

What Moves Us? How Mobility and Movement Are at the Center of Human Evolution

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Movement is central to the survival of all free-living organisms. Consequently, movement and what anthropologists often refer to as mobility, which is the sum of small-scale movements tracked across larger geographic and temporal scales, are key targets of selection. Movement and mobility also underpin many of the key features that make us human and that allowed our lineage to adapt to changing environments across the globe. The most obvious example is the evolution of humans' singular mode of locomotion. Bipedalism is arguably the most important derived anatomical trait of the hominin lineage. The mechanisms and circumstances that gave rise to this novel mode of movement remain subjects of intense research.

You got to move
 You got to move
 You may be high, you may be low
 You may be rich, child, you may be poor
 But when the Lord gets ready,
 you got to move
 (traditional)

Hominins are also unique among primates with respect to their extensive geographic distribution, which, in turn, has had important consequences for global trajectories of cultural and biological evolution. The multiple dispersals of early *Homo* beg a range of questions about the abilities of homi-

nins to cover ground and find their ways around unfamiliar habitats. Many explanations for the dispersal of *H. sapiens*, as well as our species' interactions with other indigenous hominin taxa, highlight social networks and cultural transmission, two phenomena that emerge partially, if not wholly, from the movements of groups and individuals.

We also point to the long-recognized fact that hominins are uniquely omnivorous primates. Flexibility in hominin diet was crucial to global expansion, while the addition of nutrient-dense foods to diets is widely considered to be necessary for encephalization. Variation

in diet directly implicates movement: Shifts in trophic levels among humans and other mammals are invariably accompanied by changes in the scale and patterns of mobility associated with foraging and resource transport.^{1,2}

While many of us think about movement and mobility, we often conceive of these phenomena in very different ways. These differences are expressed in the divergent scales over which movement can be observed and conceptualized, which range from the neuromuscular and cognitive scaffolds of somatic movement to the dispersal of populations across continents. These differences also appear in thinking about individual versus group patterns of movement and the evidence they leave behind. To a certain extent, the different subfields that contribute to research on human evolution focus on movement at different scales. Skeletal biologists examine mobility in terms of biomechanics, though they are mindful of the larger-scale phenomena such as predator avoidance and foraging, which served as the contexts for selection on the skeleton. Archeologists typically study aggregate, time-transgressive records of behavior at the scale of sites or landscapes. Perspectives from genetics take the scale up one more level, examining population dynamics at a continental or subcontinental scale.

The aim of this special issue and the 2014 symposium that preceded it, is to help tie together some of the disparate fields, methods, and modes of inquiry into a more unified approach to understanding both the evolution and the evolutionary consequences of hominin movement. In this introductory section we adopt the "movement ecology paradigm"

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Key words: mobility; movement ecology; foraging; locomotion; territory

developed by Nathan et al.³ in an attempt to unify some of the disparate perspectives on movement within paleoanthropology as well as to establish a context for the contributions that follow in this issue. Studies of movement ecology seek to bring together an understanding of biomechanics and physiology with larger scale phenomena (search strategy, navigation, and migration) to fully understand how selection acting on mobility influences a particular species or lineage. While the framework proposed by Nathan and colleagues³ does not capture the full complexity of the causes and consequences of human movement, it is a good place to start. Viewing human movement and mobility within this framework can help us to identify the questions we are not currently asking, questions that will help us understand the selective forces that ultimately shaped the evolution of human movement and the ways that this, in turn, affected the long-term evolutionary trajectory of the human lineage. In addition, the movement ecology framework brings a novel perspective on long-standing debates and, in the case of paleoanthropology, may help us resolve questions that remain unanswered after years of careful comparative morphological analyses.

MOVEMENT ECOLOGY FRAMEWORK

According to Nathan et al.,³ movement is driven primarily by four interrelated phenomena. By understanding each of these and the links between them, researchers can more fully describe the evolutionary forces that shaped movement in a particular lineage. First, an internal state motivates creatures to move. This state can be reward-based, decision-based, or a combination of the two. Second, motion capacity, the biomechanical constraints on the movement of an organism, influences how it moves. The third component is the navigation capacity of individuals. This component, which encompasses the diverse cognitive challenges of movement, determines where an animal will move. Finally, there are external factors that both influence

motivation and channel actual movement patterns. These external factors include topography, distributions of resources within a habitat, interactions with conspecifics, and predator distributions.

The relationships among these four factors ultimately determine the movement of an individual on the landscape.³ If we make the reasonable assumption that movement on a landscape underlies many fitness-enhancing behaviors, such as foraging, predator avoidance, finding mates, and locating new territories, then the selection pressures that shape these factors and the relationships among them are important components in determining the evolutionary path of a species. Here we consider each of these factors in detail and briefly review the current

movement and mobility play key roles in descriptions of the evolution and dispersal of genus *Homo*.

state of knowledge in what might be called hominin movement ecology. It is our hope that this review will not only stimulate thinking about what information is lacking in our understanding of the evolution of human movement, but clarify the kinds of future work that could fill these gaps. As we will describe in more detail, the study of human movement at a variety of scales has raised fundamental questions within paleoanthropology. These questions become more vexing as new fossils are continually discovered⁴⁻⁷ and dates for initial colonization of different habitats are reevaluated.⁸⁻¹² We suggest that, as a complement to more traditional analyses of comparative anatomy, the incorporation of novel elements of the movement ecology framework can be crucial in resolving some of these key debates.

We focus our discussion of movement ecology on the genus *Homo*.

The main reason for this focus, aside from the nature of the articles in this issue, is that it allows us to bring multiple lines of evidence to bear on changes in movement and mobility over the last ~1.8 million years that do not exist for earlier hominins. These lines of evidence include, for example, archeological data, habitat differences, and geographic ranges. As we will discuss, movement and mobility play key roles in descriptions of the evolution and dispersal of genus *Homo*. However, there is considerable debate over what changed in this lineage, and when. By exploring all elements of the movement ecology framework for the genus *Homo*, we hope to identify areas of research that may prove particularly fruitful in resolving these debates. We suggest that this case study provides a blueprint for the exploration of movement ecology in other members of the human lineage (for example, early hominins) and may prove useful for studying selection pressures acting on mobility in extant humans and nonhuman primates.

MOTION CAPACITY (HOW TO MOVE)

Motion capacity refers to the biomechanical capabilities and constraints that determine how an animal moves on the landscape.³ This area of the movement ecology framework has received the most attention within biological anthropology. A complete review of hominin locomotor evolution is beyond the scope of our discussion here. Instead, we focus our discussion on the longstanding view in paleoanthropology that changes in movement capacity underlie or accompany the origins and evolution of the genus *Homo*.

Many researchers have suggested that by 1.8 Ma our ancestors had shifted toward habitual movement patterns such as long-distance trekking and endurance running, which required greater endurance and possibly higher speeds.¹³⁻¹⁶ This shift is often viewed in the context of a changing landscape and diet that led to selection for increased travel distance associated with new strategies of hunting and foraging.¹³⁻¹⁶ In

support of these claims, authors have suggested that changes in body size, limb length, and other key morphological parameters, such as increased semi-circular canal radii and long spring-like tendons in the distal hindlimbs, are adaptations to long-distance travel and, possibly, endurance running.^{13,14,17} Many of these features are shared with other mammals that incorporate long-distance endurance activities into their mobility patterns, suggesting convergent evolution in the genus *Homo* for some degree of cursoriality.^{13,14}

These changes in locomotor behavior imply a shift in constraints on performance, likely tied to environmental and habitat transitions that allowed hominins to exploit novel resources such as hunting or scavenging for meat.¹⁵ However, while this major locomotor shift has some support, new work has presented contrary evidence that requires reevaluation of locomotor differences between *Homo* and earlier hominins.^{18–20} For example, new fossil finds of australopiths suggest that there may not have been such a great shift in body size or limb length between the two hominin grades.²⁰ Reanalysis of material from *H. erectus* suggests that features of its upper body morphology may not be well-suited for distance running.^{18,19} Fossil specimens of early *Homo* and early *H. erectus* also show a great deal of variation in size and structure, notably the small body size of Dmanisi *H. erectus* and a relatively wide pelvis in the Gona hominin, which its finders attribute to *H. erectus* (but see Ruff²² for an alternate view of the Gona pelvis).^{5,21} Thus, conflicting analyses leave open the possibility that evolutionary changes in locomotor capabilities during the evolution of the genus *Homo* may not have been unique to our genus, and may not be the main selection pressures that shaped our lineage.

We believe the ambiguity of morphological analysis requires clarification from outside of the specific study of locomotor biomechanics. Decades of productive comparative morphological studies have not completely resolved our understanding of evolutionary patterns of human move-

ment.²⁰ As new fossils are discovered and old fossils are reanalyzed, our understanding of the complexity of movement patterns in contemporaneous species is bound to increase. The incorporation of other elements of the movement ecology framework may help us better understand these changes in locomotion during human evolution. These other elements present their own challenges in understanding the movement ecology of fossil taxa, yet we hope that identifying areas with converging lines of evidence can help resolve debates over the evolutionary pattern of human locomotor variation.

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MOVEMENT PATH

The motion capacity of an organism allows physical movement across space. Movement path, which refers to the pattern of movement on the landscape, is the physical manifestation of the motion capacity of an organism and its navigation capacity. Because movement path describes a series of actual events rather than a capacity, it provides a link between biomechanics (what an organism can do) and archeological or contemporary data (what it did or does do). A greater understanding of movement paths in the present could help us

better incorporate the remnants of these paths (for example, archeological data) into reconstructions of past hominin mobility and thus inform the debate over changes in movement patterns during evolution of the genus *Homo*. For example, interpreting the distributions of artifacts on ancient landscapes through the filter of aggregate movement patterns will provide better estimates of the sizes of home ranges and foraging territories. In this way, the mapping of paths as a part of the movement ecology framework can help to fill in gaps in understanding that biometric studies have failed to resolve.

Paths of movement are often broken down into steps, which are defined by movements between two points followed by some change (either a pause or change in movement direction). The study of movement paths has focused mainly on the strategy for linking move steps on the landscape in a way that supports particular goals, such as foraging or migration. Recent research, underwritten by technological developments that allow researchers to more easily track the locations of individuals in real time, investigates general patterns in the movements of individuals: this is what Nathan et al.³ termed the “Lagrangian” perspective on mobility. Newly acquired data on the distributions of path segment lengths in the routes individuals take reveal surprising commonalities across species. For example, so-called Levy walks or flights, in which path-segment lengths are distributed according to a particular subclass of power-law functions,^{23,24} seem to occur in a wide range of species and situations. Humans,^{25–29} some non-human primates,^{30,31} and a wide range of other organisms (see Viswanathan et al.²⁴ for review) sometimes, but not always, exhibit Levy-walk-like behavior. Viswanathan et al.³² proposed that Levy flights are optimal search strategies when foraging, with little prior information, for resources in patchy environments. These observations beg the question of whether documented patterns of movement are direct outgrowths in various organisms of an evolved capacity to switch among alternative search

patterns or whether they emerge spontaneously from the execution of simpler, more flexible search patterns in particular sorts of environments. Regardless of how these patterns arise, analyzing movement paths in this way provides a new avenue for predicting movement patterns in the past.

Even though individuals may be invisible to archeologists under most circumstances, their habits and tendencies are still implicit in the data, and their movement paths can leave a record on the landscape. The displacements of artifacts and lithic raw materials are the most direct evidence we have of the habitual movements of hominins across ancient landscapes from the Oldowan to the Upper Paleolithic.^{33–37} Before the development of bulk exchange of commodities and vehicular transport, the movement of artifacts tracked the movement of individuals quite closely. Thus, the ways hominins typically moved around played a central role in structuring how artifacts were shifted across landscapes and where they were disposed. Displacements of artifacts in the modern world sometimes follow Levy-like patterns.²⁵ Moreover, modeling work shows how the summed movement tendencies of individuals can influence the aggregate patterns of artifact displacement that archeologists typically study.³⁸ Given temporal and practical constraints on field research, general propositions about relationships between the movement paths of individuals and the bulk displacements of artifacts and raw materials across ancient landscapes, as well as quantitative predictions, will come mainly from agent-based models. However, the predictions these models generate can certainly be tested archeologically.

While work on movement paths of living humans is in early stages, it is important to note that these paths determine much about how individuals and groups exploit their habitats. In addition, these patterns of movement influence interactions between groups or populations, and may even play a role in patterns of human migration²⁴ or intergroup cultural transmission.³⁹ Evidence from the archeological record may help us

understand how and when different movement strategies emerged during human evolution and predict how these strategies would have influenced large-scale mobility and cultural contacts. Combined with evidence from the systematic sourcing of raw materials used for making stone tools, modeling work may be able to tell us more about distance traveled on shorter time scales, helping us better understand changes in mobility when morphology is ambiguous.

Navigation capacity is a function of cognition, which provides an intriguing avenue for exploration of the evolution of human movement. If we begin with the premise that travel over long distances and/or in certain kinds of terrain places greater or lesser demands on navigation abilities, then we may explore the parts of the brain that are most closely tied to navigation ability in living taxa.

Explorations of movement paths offer a particularly important window into how hominin groups interacted with both their landscapes and other organisms. A key goal of future work should be to understand how much of search is truly random in human hunter-foragers, and how random search, resource distributions, and goal-oriented movements combine to determine changes in an individual's location across time. Linking these analyses with archeo-

logical data and agent-based models will give researchers the best possible chance of reconstructing movements and mobility patterns in human ancestors. Indeed, given a size constraint on distances traveled, certain movement patterns and paths may only arise if individuals are capable of making long-range movements within a relatively short time frame. A greater understanding of movement paths in the past may allow us to better understand the kinds of distances and speeds used throughout the evolution of *Homo*, and therefore provide novel data to the debates over mobility patterns and their evolutionary consequences.

NAVIGATION CAPACITY

A key element determining movement paths, especially those that take individuals into new areas or habitats, derives from the ways individuals determine where to move on their landscape. Navigation capacity is a function of cognition, which provides an intriguing avenue for exploration of the evolution of human movement. If we begin with the premise that travel over long distances and/or in certain kinds of terrain places greater or lesser demands on navigation abilities, then we may explore the parts of the brain that are most closely tied to navigation ability in living taxa. Presumably, a shift toward longer-distance travel, as hypothesized for the genus *Homo*, may have required a change in navigation capabilities.

In animal models, the hippocampus is often described as a key structural element of the brain that relates to spatial navigation performance because it is tied to learning and memory formation,^{40,41} both of which are essential for successful spatial navigation.⁴² In rodent studies, the size of the hippocampus predicts performance on spatial tasks, including maze performance.⁴⁰ In birds, the size of the hippocampus is correlated with migration experience,⁴³ as well as spatial memory and learning.^{44,45} In a broad sample of 46 primate species, Shultz and Dunbar⁴⁶ showed that hippocampus volume is strongly correlated with

performance on a series of cognitive tasks that emphasize learning. Finally, studies of living humans identified the hippocampus as a key element in the ability to navigate a complex environment. For example, London taxi drivers are known for their intricate spatial navigation abilities, honed by several years of structured training and requiring passage of rigorous examinations before licensing. In a classic study, Maguire et al.⁴¹ showed that the posterior hippocampus is significantly larger in taxi drivers than in control subjects. In a later study, they showed that in taxi drivers the posterior hippocampus is larger than in London bus drivers, who must deal with similar driving experiences but on defined routes.⁴⁷

There is evidence that hippocampal size has changed during human evolution, hinting at a shift in spatial memory and navigation capacity sometime after the split between the chimpanzee and hominin lineages. In a comprehensive comparison of subcortical brain structure in humans compared to that in other primates, Barger and colleagues⁴⁸ found that the human hippocampus, relative to hemispheric volume, is ~50% larger than would be predicted for an ape. Their results suggest an evolutionary shift in the size of this key navigational structure at some time after the split between chimpanzees and humans.⁴⁸ However, it is important to note that the hippocampus is involved in many other processes. Consequently, there is no way to fully test the hypothesis that the evolutionary change in the hippocampus was directly related to navigational capacity. Moreover, the relative size of brain structures may not be the key variable that determines cognitive performance.^{46,49} Recent work suggests that the absolute size of structures, which is a proxy for the total number of neurons, determines performance on key cognitive tasks.^{46,49}

Conroy and Smith⁵⁰ estimated the size of brain structures in hominin species based on scaling relationships across a wide range of primates and showed, as expected, that structures including the hippocampus increase in size across human

evolution. Seen in this way, the increased size of the hippocampus through time in human evolution may have relaxed some constraints on spatial memory needed to forage across larger ranges in more open habitats. The expanded brains of *H. erectus* would have likely had navigation capacities similar in many ways to living humans.

Assessing the size of the hippocampus more directly across human evolution is nearly impossible. However, the hippocampus is a part of the temporal lobe. The basic shape

Initiation of movements and larger-scale mobility have both proximate (motivational) and ultimate (evolutionary) mechanisms and goals. For example, predator evasion will have a proximate mechanism (activation of the flight or fight response, cortisol response, adrenaline response) and an ultimate goal (survival).

of this area of the brain is preserved in hominin endocasts. Studies of endocasts have identified the temporal lobe as a key brain element that has increased in size during human evolution in ways not predicted by body mass scaling alone.⁵¹ Of course the hippocampus, as a subcortical structure, may have little or no effect on expression of the temporal lobe in endocasts. However, exploring associations between the size of the hippocampus and the surface morphology of the temporal lobe may provide insights into the evolution of spatial navigation abilities during hominin evolution.

We suggest that a more focused agenda for research into spatial navigation and spatial memory may provide a novel avenue into understanding cognitive adaptations for changes in movement patterns during human evolution. In particular, the shift toward longer-distance travel may have required a change in performance in this cognitive domain and would help resolve debates over locomotion and movement patterns in early *Homo*. As for the archeological evidence, ranges of resources returned to base camps provide a first approximation of the kinds of different habitats exploited by hominins. Evidence from displacements of lithic raw materials furnish direct evidence of scales of habitual movement and could provide unique evidence of spatial memory in cases where individuals accessed the same raw materials from multiple routes. Archeological evidence of foraging in different types of habitats or resource patches would provide some control over where individuals did or did not go.⁵² A more detailed focus on the evolution of spatial cognition would complement analyses of skeletal anatomy and movement paths to help us understand whether changes in the brain supported longer-distance travel and mobility at particular times in hominin evolution.

INTERNAL STATE (WHY MOVE)

While our discussion so far has focused on how we move and where we move, a key element of investigating movement is understanding why we move. The internal state helps determine why organisms do and do not change locations in the first place. This is a complex area of research and must be viewed as a multi-layered phenomenon. Initiation of movements and larger-scale mobility have both proximate (motivational) and ultimate (evolutionary) mechanisms and goals. For example, predator evasion will have a proximate mechanism (activation of the flight or fight response, cortisol response, adrenaline response) and an ultimate goal (survival). Likewise, when a human initiates movement

to find food, this move was likely motivated by a combination of hunger (brought about by hormonal interactions), higher-level cognition (planning, decision-making, cost-benefit analyses), and social interactions (food needs of mates, prospective mates, or offspring). Viewed through this lens, the internal state is a fertile ground for linking physiology, neurobiology, and sociality to determine key mobility drivers during periods of hominin evolution.

Researchers have investigated the internal motivators of both spontaneous physical activity (SPA) and purposeful activity in animal models and in humans, mainly within the realm of obesity research.^{53,54} This area of work focuses on proximate causes of movement, including a sequence of interconnected neuropeptides, as well as reward-based neurotransmitter systems such as dopamine, opioids, or endocannabinoids.^{53–57} These proximate mechanisms likely form the foundation for individual decisions about when, where, and how far to move. Therefore, selection may act strongly on these physiological systems when overall movement and mobility are changing. While understanding the internal state as it relates to the evolution of hominin movement is a challenge, it is possible to explore these proximate mechanisms using comparative studies of exercise physiology and neurobiology.

A full account of the neuroregulation of SPA is beyond the scope of this review, but several neuropeptides have been implicated in the initiation of SPA.⁵⁴ Currently, researchers believe that SPA is regulated by a suite of neuropeptide systems, including cholecystokinin, corticotropin-releasing hormone, neuromedin U, neuropeptide Y, leptin, agouti-related protein, orexins, and ghrelin (see Garland et al.⁵³ and Teske et al.⁵⁴ for more complete discussions). These peptides modulate neuronal communication in brain areas that are important for movement, motivation, and reward, including the mesencephalic locomotor region, locus coeruleus, ventral tegmental area, substantia nigra, nucleus accumbens, and striatum⁵⁴). Interestingly, these neuropep-

tides are also heavily involved in feeding behaviors,⁵³ suggesting a role for dietary needs in inducing SPA. This kind of internal-state mechanism is logical, since a driving factor in movement is acquiring food energy.⁵⁸ It is possible that comparative studies of these neuropeptides and movement patterns may help us understand whether these internal drivers of SPA shifted during human evolution. For example, rats from lines considered to be resistant to obesity are more sensitive than others to orexin-A and thus have increased SPA.^{53,54} Evolutionary changes that act on variation in the effects of neuropeptides on movement could have played a role in the hypothesized increase in physical activity during the evolution of *Homo*.

Diet composition can influence SPA in ways that may help us interpret the effects of dietary transitions on movement ecology in hominin evolution. For example, the Western diet, with an emphasis on high-fat foods, reduces SPA in most rodent models.⁵³ However, in a group of rodents bred to run long distances voluntarily (high-runner or HR mice; see Wallace and Garland⁵⁹) a high-fat diet actually leads to increased voluntary locomotion.⁶⁰ These HR mice have often been described as a model for the evolution of high levels of physical activity in humans.^{53,61} Thus, it is possible that neurobiological changes associated with the evolution of high physical activity may lead to increased voluntary locomotion in the presence of a high-fat diet. Although we are not aware of similar studies in humans, these results provide a strong basis for exploring the relationship between diet and SPA in human athletes.

In addition to neuropeptides, researchers have explored the role of neurobiological reward systems (for example, dopamine, endorphins, and endocannabinoids) in human and nonhuman mammalian movement.^{53,55,56,62} Of note, experiments on HR mice suggest that rewards associated with increased voluntary locomotion can evolve.^{62,63} For example, Keeney et al.⁶² discovered that in HR mice, as compared to controls, a selective cannabinoid receptor antagonist (Rimonabant) differentially

decreases wheel-running behaviors, suggesting a role for endocannabinoid signaling in the evolution of voluntary wheel-running in these mice.

Similarly, aspects of the dopamine signaling system are altered in selected mice compared to controls.⁶³ This line of research spurred a comparative analysis of endocannabinoid signaling in humans, dogs, and ferrets, which showed that peripheral levels of a key endocannabinoid, anandamide, do not increase in response to exercise in all mammals.⁵⁶ In this narrow taxonomic sample, only humans and dogs experienced an increase in this reward-inducing compound.⁵⁶ These results suggested that there may be some convergence in rewards induced by physical activity and that humans appear more like dogs than the more sedentary ferrets. Using comparative methods like this, we can begin to tease apart exactly how selection may have acted on reward systems during our evolutionary history and determine what proximate mechanisms were targeted.

On a broader scale, researchers have explored possible genetic aspects of personality type that may fit within the internal state element of the movement ecology paradigm. Chen et al.⁶⁴ found that patterns of polymorphisms in the dopamine receptor D4 (DRD4) gene correlate with migratory distance from the presumed African origin of *Homo sapiens*. Specifically, variants in this gene correlate with high novelty-seeking personality traits (7R variant) and low novelty-seeking personality traits (4R variant). Chen et al.⁶⁴ suggested that higher numbers of individuals with the 7R allele in populations farther from Africa indicate that novelty-seeking will be preferentially found in individuals with a propensity to explore new areas and possibly to migrate. This intriguing suggestion has received some criticism,⁶⁵ but has also received support from a later analysis by Mathews and Butler,⁶⁶ who showed that increased frequency of novelty-seeking alleles (7R and 2R) is associated with population histories of migration, and that genetic drift cannot explain these results. Although

this association between genetics, behavior, and outcome is likely simplistic, and the causes of migration events are surely a more complex interaction of cognition and personality, studies like these, which provide comparative evidence of internal movement motivation, hold a promise with regard to understanding the evolution of human mobility from a broad perspective.

In addition to these proximate physiological motives, humans must navigate a complex interpersonal world that affects motivations for movement. Humans move across social landscapes as much as they do across biotic and geologic ones. Thus, we must consider the scale and structure of social worlds, as well as social cognition, in any account of the evolution of human movement at a large scale. Social motives can both push and pull movements. There are positive inducements to seek out new places to live and new individuals to interact with, whether from the potential of finding mates or the likelihood of learning new things.⁶⁷ On the other hand, social tensions within groups, growing out of imbalances between populations and food supplies or even simple scalar effects, may push individuals to move out of comfortable situations into less well-known places. Consequently, the sizes of residential groups and extensions of social networks may have been important in the past in motivating people to move over long distances or inhibit their movement.

EXTERNAL FACTORS

External factors that influence movement include environmental structure, climatic events and associated habitat changes, predator distributions on the landscape, and group-level interactions within and between hominin species. This is one area in which we can draw on a range of data sources that are independent of hominin skeletal biology and physiology in order to test models about the evolution of movement. Archeological data, paleoenvironmental proxies, and a basic understanding

of geomorphology help to fill out the context in which hominins made decisions about how and where to move.

In fact, external (environmental) factors have been implicated in some of the major evolutionary transitions in human movement. Most obviously, the origins of the genus *Homo* is often described within the context of a large-scale habitat shift from woodlands and forests to more open, broken savannah landscapes in East Africa.⁶⁸ It has long been argued that this ecological change may have provided the backdrop for an increase in the distances over which early

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members of the genus *Homo* moved on a daily or long-term basis. While the “Savannah hypothesis” has been repeatedly challenged on the basis of ecological reconstructions for earlier hominins during the origins of bipedalism,^{69,70} few would dispute the broader assertion that resource distributions played a large role in motivating and structuring hominin movement. Moreover, as hominins expanded their geographic and ecological ranges out of the tropics and subtropics, survival in less productive environments would have necessitated further extension of the habitual range of movement. Comparatively sparse and patchy distribu-

tions of potential food sources in cold, temperate environments of Eurasia would have constrained dispersing hominins to cover landscapes in new ways.

Among the disciplines focused on the study of human evolution, archeology has been most concerned with the large-scale movements of groups (what Nathan et al.³ call “Eulerian” mobility) and their material consequences. Since the early twentieth century, archeologists have recognized that mobility is important in structuring the archeological record. Insights from researchers such as Taylor⁷¹ and Winters⁷² drew researchers’ attention to the ways the distribution of resources in time and space influenced human decisions about when to move and where to go. Binford’s and Kelly’s seminal works^{73–76} resulted in a coherent approach to describing the movements of hunter-gatherer groups. Binford and Kelly are responsible for two fundamental insights. First, they proposed that variation in group mobility amounted to much more than a binary opposition, nomadism versus sedentism. They identified a series of strategies for moving resources to people or people to resources. Second, they showed how frequencies and scales of different strategies varied according to the structure of environments, with overall biotic richness and spatial and temporal patchiness playing key roles. Concepts such as residential and logistical mobility still form the basis for much archeological thinking on the topic,^{39,77,78} although researchers are beginning to consider factors such as information and mating opportunities in conditioning decisions about where and when to move.^{67,77,79}

Thinking about group-level mobility and its archeological consequences has certainly had an influence on paleoanthropology, although the relevance of the concepts has yet to be fully explored. It is widely recognized that the material record of hominins is strongly structured by movements of groups and individuals, and that the distributions of artifacts and “fragmentation” of manufacture sequences from the

Oldowan to the Upper Paleolithic carries information about regular patterns of mobility.^{38,80–84} Methods enabling us to attribute raw materials to specific source locations can even enable researchers to draw inferences about the scale and direction of habitual movements, although the logical linkages are not always as simple as they initially appear to be. By combining information about lithic artifact manufacture, raw material movement, and faunal resource exploitation, researchers have been able to investigate the ways hominins responded to climatically linked changes in resource distributions by altering their strategies for positioning themselves on the landscape, providing new insights into the adaptive flexibility of Neanderthals, for example.^{81,85,86} On a more theoretical level, links between scales and patterns of mobility and cultural transmission have been proposed.^{38,67,79}

Although mobility is a nearly ubiquitous theme in Paleolithic archeology in the early twenty-first century, it is clear that the archeological record has much more to tell us about the movement ecology of hominins as it relates to the major evolutionary developments we described in the opening paragraphs. Major shifts in diet and trophic level, such as those hypothesized to have accompanied the early development of the genus *Homo*, would have required compensatory responses in mobility. We know, for example, that feeding higher in the trophic pyramid requires larger foraging territories, holding group and body sizes constant.^{1,2,87,88} Less well understood are the demands that expanded or refocused diets would have placed on both physiology and cognition, as hominins had to locate a range of resources, position themselves to exploit them, and reconcile the spatial and temporal availabilities of individual foods. The development of processing-intensive feeding strategies involving fire^{89–91} may have placed very different constraints on where and when early hominins could move.

Major episodes of hominin dispersal, whether in the early Pleistocene or later, also implicate movement at a smaller scale. Dispersal through

demic expansion, as opposed to directed exploration, should emerge from habitual movement across landscapes as part of foraging, mate seeking, and other proximate responses to biological needs. Yet we know little about how strategies of movement within regular foraging territories can scale up. Is habitual, daily movement alone sufficient to produce waves of expansion in particular ecological circumstances or are evolved tendencies toward explo-

feeding higher in the trophic pyramid requires larger foraging territories, holding group and body sizes constant.^{1,2,87,88} Less well understood are the demands that expanded or refocused diets would have placed on both physiology and cognition, as hominins had to locate a range of resources, position themselves to exploit them, and reconcile the spatial and temporal availabilities of individual foods.

ration necessary precursors to large-scale population dispersal? In a world with more than seven billion people, bound within a vast web of defended political boundaries, it is unlikely that we will ever be able to directly observe the uninterrupted geographic expansion of a single human population. Future insights about relationships between meso-scale movement within foraging territories and population dispersal will

have to come first from silicon-based modeling exercises and animal models. Meanwhile, rates and routes of population dispersal ought to be strongly influenced by environmental structure, whether topographic or biotic. Here, improvements in technology (remote sensing, digital elevation models, etc.) and increasingly fine-grained paleoclimate models make it more practical to map the local effects of climate change onto potential pathways of dispersal. In the near future, these approaches should produce better hypotheses about the timing and direction of various movements “out of Africa,” which can then be tested using geological and archeological data.^{92–94}

Technology, specifically the widespread availability of geographic information systems (GIS) software and digital topographic models, is also invaluable in studying external constraints on movement at an intermediate scale. These tools enable researchers to assess topographic limitations on movement and to identify least-cost or least-effort pathways through actual landscapes. Such constructs hold the potential for building and testing realistic models of how past human groups moved through the physical geographies they inhabited and how physical geography, in turn, channeled access to resources and contacts with other human groups.

WHAT DO WE DO NOW?

Given both tradition and methodological constraints, the diverse subfields that contribute to human evolution research adopt different perspectives on human movement and mobility. Archeology and genetics are in the best position to examine how external forces affected movement at large and mid-range spatial scales. While archeologists tend to focus on aggregate, group-level tendencies, the record with which they work is ultimately a product of individual episodes of movement. Studies of fossil anatomy help us understand constraints and the outcome of long-term selection pressures. Studies of living

humans, nonhuman primates, and other mammalian models provide insight into how external factors constrain mobility on many scales and patterns of habitual movement. Such research also provides the main comparative source of theories about the cognitive correlates of movement. A fertile area of future work includes more detailed examination of the evolution of spatial navigation abilities in humans through neuroanatomical and neurophysiological studies exploring the evolution of internal motivators of movement. Through studies of comparative physiology, we can find complementary lines of evidence for changes in movement ecology across human evolution. Ethnographic studies alone can tell us about the unique ways humans impose social and symbolic structure on the physical landscapes over which they move. In addition, agent-based modeling is likely to be the best source of theory about how movement at one scale influences movement at another. In the end, we believe this more integrative view of mobility in human evolution will help us better define and test hypotheses about how selection shaped the hominin lineage through changes in movement ecology. In this way, a movement ecology framework provides a framework for new collaborations across all major subfields studying human evolution.

This introduction has attempted to link together varied and disparate areas of research to explore how we might rethink perspectives on changes in movement and mobility during evolution of the genus *Homo*. While morphological studies suggest that there were great changes in locomotor capabilities with the evolution of *H. erectus*, a stronger case would come from converging lines of evidence outside of the fossil record. If changes in the environment coincided with improved navigation capacity and evolutionary shifts in internal motivators, a fuller picture of the evolution of the genus *Homo* would emerge. Properly used, archeological evidence could provide a test-bed for hypotheses about changes in both internal and exter-

nal factors. Currently, the disparate lines of evidence support a view of large-scale movements by *H. erectus* and later members of the genus *Homo*. Changes in anatomy in some fossil finds, combined with comparative evidence from internal state (rewards for endurance locomotion) and suggested increased navigation capabilities indicate that when the landscape changed and our ancestors found themselves in more open environments, selection shifted movement patterns to increase distance traveled. How this increase in

Studies of fossil anatomy help us understand constraints and the outcome of long-term selection pressures. Studies of living humans, nonhuman primates, and other mammalian models provide insight into how external factors constrain mobility on many scales and patterns of habitual movement.

movement summed to changes in mobility requires more detailed archeological study, but we clearly see the imprints of changes in movement on human physiology and health today.^{95,96}

This exploration of human movement ecology may serve as a framework for how to proceed in testing the hypothesis that evolution of the genus *Homo* was precipitated by selection for a novel movement and mobility pattern. Beyond this specific case, though, we suggest that the incorporation of these research areas will prove useful to our understanding of the evolution of hominins throughout the last 5 million years. From the effects of climate on

mobility in European Neanderthals to the use of arboreal substrates in early hominins, a movement ecology framework may open new avenues of inquiry that can help reframe old debates. The papers that follow begin to do so by incorporating new ways of exploring old themes in the study human mobility.

PAPERS IN THIS SPECIAL ISSUE

These papers come out of a symposium organized by two of the authors of this paper (SLK and AEC) at the 2014 meeting of the Society for American Archaeology in Austin, Texas. Although this was an archeology meeting, the participants represented a wide range of disciplines, including biological anthropology, ethnography, and even cognitive science. The various papers tackled questions of movement at a range of scales, from biomechanics to territory sizes.

The paper by Wallace and Garland is the most biological and “micro-scale” of the group. In it, the authors describe the results of a series of selection experiments on laboratory mice. Mice selectively bred for high amounts of voluntary wheel-running exhibit a range of physiological and neurological characteristics. Some of these, such as larger joint surfaces, are predictable compensatory adaptations; others, such as changes in the size and proportions of the brain, are unexpected. On one hand, these results bear directly on hypotheses concerning the role of endurance running in human evolution. More generally, they implicate the complex network of interrelated traits that constrain and are constrained by habitual patterns of movement.

Bird and coworkers examine how landscape structure affects foraging decisions of members of an Australian aboriginal community in the arid Western Desert, but also how range burning, a foraging-related activity, affects landscape structure. The Martu people move across expanses of bush that they have, to a surprising degree, remade themselves. Human manipulation of habitats introduces a nonlinear element of niche construction into

conceptualizations of movement as a response to resource availability.

Churchill and colleagues turn to animal models as a source of insights into scales of the foraging territories of extinct hominins, particularly Neanderthals. Using dedicated predators such as wolves as the main referent, they generate a series of predictions about spatial scale of Neanderthal territories in different habitats. As the authors point out, such predictions are only a first step. Working between expectations from ecological and energetic models such as this one, and empirical findings from studies of artifact movement, we should be able to come to a clearer understanding of the actual sizes of hominin foraging territories and the environmental and demographic factors that shaped them.

Hamilton and coworkers take an alternative perspective on the phenomena of regular movement patterns across foraging territories. Starting from the theoretical framework of metabolic ecology and using basic energetic principles, they derive a series of predictions about how far hominins ought to move on a regular basis in different environmental circumstances. As they show, these expectations fit reasonably well with observations from ethnographic sources. Departures from expectations point to additional factors not considered in the original models.

Guiducci and Burke's contribution unites two components of the movement ecology framework, navigation and the external factors that constrain movement patterns. Beginning from the premise that navigation presents important cognitive challenges, they explore how the structure of topographic relief can affect the legibility of landscapes, or the degree to which they are conducive to way-finding. While the research is in its early stages, it offers the possibility of being able to evaluate how topography and geomorphology would have made some landscapes more navigable or learnable than others. Such information would, in turn, provide a new level of sophistication to hypotheses about the pathways of dispersal and colonization.

Three of the papers are more strictly archeological in focus. Two of them concern the spatial layout of campsites and the movement of individuals when groups are essentially stationary. Surovell and O'Brien present preliminary results from an innovative study of the ways people use space within a campsite occupied by a group of nomadic herders in Mongolia. They systematically document, for the first time, the kinds of small-scale choices that individuals make when moving within sites. The findings from this project promise to provide entirely new perspectives on archeological studies of site structure and of micro-scale movement of individuals. Clark's paper begins from the opposite direction. To our knowledge, this is the first broad systematic comparative study of spatial structures of a series of Middle Paleolithic sites occupied by Neanderthals, and the only study of Neanderthal site layout conducted at a scale large enough to capture the true size of the average hunter-gatherer camp. Analyses of the fundamental spatial makeup of the sites and the movement of different classes of artifacts within the site enable Clark to draw conclusions about the ways individual sites fit into a larger system of regional movement. This study is also an example of the potential usefulness of high-quality, highly comparable data generated by rescue archeology projects. Tomasso and Porraz take on conventional interpretations of evidence of lithic raw material movements in the Paleolithic. They argue that common assumptions about "embedded procurement," which assume that usable stone was collected as part of other foraging activities and therefore had little or no marginal cost, are incomplete. Using case studies from the Upper Paleolithic, they make a strong claim that people could be very selective about raw material properties, and that both indirect procurement (exchange) and strategic procurement of highly desirable raw materials also played a role in structuring the record. These results have important implications with regard to how we can translate evidence of movements of artifacts into models of the movements of people in the past.

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