belong to a radiation that began with a population of Miocene apes whose descendants had different evolutionary fates. Some no doubt disappeared without descendants themselves, some evolved into each of the living great apes, and some evolved eventually into modern people. Since selection can only operate on what is already there, identifying let alone explaining any evolutionary transition along the way requires presuming both pre- and post-transition states. The distribution of features among living descendants guides hypotheses about ancestral states as features common to most members of a radiation are good candidates for features of their common ancestor. Features shared among modern hunter-gatherers and all other living hominids are likely nominees for features of the ancestor we share, and, if so, of all the populations linking us to them.

Phylogeny sets the possibilities, but selection can result in similar adjustments in species that are phylogenetically very distant from each other. Our collaboration started from costs and benefits of foraging strategies among modern hunter-gatherers with variation in fitness tradeoffs by age, sex and local ecology leading to other aspects of social behavior. Concepts and methods that reveal and explain variation in animals phylogenetically distant from humans have been essential. Lack's demonstration that offspring quality/quantity tradeoffs can account for clutch size variation in birds was background to NBJ and Sibly's (1978) model of Bushmen birth spacing. Charnov (1976a) used observations on mantid foraging to explain and evaluate the empirical utility of his optimal diet model. Geoff Parker (1974) learned from observing golden dungflies that more male competitors increase time spent mate guarding, laying the foundation for subsequent recognition of adult sex ratio effects on mating strategies.

Both phylogenetic similarity and likely common selection pressures continue to make comparisons and contrasts with other primates especially useful. Sarah Hrdy (e.g., 1999, 2009) has provided widely influential guidance about primate comparisons. Among other things, she identified the distinctive importance of allomothering in our own species and so categorized humans as cooperative breeders. That label was previously used for species in which social groups contain only a single breeding female with non-breeding helpers, not a pattern found in humans. But like other cooperative breeders humans rely on dependent provisioning by allomothers. Hrdy highlighted the important contrast between human childrearing and the independent mothering of all the great apes, strong basis for assuming that independent mothering was the pattern in our common ancestor. In primates, it is only humans and the small New World callitrichid monkeys that rely on dependent provisioning from individuals other than the mother.

Longstanding interest in the treatment of primate infants led Hrdy (2009) to identify features that distinguish contexts where mothers allow others to handle their infants from those where they do not. As quality-quantity tradeoffs would predict, when social relationships assure the infant will be safely returned, mothers can net fitness benefits by foraging unencumbered while trusted others hold their infant (Hawkes et al., 2017). That suggests cooperative breeding may be one extreme of variation in maternal protectiveness that correlates with variation in the composition of social groups. Hrdy (1999, 2009) examined similarities in social predispositions between humans and callitrichids, marmosets and tamarins. These tiny monkeys are at the opposite end of the primate range of variation in life history from humans. Mortality is high, first birth within 2 years, and fertility astonishing: They produce twins, sometimes even triplets—sometimes two sets a year. Also unlike humans it is males that supply the allomothering, carrying infants, which they only return to the mother for milk. We share with them altered fitness tradeoffs for mothers due to reliance on allomothers so that both callitrichid and human mothers—unlike other primates—may abandon infants when they lack adequate support (Hrdy, 1999, 2009).

Tamarins and marmosets produce litters; and human stacking of multiple dependents Robson et al., 2006) makes us more like litter-bearers than producers of singletons (Hrdy, 1999). There is competition for the attention of both mothers and allomothers, which is crucial for infant welfare. Infant babbling, seen only in these taxa, may have been favored by selection because it attracts that attention (Hrdy, 2009). Selection on distinctive social tendencies and capacities to actively engage the commitment of mothers and others is especially prominent in humans (Hrdy, 1999, 2009; Hawkes, 2014). Perhaps larger social groups in humans contribute to that. In callithrichids the single breeding female family is usually *the* social group, members remaining close together and defending their territory against others. Humans, like several other primate species form multi-level social groups in which core units comprised of a male and one or more females with offspring are part of larger communities (Greuter, Chapais, & Zinner, 2012).

In our multifamily communities, relationships among men shape a great deal of social life (Rodseth, 2012). From that perspective the infant carrying and provisioning by callitrichid males is not convergent with the 'sexual division of labor' in humans. Only in rare recent settings is caring for infants a central responsibility of men. Our hypothesis about the evolution of men's work identifies the importance of reputation competition (Speth, 2010). We interpret the accumulated data to show that men generally prioritize public over domestic effort. The importance of the resulting public goods, a hallmark of our lineage, is overshadowed—inappropriately—by continuing claims that hunting is family provisioning. Labels may contribute to what seem persistent misunderstandings. As noted by NBJ (Blurton Jones, 2016a), disclaimers seem in order.

Showoffs in the initial showoff versus provisioner game (Hawkes, 1990) are not presumed to be bragging self-aggrandizers. In that game a showoff "feeds himself a bit and then seeks resources which he often fails to capture but which give him occasional bonanzas big enough to feed more than a family. Because of the size and asynchrony of these jackpots, others could readily claim the extra which would be of little direct nutritional value to the hunter himself since he would be replete on consumption of only a portion of it (Blurton Jones, 1984)... [T]hose who adopt the high-variance, "showoff" strategy, which results in intermittent bonanzas, are desirable band companions for all because of the occasional feasts they provide. Since their average returns are low and the bonanzas they bring in are unpredictable, others cannot use them as a source of dependable support. But by not supporting a few they become sources of unpredictable benefits to many. The value of the occasional large packages brought by the showoffs leads other adults to act toward them in ways which increase the chances that they will remain with the group and continue to supply extra food to all." The contrast is with provisioners "who adopt the low variance provisioning strategy, which earns a steady daily income for a wife and children, [but] never earn enough excess for others to claim without dispute. Because of this their presence in a band is of no advantage to any but their wives and children" (Hawkes, 1990, p. 155).

The showoff label can also seem misleading to those who know that hunter-gatherer men do not tout their successes. Those connotations of the label are unintended and in the way. "Lee's famous anecdote about the properly self-effacing behavior of !Kung hunters captures the common pattern (Lee, 1969). But !Kung men talk endlessly about hunts and hunting, rehearsing the "minutest details."... All those who listen to the storytelling soon know which man it was that made every kill. The self-effacing style also characterizes Aché hunters, who arrive at the evening's forest camp without a word, whether they have taken any prey or not. Ten minutes or more may pass before the men begin to talk quietly of the day. Then, without fanfare, someone else, perhaps a boy, will step outside the circle of fires and drag in any prey left discretely at the margins of the camp" (Hawkes & Bliege Bird, 2002, p. 64).

This absence of bragging is especially important to highlight because its likely association with unpredictability may contribute to the famously "egalitarian" character of many modern foraging societies. "Using the Hadza rates as the example, even the best hunter usually fails to score, and the least skilled and experienced sometimes succeeds. The two-sided consequence, that good hunters cannot be relied on to succeed and that even boys can sometimes provide a bonanza for all, regularly undercuts hierarchical rankings. Any hunter's success on one day will always be followed by failures, limiting the extent to which anyone can maintain superiority over others. ... Anyone who brags about his superiority will have his claims soon countered by the success of another" (Hawkes, 2000, p. 72).

This is an alternative to the common view that hunter-gatherers are egalitarian because they do not accumulate wealth. Wealth accumulation hypotheses not only ignore the steep hierarchies found in other primates, they also leave Aboriginal Australia as a puzzling exception. "[E]thnographers working in Australia described "gerontocracies" in which old men, no richer than hun[illegible]to elsewhere, wielded power over young; and polygyny was common" (Hawkes, 2000, p. 76). These male gerontocracies are not based on wealth differences, but there is an ecological feature that may help explain the "exception." "[I]n Australia, unlike all other continents occupied by humans, the terrestrial vertebrate populations persisting into the Holocene included no very large bodied species. ...[W]ithout big-game hunting to eclipse the prominence of senior men, the fact that they would always have prior claims and previously established allies could allow the older men to successfully hold wives against more weakly competitive younger men. The distinctive complexity of Australian marriage arrangements could arise when mate-guarding conventions are generally in use but male hierarchies are no longer undercut by the constantly anticipated but always unpredictable capture of large prey" (Hawkes, 2000, p. 76).

Another likely source of misunderstanding about the showoff hypothesis needs mention. The showoff–provisioner opposition may suffer from confounding with a different binary opposition, "dads versus cads." Although parenting versus mating effort is at issue in both cases, the oppositions are not equivalent. Showoffs supply bonanzas that are of benefit to all. Formulated in the collective action framework, it is their contribution to common or public goods that earns them reputation benefits. "Various versions of that showoff hypothesis propose that hunters attract the favorable attention of many potential consumers by acquiring foods that are widely consumed... When hunters target large prey, and when others can learn about and compare their successes, hunting reputation becomes a prominent determinant of how desirable a neighbor and ally, and how dangerous a rival, a man might be" (Hawkes & Bliege Bird, 2002, p. 59). "The hyperbole that [Elizabeth Marshall] Thomas (1959, p. 182) captures in her description of one influential !Kung man indicates just this effect.... 'it was said of him that he never returned from a hunt without having killed at least a wildebeest, if not something larger. Hence the people connected with him ate a great deal of meat and his popularity grew'" (Hawkes, et al., 2001a, p. 134). Effort allocated to hunting big animals like effort to other public goods, such as political leadership or community defense trades off with domestic effort. Reputation benefits may help explain such effort fitting it to the showoff, costly signaling framework.

Many, though not all, of our papers give substantial attention to alternative hypotheses—something not done here. We hope interested (or irritated) readers will seek both observations and arguments covered much more fully in the papers cited. Aiming here to explain where our favored hypotheses came from, what questions they address, and where they have taken us, we have not even begun to cover the rich field of hunter-gatherer studies. The hypotheses discussed continue to be productive so far. They have earned standing as possibilities, supplying productive guidance for interrogating many lines of evidence about the variation in the living world to understand both the living variation *and* to guess at how we got here from a different past.

ACKNOWLEDGMENTS

We are grateful for support for this research from the National Science Foundation grant numbers BNS-8121209, BNS-8309834, BNS-8507859, BNS-8807436, and BCS-1534554, the National Institutes of Health grant number 1 RO1 HD16221-01A2, and the Australian Research Council grant number DP160101597. This work has also been supported by the University of California at Los Angeles, the University of Utah, and Bettina Bancroft. Jeanette Hanby and David Bygott provided invaluable support during our Hadza fieldwork.

ORCID

Kristen Hawkes http://orcid.org/0000-0002-0558-4856

WORKS CITED

Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle: University of Washington Press.

Barry, H., Child, I., & Bacon, M. (1959). The relation of child training to subsistence economy. *American Anthropologist*, *61*, 51–63.

Birdsell, J. B. (1968). Some predictions for the Pleistocene based on equilibrium systems among recent hunter-gatherers. In R.B. Lee & I. DeVore (Eds.) *Man the hunter* (pp. 229–240). New York: Aldine.

Binford, L. R. (1977). Olorgesailie deserves more than an ordinary book review. *Journal of Anthropological Research*, *33*, 493–502.

Binford, L. R. (1981). *Bones: Ancient men and modern myths*. Academic Press: New York.

Binford, L. R., & O'Connell, J. F. (1984). An Alyawara day: The stone quarry. *Journal of Anthropological Research*, *40*, 406–432.

Bliege Bird, R. (1999). Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology*, *8*, 65–75.

Blurton Jones, N. G. (1972). *Ethological studies of child behaviour*. London: Cambridge University Press.

Blurton Jones, N. G. (1975). Ethology, anthropology and childhood. In R. Fox (Ed.) *ASA studies – biosocial anthropology* (pp. 69–92). London: Malaby Press.

Blurton Jones, N. G. (1984). A selfish origin for human food sharing: Tolerated theft. *Ethology and Sociobiology*, *5*, 1–3.

Blurton Jones, N. G. (1986). Bushman birth spacing: A direct test for optimal interbirth intervals. *Ethology and Sociobiology*, *7*, 91–105.

Blurton Jones, N. G. (1987). Bushman birth spacing: Direct tests of some simple predictions. *Ethology and Sociobiology*, *8*, 183–203.

Blurton Jones, N. G. (1987). Tolerated theft. Suggestions about the ecology and evolution of sharing, hoarding, and scrounging. *Social Science Information*, *26*, 31–54.

Blurton Jones, N. G. (1989). The costs of children and the adaptive scheduling of births. Towards a sociobiological perspective on demography. In A. Rasa, C. Vogel & E. Voland (Eds.) *Sociobiology of sexual and reproductive strategies* (pp. 265–282). London and New York: Chapman and Hall.

Blurton Jones, N. G. (2016a). *Demography and evolutionary ecology of Hadza hunter-gatherers*. Cambridge: Cambridge University Press.

Blurton Jones, N. G. (2016b). Why do so few Hadza farm? In K.L. Kramer & B.F. Codding (Eds.) *Twenty-first century hunters and gatherers* (pp. 113–136). Santa Fe: SAR Press.

Blurton Jones, N. G., Hawkes, K., & Draper, P. (1994a). Differences between Hadza and !Kung children's work: Affluence or practical reason? In E. S. Burch, Jr., and L. J. Ellanna (Eds.) *Key issues in hunter-gatherer research* (pp. 189–215). Oxford: Berg.

Blurton Jones, N. G., Hawkes, K., & Draper, P. (1994b). Foraging returns of !Kung adults and children: Why didn't !Kung children forage?. *Journal of Anthropological Research*, *50*, 217–248.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (1996). The global process and local ecology: How should we explain differences between the Hadza and the !Kung. In S. Kent (Ed.) *Cultural diversity among twentieth century foragers: An African perspective* (pp. 159–187). Cambridge: Cambridge University Press.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (1997). Why do Hadza children forage? In N.L. Segal, G.E. Weisfeld & C.C. Weisfeld (Eds.) *Genetic, ethological and evolutionary perspectives on human development. Essays in honor of Dr. Daniel G. Freedman* (pp. 279–313). Washington DC: American Psychological Association.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (2002). Antiquity of postreproductive life: Are there modern impacts on hunter-gatherer postreproductive life spans?. *American Journal of Human Biology*, *14*, 184–205.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (2005a). Older Hadza men and women as helpers: Residence data. In B.S. Hewlett & M.E. Lamb (Eds.) *Hunter-gatherer childhoods: Evolutionary, developmental and cultural perspectives* (pp. 214–236). New Brunswick NJ: Aldine Transaction Publishers.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (2005b). Hadza grandmothers as helpers: Residence data. In E. Voland, A. Chasiotis & W. Schiefenhovel (Eds.) *Grandmotherhood: The evolutionary significance of the second half of life* (pp. 160–176). New Brunswick NJ: Rutgers University Press.

Blurton Jones, N. G., & Konner, M. J. (1973). Sex differences in behaviour of London and Bushman children. In R.P. Michael & J.H. Crook (Eds.) *Comparative ecology and behaviour of primates* (pp. 689–750). London: Academic Press.

Blurton Jones, N. G., & Konner, M. J. (1976). !Kung knowledge of animal behavior (or: The proper study of mankind is animals). In R. B. Lee & I. DeVore (Eds.) *Kalahari hunter-gatherers: Studies of the !Kung San and their neighbors* (pp. 326–348). Cambridge: Harvard University Press.

Blurton Jones, N. G., & Marlowe, F. W. (2002). Selection for delayed maturity: Does it take 20 years to learn to hunt and gather?. *Human Nature*, *13*, 199–238.

Blurton Jones, N. G., Marlowe, F. W., Hawkes, K., & O'Connell, J. F. (2000). Hunter-gatherer divorce rates and the paternal provisioning theory of human monogamy. In L. Cronk, N. Chagnon, & W. Irons (Eds.) *Adaptation and human behavior: An anthropological perspective* (pp. 65–84). New York: Aldine de Gruyter.

Blurton Jones, N. G., & Sibly, R. M. (1978). Testing adaptiveness of culturally determined behavior: Do Bushman women maximize their reproductive success by spacing births widely and foraging seldom? In N.G. Blurton Jones & V. Reynolds (Eds.) *Human behavior and adaptation (pp. 135–159). Symposium No. 18 of the Society for the Study of Human Biology*. London: Taylor and Francis.

Blurton Jones, N. G., Smith, L. C., Hawkes, K., O'Connell, J. F., & Kamuzora, C. L. (1992). Demography of the Hadza, an increasing and high density population of savanna foragers. *American Journal of Physical Anthropology*, *89*, 159–181.

Brink, A. S. (1957). The spontaneous fire-controlling reactions of two chimpanzee smoking addicts. *South African Journal of Science*, *53*, 241–247.

Broude, G. J., & S. J. Greene, (1980). Cross-cultural codes on twenty sexual attitudes and practices. In H. Barry III & A. Schlegel (Eds.) *Cross-cultural samples and codes* (pp. 313–333). Pittsburgh: University of Pittsburgh Press.

Carr-Saunders, A. M. (1922). *The population problem: A study in human evolution*. Oxford at the Clarendon Press.

Chan, M. H., Hawkes, K., & Kim, P. S. (2016). Evolution of longevity, age at last birth and sexual conflict with grandmothering. *Journal of Theoretical Biology*, *393*, 145–157.

Chan, M. H., Hawkes, K., & Kim, P. S. (2017). Modelling the evolution of traits in a two-sex population, with an application to grandmothering. *Bulletin of Mathematical Biology*, *79*, 2132–2148.

Charnov, E. L. (1976a). Optimal foraging: Attack strategy of a mantid. *American Naturalist*, *110*, 141–151.

Charnov, E. L. (1976b). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136.

Charnov, E. L. (1982). *The theory of sex allocation*. Princeton: Princeton University Press.

Charnov, E. L. (1991). Evolution of life history variation in female mammals. *Proceedings of the National Academy of Sciences (USA)*, *88*, 1134–1137.

Charnov, E. L. (1993). *Life history invariants: Some explorations of symmetry in evolutionary ecology*. Oxford: Oxford University Press.

Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? *Or* life in the slow lane. *Evolutionary Anthropology*, *1*, 191–194.

Clutton-Brock, T., & Parker, G. (1995). Sexual coercion in animal societies. *Animal Behaviour*, *49*, 1435–1465.

Coale, A. J., & Demeny, P. (1983). *Regional model life tables and stable populations*. 2nd edition, Princeton: Princeton University Press.

Coxworth, J. E., Kim, P. S., McQueen, J. S., & Hawkes, K. (2015). Grandmothering life histories and human pair bonding. *Proceedings of the National Academy of Sciences (USA)*, *112*, 11806–11811.

Daly, M., & Wilson, M. (1987). The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation*, *35*, 91–144.

Daly, M., Wilson, M., & Weghorst, S. (1982). Male sexual jealousy. *Ethology and Sociobiology*, *3*, 11–27.

Davies, N. B. (1991). Mating systems. In J. Krebs & N. Davies (Eds.) *Behavioural ecology: An evolutionary approach*, 3rd edition (pp. 263–94). Oxford: Blackwell Scientific Publications.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology*, 4th Ed. Oxford: Wiley Blackwell.

de Waal, F. B. M. (1982). *Chimpanzee politics*. Baltimore: Johns Hopkins University Press.

Draper, P. (1976). Social and economic constraints on child life among the !Kung. In R.B. Lee & I. DeVore (Eds.) *Kalahari hunter-gatherers* (pp. 199–217). Cambridge: Harvard University Press.

Draper, P., & Cashdan, E. (1988). Technological change and child behavior among the !Kung. *Ethnology*, *27*, 339–365.

Emery Thompson, M., Jones, J. H., Pusey, A. E., Brewer-Marsden, S., Goodall, J., Marsden, D., . . . Wrangham, R. W. (2007). Aging and fertility in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, *17*, 2150–2156.

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Oxford University Press.

Flannery, K. V. (1969). Origins and ecological effects of early domestication in Iran and the Near East. In P.J. Ucko & G.W. Dimbleby (Eds.) *The domestication and exploitation of plants and animals* (pp. 73–100). Chicago: Aldine.

Flinn, M. V. (1988). Mate guarding in a Caribbean village. *Ethology and Sociobiology*, *9*, 1–28.

Fried, M. H. (1967). *The evolution of political society*. New York: Random House.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge Mass: Belknap Press of Harvard University Press.

Goodenough, W. H. (1970). *Description and comparison in cultural anthropology*. Chicago: Aldine.

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517–546.

Grueter, C. C., Chapais, B., & Zinner, D. (2012). Evolution of multilevel social systems in nonhuman primates and humans. *International Journal of Primatology*, *33*, 1002–1037.

Gurven, M. (2004). To give or to give not: An evolutionary ecology of human food transfers. *Behavioral and Brain Sciences*, *27*, 543–583.

Gurven, M., & Hill, K. (2009). Why do men hunt? A re-evaluation of "Man the Hunter" and the sexual division of labor. *Current Anthropology*, *50*, 51–74.

Gurven, M., & Kaplan, H. (2007). Longevity among hunter-gatherers: A cross-cultural examination. *Population and Development Review*, *33*, 321–365.

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, *12*, 12–45.

Hawkes, K. (1987). How much food do foragers need? In M. Harris & E. Ross (Eds.) *Food and evolution: Toward a theory of human food habits* (pp. 341–355). Philadelphia: Temple University Press.

Hawkes, K. (1990). Why do men hunt? Some benefits for risky strategies. In E. Cashdan (Ed.) *Risk and uncertainty in tribal and peasant economies* (pp. 145–166). Boulder: Westview Press.

Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology*, *12*, 29–54.

Hawkes, K. (1992a). Sharing and collective action. In E.A. Smith & B. Winterhalder (Eds.) *Evolutionary ecology and human behavior* (pp. 269–300). New York: Aldine de Gruyter.

Hawkes, K. (1992b). On sharing and work (a comment on Bird-David). *Current Anthropology*, *33*, 404–407.

Hawkes, K. (1993a). Why hunter-gatherers work: An ancient version of the problem of public goods. *Current Anthropology*, *34*, 341–361.

Hawkes, K. (1993b). On why male foragers hunt and share food: Reply to Hill and Kaplan. *Current Anthropology*, *34*, 706–710.

Hawkes, K. (2000). Big game hunting and the evolution of egalitarian societies: Lessons from the Hadza. In M. Diehl (Ed.) *Hierarchies in Action: Cui Bono? Center for Archaeological Investigations, Occasional Paper 27* (pp. 59–83). Carbondale: Southern Illinois University Press.

Hawkes, K. (2001). Is meat the hunter's property? Ownership and explanations of hunting and sharing. In C. Stanford & H. Bunn (Eds.) *Meat-eating and human evolution* (pp. 219–236). Oxford: Oxford University Press.

Hawkes, K. (2004). Mating, parenting and the evolution of human pair bonds. In B. Chapais & C. Berman (Eds.) *Kinship and behavior in primates* (pp. 443–473). Oxford: Oxford University Press.

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, *15*, 380–400.

Hawkes, K. (2006). Slow life histories and human evolution. In K. Hawkes & R. Paine (Eds.) *The evolution of human life history* (pp. 95–126). Santa Fe: School of American Research Press.

Hawkes, K. (2014). Primate sociality to human cooperation, why us and not them?. *Human Nature*, *25*, 28–48.

Hawkes, K. (2016). Ethnoarchaeology and Plio-Pleistocene sites: Some lessons from the Hadza. *Journal of Anthropological Archaeology*, *44*, 158–165.

Hawkes, K., & Bliege Bird, R. (2002). Showing off, handicap signaling and the evolution of men's work. *Evolutionary Anthropology*, *11*, 58–67.

Hawkes, K., Chisholm, J., Fairbanks, L. A., Johow, J., Kalcher-Somersgutter, E., Liebal, K., . . . Finaly, B. L. (2017). Primate infancies: Causes and consequences of varying care. In H. Keller & K. A. Bard (Eds.) *The cultural nature of attachment: Contextualizing relationships and development* (pp. 69–107). Cambridge: MIT Press.

Hawkes, K., & Coxworth, J. E. (2013). Grandmothers and the evolution of human longevity: A review of findings and future directions. *Evolutionary Anthropology*, *22*, 294–302.

Hawkes, K., & Blurton Jones, N. G. (2005). Human age structures, paleodemography, and the grandmother hypothesis. In E. Voland, A. Chasiotis & W. Schiefenhovel (Eds.) *Grandmotherhood: The evolutionary significance* of the second half of life (pp. 118–140). New Brunswick NJ: Rutgers University Press.

Hawkes, K., Hill, K., & O’Connell, J. F. (1982). Why hunters gather: Optimal foraging and the Aché of Eastern Paraguay. *American Ethnologist*, *9*, 379–398.

Hawkes, K., & O’Connell, J. F. (1981). Affluent hunters? Some comments in light of the Alyawara case. *American Anthropologist*, *83*, 622–626.

Hawkes, K., & O’Connell, J. F. (1985). Optimal foraging models and the case of the !Kung. *American Anthropologist*, *87*, 401–405.

Hawkes, K., & O’Connell, J. F. (1992). On optimal foraging models and subsistence transitions. *Current Anthropology*, *33*, 63–66.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (1989). Hardworking Hadza Grandmothers. In V. Standen & R.A. Foley (Eds.) *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 341–366). London: Basil Blackwell.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (1991). Hunting income patterns among the Hadza: Big game, common goods, foraging goals, and the evolution of the human diet. *Philosophical Transactions of the Royal Society*, Section B, *334*, 243–251.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (1995b). Hadza children’s foraging: Juvenile dependency, social arrangements and mobility among hunter-gatherers. *Current Anthropology*, *36*, 688–700.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (1997). Hadza women’s time allocation, offspring provisioning and the evolution of post-menopausal lifespans. *Current Anthropology*, *38*, 551–577.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (2001a). Hadza meat sharing. *Evolution and Human Behavior*, *22*, 113–142.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (2001b). Hunting and nuclear families: Some lessons from the Hadza about men’s work. *Current Anthropology*, *42*, 681–709.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (2003). Human life histories: Primate tradeoffs, grandmothering socioecology, and the fossil record. In P. Kappeler & M. Pereira (Eds.) *Primate life histories and socioecology* (pp. 204–227). Chicago: University of Chicago Press.

Hawkes, K., O’Connell, J. F., & Blurton Jones, N. G. (2014). More lessons from the Hadza about men’s work. *Human Nature*, *25*, 596–619.

Hawkes, K., O’Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences (USA)*, *95*, 1336–1339.

Hawkes, K., O’Connell, J. F., Blurton Jones, N. G., Alvarez, H. P. & Charnov, E. L., (2000). The grandmother hypothesis and human evolution. In L. Cronk, N. Chagnon & W. Irons (Eds.) *Adaptation and human behavior: An anthropological perspective* (pp. 231–252). New York: Aldine de Gruyter.

Hawkes, K., O’Connell, J. F., & Coxworth, J. E. (2010). Family provisioning is not the only reason men hunt. *Current Anthropoogy*, *52*, 259–264.

Hawkes, K., O’Connell, J. F., Hill, K., & Charnov, E. L. (1985). How much is enough? Hunters and limited needs. *Ethology and Sociobiology*, *6*, 3–15.

Hawkes, K., Rogers, A. R., & Charnov, E. L. (1995a). The male’s dilemma: Increased offspring production is more paternity to steal. *Evolutionary Ecology*, *9*, 662–677.

Hawkes, K., & Smith, K. R. (2010). Do women stop early? Similarities in fertility decline between humans and chimpanzees. *Annals of the New York Academy of Science*, *1204*, 43–53.

Herzog, N. M., Keefe, E. R., Parker, C. H., & Hawkes, K. (2015). What’s burning got to do with it? Primate foraging opportunities in fire-modified landscapes. *American Journal of Physical Anthropology*, *159*, 432–441.

Herzog, N. M., Parker, C. H., Keefe, E. R., Coxworth, J. E., Barrett, A., & Hawkes, K. (2014). Fire and home range expansion: A behavioral response to burning among savannah dwelling vervet monkeys (Chlorocebus aethiops). *American Journal Physical Anthropology*, *154*, 554–560.

Hill, K. (1988). Macronutrient modifications of optimal foraging theory: An approach using indifference curves applied to some modern foragers. *Human Ecology*, *16*, 157–197.

Hill, K., & Hawkes, K. (1983). Neotropical hunting among the Aché of Eastern Paraguay. In R. Hames & W. Vickers (Eds.) *Adaptive responses of Native Amazonians* (pp. 139–188). New York: Academic Press.

Hill, K., Hawkes, K., Hurtado, A. M., & Kaplan, H. (1984). Seasonal variance in the diet of Aché hunter-gatherers in Eastern Paraguay. *Human Ecology*, *12*, 145–180.

Hill, K., & Hurtado, A. M. (1996). *Aché life history: The ecology and demography of a foraging people*. New York: Aldine de Gruyter.

Hill, K., Kaplan, H., Hawkes, K., & Hurtado, A. M. (1985). Men’s time allocation to subsistence work among the Aché of Eastern Paraguay. *Human Ecology*, *13*, 29–47.

Hill, K., Kaplan, H., Hawkes, K., & Hurtado, A. M. (1987). Foraging decisions among Aché hunter-gatherers: New data and implications for optimal foraging models. *Ethology and Sociobiology*, *8*, 1–36.

Howell, N. (1979). *Demography of the Dobe !Kung*. New York: Academic.

Howell, N. (1976). Toward a uniformitarian theory of human paleodemography. *Journal of Human Evolution*, *5*, 25–40.

Hrdy, S. B. (1999). *Mother nature: A history of mothers, infants, and natural selection*. New York: Pantheon Books.

Hrdy, S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge: Harvard University Press.

Hurtado, A. M., Hawkes, K., Hill, K., & Kaplan, H. (1985). Female subsistence strategies among the Aché of Eastern Paraguay. *Human Ecology*, *13*, 1–28.

Hurtado, A. M., & Hill, K. (1992) Paternal effect on offspring survivorship among Aché and Hiwi hunter-gatherers: Implications for modeling pair-bond stability. In B. S. Hewlett (Ed.) *Father–child relations: Cultural and biosocial contexts* (pp. 31–55). New York: Aldine de Gruyter.

Isaac, G. L. (1968). Traces of Pleistocene hunters: An East African example. In R.B. Lee & I. DeVore (Eds.) *Man the hunter* (pp. 253–261). New York: Aldine.

Isaac, G. L. (1978). The food sharing behavior of protohuman hominids. *Scientific American*, *238*, 90–108.

Jones, D. (1996). An evolutionary perspective on physical attractiveness. *Evolutionary Anthropology*, *5*, 97–109.

Jones, K. T. (1983) Forager archaeology: The Aché of eastern Paraguay. In G.M. Lemoine, A.S. MacEachern (Eds.) *Carnivores, human scavengers and predators: A question of bone technology* (pp. 171–191). Calgary: Department of Anthropology, University of Calgary.

Jones, K. T. (1993). The archaeological structure of a short term camp. In J. Hudson (Ed.) *From bones to behavior: Ethnoarchaeological and experimental contributions to the interpretation of faunal remains*. Occasional Paper 21 (pp. 101–114). Carbondale: Center for Archaeological Investigations, Southern Illinois University.

Jones, K. T. (2012). *The shrinking jungle*. Salt Lake City: University of Utah Press.

Kaplan, H., Hill, K., Hawkes, K., & Hurtado, A. M. (1984). Food sharing among Aché hunter-gatherers of Eastern Paraguay. *Current Anthropology*, *25*, 113–115.

Kaplan, H., & Hill, K. (1985). Aché food sharing: Tests of some explanatory hypotheses. *Current Anthropology*, *26*, 223–245.

Kaplan, H., Hill, K., & Hurtado, A. M. (1990). Risk, foraging, and food sharing among the Aché. In E. Cashdan (Ed.) *Risk and uncertainty in tribal and peasant economies* (pp. 107–143). Boulder: Westview Press.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185.

Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, *21*, 919–948.

Kim, P. S., Coxworth, J. E., & Hawkes, K. (2012). Increased longevity evolves from grandmothering. *Proceedings of the Royal Society B*, *279*, 4880–4884.

Kim, P. S., McQueen, J. S., Coxworth, J. E., & Hawkes, K. (2014). Grandmothering drives the evolution of longevity in a probabilistic model. *Journal of Theoretical Biology*, *353*, 84–94.

Lack, D. (1954). *The natural regulation of animal numbers*. Oxford: Oxford University Press.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.

Lancaster, J., & King, B. (1985). An evolutionary perspective on menopause. In J. Brown & V. Kerns (Eds.) *In her primer: A new view of middle-aged women* (pp. 13–20). South Hadley, MA: Bergen and Garvey.

Lee, R. B. (1968). What hunters do for a living, or, how to make out on scarce resources. In R.B. Lee & I. DeVore (Eds.) *Man the hunter* (pp. 30–48). New York: Aldine.

Lee, R. B. (1969). Eating Christmas in the Kalahari. *Natural History*, *1969*, 60–64.

Lee, R. B. (1972). Population growth and the beginnings of sedentary life among the !Kung Bushmen. In B. Spooner (Ed.) *Population growth: Anthropological implications* (pp. 329–342). Cambridge MA: MIT Press.

Lee, R. B. (1979). *The !Kung San: Men, women, and work in a foraging society*. Cambridge: Cambridge University Press.

Lee, R.B., & DeVore, I., Eds. (1968). *Man the hunter*. New York: Aldine.

Loo, S. L., Chan, M. H., Hawkes, K., & Kim, P. S. (2017). Further mathematical modelling of mating sex ratios and male strategies with special relevance to human life history. *Bulletin of Mathmatical Biology*, *79*, 1907–1922.

Loo, S. L., Hawkes, K., & Kim, P. S. (2017). Evolution of male strategies with sex-ratio dependent payoffs: Connecting pair bonds with grandmothering. *Philosophical Transactions of the Royal Society B*, *372*, 20170041.

Lupo, K. D. (1993). A taphonomic analysis of Hadza-produced bone assemblages. Ph.D. dissertation, University of Utah, Salt Lake City.

MacArthur, R. H. (1972). *Geographical ecology: Patterns in the distributions of species*. New York: Harper and Row.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*, 603–609.

Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Berkeley: University of California Press.

Morin, P. A. (1993). Reproductive strategies in chimpanzees. *Yearbook of Physical Anthropology*, *361*,79–212.

Muller, M. N., Emery Thompson, M., & Wrangham, R. W. (2006). Male chimpanzees prefer mating with old females. *Current Biology*, *16*, 2234–2238.

Murdock, G. P. (1949). *Social structure*. New York: Macmillan.

O'Connell, J. F. (1987). Alyawara site structure and its archaeological implications. *American Antiquity*, *57*, 74–108.

O'Connell, J. F. (1995). Ethnoarchaeology needs a general theory of behavior. *Journal of Archaeological Research*, *3*, 205–255.

O'Connell, J. F. (2011). Remembering Lew Binford. *Mitteilungen der Gesellschaft für Urgeschichte*, *20*, 79–89.

O'Connell, J. F., & Hawkes, K. (1981). Alyawara plant use and optimal foraging theory. In B. Winterhalder & E.A. Smith (Eds.) *Hunter-gatherer foraging strategies: Ethnographic and archaeological analysis* (pp. 99–125). Chicago: University of Chicago Press.

O'Connell, J. F., & Hawkes, K. (1984). Food choice and foraging sites among the Alyawara. *Journal of Anthropological Research*, *40*, 504–535.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1988a). Hadza hunting, butchering, and bone transport and their archaeological implications. *Journal of Anthropological Research*, *44*, 113–161.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1988b). Hadza scavenging: Implications for Plio-Pleistocene hominid subsistence. *Current Anthropology*, *29*, 356–363.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1990). Reanalysis of large mammal body part transport among the Hadza. *Journal of Archaeological Science*, *17*, 301–316.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1992). Patterns in the distribution, site structure and assemblage composition of Hadza kill-butchering sites. *Journal of Archaeological Science*, *19*, 319–345.

O'Connell, J. F., Hawkes, K., & Blurton Jones, N. G. (1999). Grandmothering and the evolution of *Homo erectus*. *Journal of Human Evolution*, *36*, 461–485.

O'Connell, J. F., Hawkes, K., Lupo, K. D., & Blurton Jones, N. G. (2002). Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution*, *43*, 831–872.

Olson, M. (1965). *The logic of collective action: public good and the theory of groups*. Cambridge, Harvard University Press.

Parker, C. H., Keefe, E. R., Herzog, N. M., O'Connell, J. F., & Hawkes, K. (2016). The pyrophilic primate hypothesis. *Evolutionary Anthropology*, *25*, 54–63.

Parker, G. A. (1974). Courtship persistence and female-guarding as male time investment strategies. *Behaviour*, *48*, 157–184.

Parker, G. A. (2006). Behavioural ecology: Natural history as science. In L.W. Simmons & J. Lucas (Eds.) *Essays in animal behavior* (pp. 23–56). San Diego: Elsevier Academic.

Promislow, D. E. L., & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life history variation among mammals. *Journal of Zoology (London)*, *220*, 417–437.

Pruetz, J. D., & Herzog, N. M. (2017). Savanna chimpanzees at Fongoli, Senegal, navigate a fire landscape. *Current Anthropology*, *58*, Supplement 16, S337–S350.

Pruetz, J. D., & LaDuke, T. (2010). Brief communication: Reaction to fire by savanna chimpanzees (Pan troglodytes verus) at Fongoli, Senegal: Conceptualization of "fire behavior" and the case for a chimpanzee model. *American Journal of Physical Anthropology*, *141*, 646–650.

Robson, S. L., van Schaik, C. P., & Hawkes, K. (2006). The derived features of human life history. In K. Hawkes & R. Paine (Eds.) *The evolution of human life history* (pp. 17–44). Santa Fe: School of American Research Press.

Rodseth, L. (2013). From bachelor threat to fraternal security: Male associations and modular organization in human societies. *International Journal of Primatology*, *33*, 1194–1214.

Sahlins, M. D. (1965). On the sociology of primitive exchange. In M. Banton (Ed.) *The relevance of models for social anthropology* (pp. 139–236*). ASA Monographs 1*. London: Tavistock.

Sahlins, M. D. (1972). *Stone age economics*. Chicago: Aldine

Samuelson, P. A. (1954). The pure theory of public expenditure. *Review of Economics and Statistics*, *36*, 387–389.

Schacht, R., & Bell, A. V. (2016). The evolution of monogamy in response to partner scarcity. *Scientific Reports*, *6*, 32472.

Smith, B. H., & Tompkins, R. L. (1995). Toward A Life History of the Hominidae. *Annual Review of Anthropology*, *24*, 257–279.

Smuts, B. B., & Smuts, R. T. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior*, *22*, 1–63.

Speth, J. D. (2010). *The paleoanthropology and archaeology of big-game hunting: Protein, fat or politics*? New York: Springer.

Stanford, C. B. (1999). *The hunting apes*. Princeton: Princeton University Press.

Thomas, E. M. (1959). *The harmless people*. New York: Knopf.

Tinbergen, N. (1965). Behavior and natural selection. In J. A. Moore (Ed.) *Ideas in modern biology Proceedings Volume 6 XVI International Congress of Zoology* (pp. 519–542). Garden City NY: Natural History Press.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35–57.

Trivers, R. L. (2002). *Natural selection and social theory: Selected papers of Robert Trivers*. Oxford: Oxford University Press.

Vincent, A. S. (1985). Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of Northern Tanzania. *World Archaeology*, *17*, 131–148.

Washburn, S. L., & Lancaster, C. S. (1968). The evolution of hunting. In R. B. Lee & I. DeVore (Eds.) *Man the hunter* (pp. 293–303). Chicago: Aldine Publishing company.

West, S. A., El Mouden, C., & Gardner, A. (2011). Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior*, *32*, 231–262.

Weiss, K. (1981). Evolutionary perspectives on human aging. In P.T. Amoss & S. Harrell (Eds.) *Other ways of growing old: Anthropological perspectives* (pp. 25–58). Stanford: Stanford University Press.

Wiessner, P., Schiefenhovel, W., Eds. (1996). *Food and the status quest: An interdisciplinary perspective*. Providence: Berghan Books.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current biological thought*. Princeton: Princeton University Press.

Williams, G. C. (1957). Pleiotropy, natural selection, and evolution of senescence. *Evolution*, *11*(4), 398–411.

Wilson, M., & Daly, M. (1992). The man who mistook his wife for a chattel. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.) *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 289–322). New York: Oxford University Press.

Winterhalder, B. (1996). Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology*, *5*, 46–57.

Wood, B. M., & Marlowe, F. W. (2013). Household and kin provisioning by Hadza men. *Human Nature*, *24*, 280–317.

Woodburn, J. C. (1968a). An introduction to Hadza ecology. In R.B. Lee & I. DeVore (Eds.) *Man the Hunter* (pp. 49–33). Chicago, Aldine.

Woodburn, J. C. (1968b). Stability and flexibility in Hadza residential groupings. In R.B. Lee & I. DeVore (Eds.) *Man the Hunter* (pp. 103–110). Chicago, Aldine.

Woodburn, J. (1998). Sharing is not a form of exchange: An analysis of property sharing in immediate return hunter-gatherer societies. In C.M. Hann (Ed.) *Property relations: Renewing the anthropological tradition* (pp. 48–63). Cambridge: Cambridge University Press.

Wrangham, R. W. (2007). The cooking enigma. In P.S. Ungar (Ed.) *Evolution of the human diet: The known, the unknown, and the unknowable* (pp. 308–323). Oxford: Oxford University Press.

Wrangham, R. W. (2009). *Catching fire: How cooking made us human*. New York: Basic Books.

Wrangham, R. W., & Carmody, R. (2010). Human adaptation to the control of fire. *Evolutionary Anthropology*, *19*, 187–199.

Wrangham, R. W., & Conklin-Brittain, N. (2003). Cooking as a biological trait. *Comparative Biochemistry and Physiology*, *Part A*, *136*, 35–46.

Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. (1999). The raw and the stolen: Cooking and the ecology of human origins. *Current Anthropology*, *40*, 567–594.

Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behaviour*. Edinburgh and London, Oliver and Boyd.

Wynne-Edwards, V. C. (1965). Self-regulating systems in populations of animals. *Science*, *147*, 1543–1548.

Yellen, J. E., & Lee, R. B. (1976). The Dobe-/Du/da environment: Background to a hunting and gathering way of life. In R. B. Lee & I. DeVore (Eds.) *Kalahari hunter-gatherers* (pp. 28–46). Cambridge: Harvard University Press.

Zahavi, A. (1975). Mate selection: Selection for a handicap. *Journal of Theoretical Biology*, *53*, 205–214.

Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, *67*, 603–605.

Zahavi, A. (1995). Altruism as a handicap-the limitations of kin selection and reciprocity. *Avian Biology*, *26*, 1–3.

How to cite this article: Hawkes K, O'Connell J, Blurton Jones N. Hunter-gatherer studies and human evolution: A very selective review. *Am J Phys Anthropol*. 2017;00:1–24. https://doi.org/10.1002/ajpa.23403