Origins of house mice in ecological niches created by settled hunter-gatherers in the Levant 15,000 y ago

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Reductions in hunter-gatherer mobility during the Late Pleistocene influenced settlement ecologies, altered human relations with animal communities, and played a pivotal role in domestication. The influence of variability in human mobility on selection dynamics and ecological interactions in human settlements has not been extensively explored, however. This study of mice in modern African villages and changing mice molar shapes in a 200,000-y-long sequence from the Levant demonstrates competitive advantages for commensal mice in long-term settlements. Mice from African pastoral households provide a referential model for habitat partitioning among mice taxa in settlements of varying durations. The data reveal the earliest known commensal niche for house mice in long-term forager settlements 15,000 y ago. Competitive dynamics and the presence and abundance of mice continued to fluctuate with human mobility through the terminal Pleistocene. At the Natufian site of Ain Mallaha, house mice displaced less commensal wild mice during periods of heavy occupational pressure but were outcompeted when mobility increased. Changing food webs and ecological dynamics in long-term settlements allowed house mice to establish durable commensal populations that expanded with human societies. This study demonstrates the changing magnitude of cultural niche construction with varying human mobility and the extent of environmental influence before the advent of farming.

house mouse | sedentism | Natufian hunter-gatherers | commensalism | niche construction

Reductions in hunter-gatherer mobility during the Late Pleistocene and development of sedentary ways of life altered human relations with plant and animal communities and played a pivotal role in domestication. Niche construction activities of settled hunter-gatherers, such as building, food storage, and waste accumulation, influenced food webs and exerted novel selection pressures on animal populations in human settlements (1–3). These factors resulted in changes in the abundance, ecology, and evolutionary trajectories of a range of animal species. Wild boars and wolves are thought to have been attracted to food sources in settlements following commensal pathways before developing long-term mutualism characteristic of domestication (4–6). Domestication of other animals, like goats or cattle, may have followed from hunting pressures exerted by settled communities and consequent shifts in hunting strategies (7–9). There is limited empirical evidence, however, on when pivotal shifts in mobility and selection pressures on animals in human settlements first occurred. Little is known about changing selection dynamics or competition among commensal taxa with changing occupational pressures. Despite acknowledged relationships between hunter-gatherer sedentism and domestication, scholars also hold widely divergent views regarding the level of hunter-gatherer versus early farmer impacts on ancient landscapes.

Our study of the beginnings of mouse commensalism in the Levantine region offers high-resolution data on the effect of fluctuations in human mobility on selection in human settlements, niche partitioning among mice species, and niche dynamics through time. The Levant is the likely place of origin of the commensal niche of house mice (*Mus musculus domesticus*; hereafter, *domesticus*) and the springboard for global human-mediated expansion of this species (10–14). Sites dating to the Early Holocene (*ca.* 12,000 B.P., all dates are calibrated radiocarbon years before present), a short time before the Neolithic, furnish the earliest known fossil evidence of *domesticus* (11, 13). Evidence for Early Holocene house mice was preceded by several millennia of decreased settlement mobility, social elaboration, and subsistence shifts among complex hunter-gatherers in the southern Levant (15). Wild grain collection, hunting, and reliance on small mammals intensified from as early as 25,000–23,000 B.P (16, 17). The appearance of the Natufian culture *ca.* 15,000 B.P. has been perceived by many as marking a punctuated transition to sedentism and built settlement environments in the region (18). As a result, it has been suggested that rather than emerging with farming, preagricultural human sedentism led to commensalism in the *domesticus* lineage (19, 20). This trajectory of reduced mobility was not unidirectional, however, and the intensities with which Natufian settlements were occupied and degree of human mobility continued to fluctuate substantially over *ca.* 3,500 y before the Neolithic (18, 21, 22).

Significance

Decreases in hunter-gatherer mobility during the Late Pleistocene altered relationships with animal communities and led to domestication. Little is known, however, about how selection operated in settlements of varying duration. This study of mice in modern African mobile settlements and ancient Levantine sites demonstrates competitive advantages for commensal mice when human mobility is low and niche partitioning with noncommensal wild mice when mobility increases. Changing mice molar shapes in a 200,000-y-long sequence from the Levant reveal that mice first colonized settlements of relatively settled hunter-gatherers 15,000 y ago. The first long-term hunter-gatherer settlements transformed ecological interactions and food webs, allowing commensal house mice to outcompete wild mice and establish durable populations that expanded with human societies.

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The Levantine Natufian-Neolithic archaeological sequence provides an exceptional opportunity to examine the evolution of mouse commensal adaptations in relation to human niche construction. Toward the end of the Pleistocene, *domesticus* and the short-tailed (ST) mouse *Mus macedonicus* (hereafter, *macedonicus*) were both present in the Levant (23). Sympatry between the closely related and competitive species may have depended on differential use of habitats in intensely settled human environments. However, few studies have so far investigated commensal dynamics in relation to competitive interactions among mice in hunter-gatherer settlements. Mechanisms of habitat partitioning are not well understood in contemporary or ancient temporary households. To address these questions, specific ecological and archaeological data are needed, because although cities are well studied, there is currently little empirical information on rodent interactions in small-scale settlements of any age.

To examine competitive interactions and habitat partitioning in human settlements occupied for varying periods, we collected ethnoarchaeological data in southern Kenya, live-trapping 192 mice in six small-scale settlements (<20 people each) occupied for varied durations. Here, a sympatric pair of species of spiny mice of the genus *Acomys* display variability in commensal habits and morphology (24, 25) relevant to interpretation of ancient sympatric *Mus* species in the southern Levant. This study provides the basis for the mouse interaction model that we use in interpretation of the archaeological data. We studied the influence of ancient hunter-gatherer settlement fluctuations on niches for commensal mice in a continuous sequence of Middle-Late Pleistocene and Early Holocene occupations in the southern Levant >200,000–10,200 B.P. (Fig. 1). To determine the presence and proportions of *domesticus* and *macedonicus* species in the archaeological deposits, we used a high-resolution geometric morphometric approach for our analysis of modern and archeological *Mus* molars (26). Mice specimens were studied from cave and open-air sites that preserved a record of fluctuations in the intensity of human occupation over time and the Natufian transition to sedentism (27–29): Middle Paleolithic levels at Tabun, Qafzeh, and Hayonim; Kebaran levels at Hayonim; Natufian levels from Ain Mallaha and Hayonim; and Pre-Pottery Neolithic A (Early Neolithic) from Netiv Hagdud (Fig. 1).

Our findings reveal niches for mice in human settlements 15,000 y ago, fluctuations in competitive dynamics among commensal mice with mobility, and the presence of dominant populations of house mice in settled hunter-gatherer households. This study also provides long-term perspectives on the variable nature of hunter-gatherer influences on commensal niches and niche construction occurring at the threshold of domestication and agriculture.

Results

Modern Referential Model. Maasai settlements studied were occupied by seasonally mobile but sedentizing herders. Over the past 40 y, the average settlement use life has increased from 3.7 to 6.4 y (30). Families stored little grain, which contributed to a neutral rather than amensal relationship with rodents. Householders did not have a negative attitude to rodents and did not kill them. We observed no intentional selection on mice in settlements. *Acomys* spp. were the most abundant species in the study, representing 60% of small mammals trapped inside the six study settlements and 72% of small mammals trapped in adjacent control sites 200–400 m from settlements. Mixture analysis and unsupervised classification with Bayesian modeling performed on tail length measurements taken from the captured *Acomys* individuals demonstrate the occurrence of two taxa (Fig. 2*A* and *Statistical Analyses*): *Acomys wilsoni*, a ST species, and *Acomys ignitus*, a long-tailed (LT) species.

A. wilsoni and *A. ignitus* occurred in both the control sites and within the settlements. The level of association between these two species and the settlements varies significantly ($\chi^2 = 39.668$, Monte Carlo $P = 0.0001$, Cramer's V = 0.456; *Statistical Analyses*). *A. ignitus* accounts for 87% ($n = 101$) of individuals captured inside the settlements but only 45% ($n = 33$) of individuals in the control sites, suggesting that among the two *Acomys* species, the LT *A. ignitus* is also the more commensal of the two (Fig. 2*B*). The difference in proportions is most pronounced when examining results of trapping inside dwellings, where 23 *A. ignitus* individuals but only one *A. wilsoni* individual were trapped (Fig. 2*B*).

Our Maasai modern reference dataset reveals notable sharing of the commensal habitat by *Acomys* species. Moreover, numbers of commensal *Acomys* do not increase with increasing use intensity of settlements within the Maasai system. Here, settlements remain small-scale and seasonal mobility involves periodic complete or partial abandonment of settlements. Using the age and extent of seasonal human occupation of the six settlements in our case study to rank-order the settlements (Table S1), only a weakly significant negative correlation exists between these settlement ranks and numbers of *A. ignitus* (Spearman's rank correlation, $r\,s = -0.9$; $P = 0.03$ using the exact permutation test;

Sites, arranged chronologically	Abb., layer	Cultural period	Radiometric chronology (BP)	Settlement-subsistence	Deposition setting	*Mus* M_1 molars
Netiv Hagdud	NTH	Pre-Pottery Neolithic A	11.5 to 10.75 Ka	Sedentary, Agricultural	Open-air	6
Ain Mallaha (Eynan)	EYN (Ib)	Final Natufian	12 to 11.5 Ka	Incipient sedentism, Pre-agricultural hunter-gatherer	Open-air	53
Ain Mallaha (Eynan)	AM1	Late Natufian	13 to 12 Ka		Open-air	10
Hayonim Cave	HaTerB				Terrace	6
Hayonim Cave	HaB	Early-Late Natufian			Cave	53
Ain Mallaha (Eynan)	AM3	Early Natufian	15 to 13 Ka		Open-air	14
Ain Mallaha (Eynan)	AM4					13
Hayonim	HaC	Kebaran	17 to 15 Ka	Mobile hunter-gatherer	Cave	21
Hayonim	HaD	Upper Paleolithic	28 to 26 Ka			29
Qafzeh	QZ_XV	Middle Paleolithic	110 to 90 Ka			25
Qafzeh	QZ_XVII					44
Qafzeh	QZ_XXI					41
Tabun	TBN		178 to 134 Ka			28
Hayonim	HaE		>200 to 70 Ka			29
Total						372

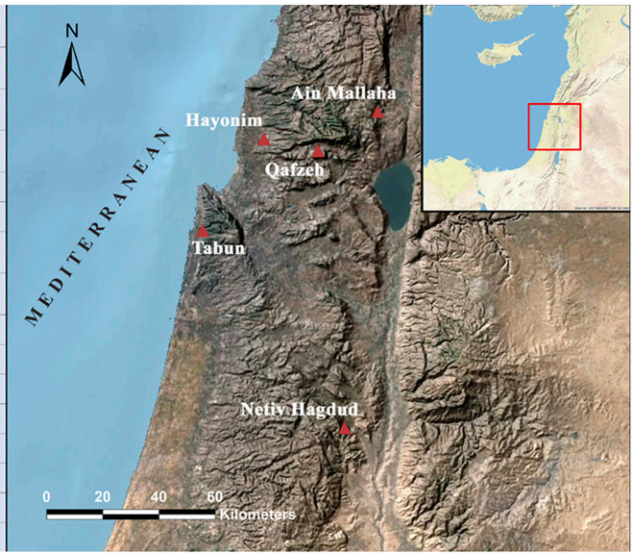

Fig. 1. Chronology (*Left*) and location (*Right*) of the archaeological contexts providing *Mus* zooarchaeological samples used in this study. Sizes of *Mus* M1 samples are given in the last column of the table. The base map was generated from Environmental Systems Research Institute (ESRI) map data using ArcGIS v.9.1; Esri, GEBCO, DeLorme, NaturalVue, United States Geological Survey, NASA, Esri Inc.

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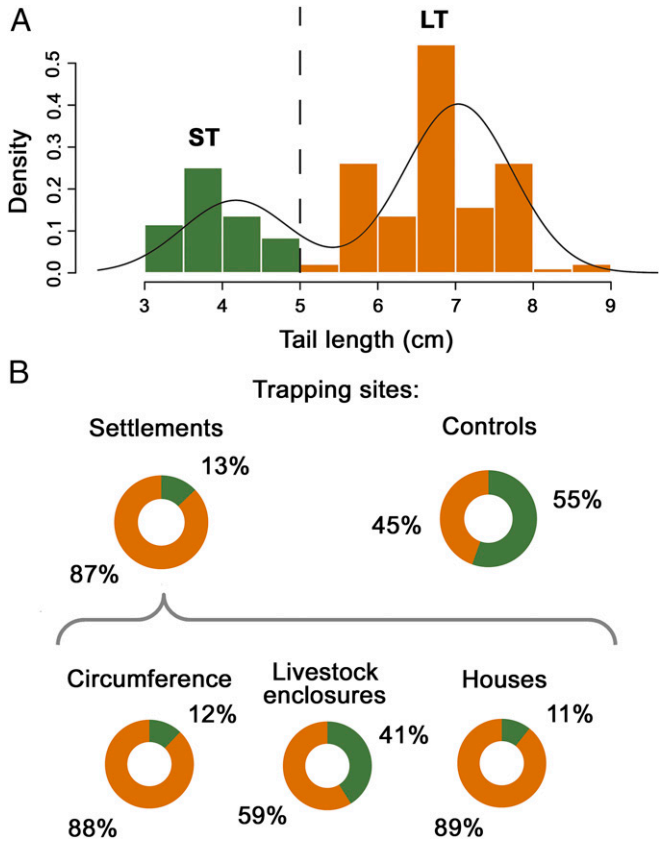

Fig. 2. Species composition of *Acomys* in Maasai settlements. (*A*) Mixture analysis combined with Bayesian modeling performed on *Acomys* tail length measurements showing the existence of two taxonomic groups: ST group and LT group. (*B*) Pie charts showing the combined proportions of the two taxa (ST/LT) in the settlements and control sites, as well as in different parts of settlements (circumference fence, animal enclosures, and houses).

Statistical Analyses). Additionally, numbers of *A. wilsoni* in the settlements and of both *Acomys* species in the control sites show no correlation with Maasai settlement intensity (*A. wilsoni* settlements: $rs = -0.8$, $P = 0.08$; *A. ignitus* controls: $rs = -0.2$, $P = 0.81$; *A. wilsoni* controls: $rs = -0.2$, $P = 0.65$).

These results indicate that the LT *A. ignitus* possesses a competitive advantage over the ST *A. wilsoni* in the settlements, thereby gaining access to preferred resources. However, because Maasai settlement use remains seasonal, *A. wilsoni* is only partially outcompeted by *A. ignitus*, indicating that absolute competitive exclusion and dominance of the commensal niche require longer term and more permanent human occupation. Dietary niche overlap and competition are thought to influence relationships among coexisting species of *Acomys* (31, 32). In human settlements, access to more optimal dietary resources for *Acomys*, including seeds and plant matter, can be enhanced due to release from competition with wild herbivores (24). Enhanced resource provisioning for mice in Maasai settlements, including herbaceous biomass and seeds, is the expected result of elevated productivity of soils fertilized by the dung from livestock herds (33).

Archaeological Samples. Samples were internally consistent and differed with stratigraphic context. The molar shape relationship among the archaeological *Mus* samples and the two modern sympatric species of *Mus* from Israel (*Statistical Analyses* and Fig. S1), showing the mean shape for each sample, is displayed by an unrooted neighbor-joining tree (Fig. 3). This phenogram clearly polarizes the sequence, showing that a single *Mus* species, *macedonicus*, was present in the entire Pre-Natufian sequence (>15,000 B.P.), including Tabun, Hayonim (HaE-C), and Qafzeh (XV, XVII, XXI) caves, as well as in the Natufian samples from Hayonim Cave (HaB, HaTerB) and the Late Natufian phase of Ain Mallaha (AM1). The presence of a single species in these samples is confirmed by Bayesian analysis, which finds only one most likely group (*Statistical Analyses* and Table S2). The earliest documented remains of *domesticus* are the remains from Early Natufian Ain Mallaha (AM3–4), where they comprise 100% of the *Mus* remains. This finding indicates a sharp replacement of *macedonicus* by *domesticus* and the presence of house mice that did not share the commensal niche with *macedonicus* (Fig. 4). A second sharp replacement is shown in the Late Natufian occupation phase of Ain Mallaha, when *macedonicus* again comprises 100% of the remains. Archaeological evidence from Ain Mallaha suggests a shift from sedentary to more ephemeral human occupation between the early and late phases of the Natufian, as evidenced by decreases in repeated use and size of stone structures and burials of individuals with personal adornments (*Archaeological Interpretation of Fluctuations in Hunter-Gatherer Site Use Intensity in the Ain Mallaha Sequence*).

Unlike any of the other samples, the sample of the Final Natufian at Ain Mallaha [Eynan (EYN)] occupies an intermediate position between the two poles of our ancient *Mus* molar shape continuum. It is the only sample where, according to Bayesian clustering models (*Statistical Analyses* and Table S2), both species occur in sympatry, but the house mouse was in the majority (79%; Fig. 3). The relative abundances of *domesticus* and *macedonicus* in this sample are closely congruent with the structure of sympatry between the two *Acomys* species within Maasai settlements (87% *A. ignitus*, the more commensal of the two species, compared with only 13% *A. wilsoni*). This finding suggests habitat partitioning in both cases and a more loose-knit facultative association of commensal mice and the human environment when the intensity of human occupation lies between sedentism and frequent seasonal movements, as seen in the Maasai context.

Combining Zooarchaeological and Referential Data. We propose three stages of niche development in commensal interactions of the house mouse (Fig. 4): N1, nonexistence or rare and opportunistic presence of house mice (archaeologically undetectable); N2, facultative association of house mice with the settlements where there is only relative dominance of house mice and competitive exclusion of *macedonicus*; and N3, obligate association of house mice with the settlements where there is absolute dominance of *domesticus* and competitive exclusion of *macedonicus*. Early Natufian occupations at Ain Mallaha show a well-developed N3 pattern, which was due to increased intensity of human occupation and dampened seasonality, and is thought to have resulted in the exclusion of *macedonicus*. It appears that increased human mobility, which has been suggested for the late phase of the Natufian, including at sites such as Ain Mallaha (*Archaeological Interpretation of Fluctuations in Hunter-Gatherer Site Use Intensity in the Ain Mallaha Sequence*), favored the return of *macedonicus* and temporary exclusion of *domesticus*, reverting to a stage N1 pattern. The fluctuating abundances of *domesticus* between the occupations of Final Natufian Ain Mallaha and Early Neolithic Netiv Hagdud seem to mirror a resumed but more gradual trend of sedentization, which is documented in the archaeological record (*Archaeological Interpretation of Fluctuations in Hunter-Gatherer Site Use Intensity in the Ain Mallaha Sequence*) and fits with a stage N2 pattern of sharing of the commensal niche among a pair of sympatric species of mice.

Discussion

Our findings from the 200,000-y sequence studied fill a critical gap in current reconstructions of the origins of commensal interactions between humans and the house mouse (*domesticus*) with reductions in human mobility. The data reveal the presence of dominant commensal populations of house mice in southern Levantine sedentary hunter-gatherer settlements as early as 15,000 B.P. Assemblages from occupations of Natufian hunter-gatherers and Early Neolithic farmers, which span the period of

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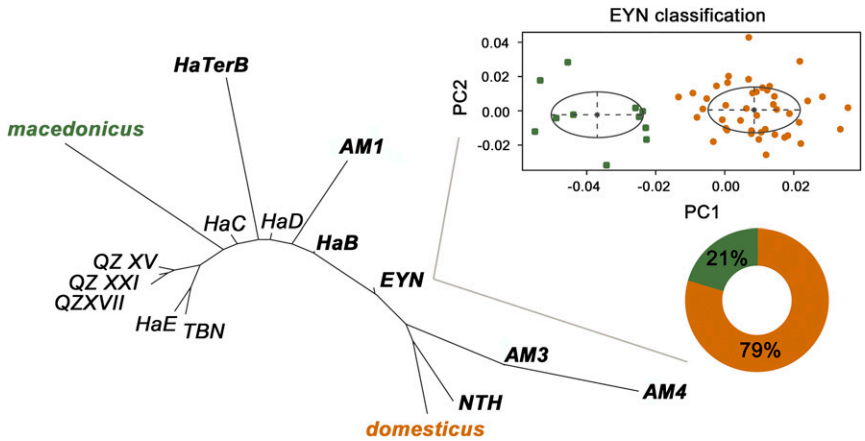

Fig. 3. (*Left*) Combined neighbor-joining tree analysis of modern and archaeological *Mus* specimens (*domesticus*, orange; *macedonicus*, green). TBN, Tabun; Ha, Hayonim; QZ, Qafzeh; AM and EYN, Ain Mallaha; NTH, Netiv Hagdud. Natufian neolithic sites in are shown in boldface. (*Right*) Species composition of EYN is shown.

sympatry of house mice and the congeneric *macedonicus* between 15,000 and 11,000 B.P., show strong temporal fluctuations in relative proportions of sympatric mice. These ecological shifts mirror documented events in the cultural record, involving alternations between periods of human sedentism and increased mobility over this period (18, 21, 22). Integrating archaeological findings with the findings from our modern referential model provides insight into the nature of early interactions between humans and commensal mice.

Commensal Origins of House Mice. Our findings demonstrate that the initial development of a commensal niche and its maintenance over time depended on long-term human occupation of settlements and sustained habitat alteration. The house mouse commensal niche appeared full-blown at the beginning of the Natufian sequence at the site of Ain Mallaha (levels 3–4, Early Natufian). Interestingly, sympatric *macedonicus* was absent in early occupation levels at Ain Mallaha and reappeared in later ones (levels 1c and Ib, Late and Final Natufian, respectively), a reconstruction that covaries with architectural shifts. This finding demonstrates that in the context of newly established sympatry between the two species, populations of house mice outcompeted their *macedonicus* counterparts, completely excluding them from the commensal niche.

Ecologists have suggested a pattern of habitat partitioning and competitive exclusion among modern populations of ST *macedonicus* and house mice in the Levant (13, 23). However, due to the urbanized and intensely agrarian nature of present-day landscapes, it has been difficult to establish whether this pattern initially emerged among early sedentary hunter-gatherers or later Neolithic famers. Evidence for the dominance of house mice in early occupations of the Natufian culture speaks to absolute habitat partitioning and competitive exclusion among populations of commensal mice. This evidence is consistent with widespread archaeological evidence for an abrupt hunter-gatherer transition to a sedentary way of life and initial construction of permanently built environments (18, 34, 35). At this time, settled hunter-gatherers introduced a new suite of selective pressures with unintentional impacts on mouse populations. Strong dependence of house mice on the commensal niche is indicated at the population level (36).

However, the establishment of a commensal niche in Natufian settlements like Ain Mallaha did not build to a trajectory of sustained dominance of commensal mice. Toward the end of the Ain Mallaha sequence, the two sympatric mouse species share the

Cultural chronology	Cultural context	Commensal niches	Ecology & population dynamics	Phylo-geography
Early Neolithic	Sedentary cultivation	100% *dom* N3	Competition & habitat partitioning	
Final Natufian	Seasonal mobility & long-term occupation	80% *dom* / 20% *mac* N2	Partial habitat partitioning	
Late Natufian	Seasonal mobility	100% *mac* N1	Breakdown in sympatry & geographic retreat of *dom*	Regional population fragmentation
Early Natufian	Hunter-gatherer sedentism & subsistence intensification	100% *dom* N3	Sympatric distributions, competition & habitat partitioning	Initial post-glacial expansion signal
Geometric K.	-	-	-	
Kebaran	Hunter-gatherer seasonal mobility	100% *mac* N1	Allopatric distributions	

Fig. 4. (*Left*) Connections between cultural, ecological, and phylogeographic factors in commensal niche dynamics in the terminal Pleistocene southern Levant (*dom*, *domesticus*; *mac*, *macedonicus*; double-headed arrows indicate transitions in commensal niches). Lack of data for the geometric Kebaran precludes determining between patterns of short-term or multiyear seasonal mobility for this period. Phylogeographic information is based on data in the study by Bonhomme et al. (14). Niche development stages N1–N3 are described in the main text. (*Right*) Maasai settlement in southern Kenya at the center of the photograph is surrounded by a grassy buffer zone, corresponding to human occupation intensity.

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commensal niche, with house mice showing only relative dominance. This pattern is rare and occurs nowhere else in the 200,000-y sequence studied (also ref. 37). In light of the correspondence that we demonstrate between our archaeological and modern reference datasets, a pattern of seasonal occupation is highly probable. This pattern may have persisted from a few years to several decades. Archaeologically, distinct occupation lenses within floors at Ain Mallaha indicate repeated use of the Final Natufian (EYN) structures despite reduced architectural investment during this period (28, 29, 38). Strong links between limited mobility, occupation pressure, and competitive advantages for *domesticus* are indicated by successive population replacements of *macedonicus* during periods of increased human sedentism. Conversely, a return to a more mobile existence in later phases of the Natufian (18, 22, 39) correlates with replacement of *domesticus* by *macedonicus*.

Fine-grained data from sites spanning a long time period allow us to evaluate the strength of ecological interactions and the resulting array of new selective pressures introduced by sedentary hunter-gatherers of the Natufian culture at a range of different scales. Direct human selection and mutualism occurred only in the very recent stages in the formal domestication of the house mouse (40), indicating the strength of indirect selection in the human niche. The response of mice to habitat alteration by sedentary Natufian hunter-gatherers was a manifest behavioral shift to a largely commensal existence and is an excellent index of the changing magnitude of cultural niche construction with varying human mobility.

Ecological Footprint of Pleistocene Hunter-Gatherers. Hunter-gatherer construction and long-term occupation of stone dwellings led to an ecological buffering effect for mice with increased resources available to them through people storing and discarding food in settlements. This activity provided a release from non-anthropogenic selection pressures, such as seasonally fluctuating food abundances and competition. Underlying mechanisms of food provisioning vary (e.g., wild grain storage, cultivation, enhanced soil fertility as in our Maasai case study), but all impacts increase with human occupation intensity. Previous research suggested that house mice became established within the commensal niche during the Early Neolithic, with the introduction of farming (13). We demonstrate that Pre-Neolithic hunter-gatherer sedentism altered selective environments for commensal species. Intensive accumulation of wild grains combined with protocultivation is now known from as early as 23,000 B.P. at the Levantine site of Ohalo II (17). Putative storage facilities are known from Natufian sites at Ain Mallaha and Hayonim Cave (41–43). Our results suggest that increased storage and greater accumulation and discard of food waste played a role in altered ecological webs, leading to the development of permanent and dominant house mouse populations in sedentary hunter-gatherer settlements.

Phenotypic traits of house mice selected for within intense anthropogenic habitats across Asia included a longer tail, shorter skull, and darker pelage relative to the phenotypic traits of sympatric mice of the same genus (44, 45). Such shifts in size, cranial morphology, and color-based phenotypic traits have been linked to brain functions organized toward reduced wariness, reactivity, and aggression, a key requirement in adaptation of domestic and commensal animals to intensely anthropized environments (46, 47). Further research is needed on trait selection in commensal habitats (48); however, the similarity in the greater tail-to-body ratio trait in commensal species from different continents, modern house mice, and *Acomys* in Maasai settlements supports links between morphological shifts and selection on mice in anthropogenic habitats. Selection for longer tails, important for agility in locomotion and possibly flight response in mice, was a likely outcome of intensified human activity in permanently settled habitats.

The beginning of sedentary living marked a turning point in human and environmental history when permanent settlement began to exert lasting impacts and ecological legacies on ancient landscapes. The contribution of commensal rodents to dampening agricultural productivity and spread of disease in later history is testimony that the transition to sedentism had a profound, long-lasting, and unpredictable influence on the human niche. Our results demonstrate that relatively large-scale and sustained anthropogenic alteration of ecological dynamics in settlements was initiated considerably earlier than previously thought. They provide evidence for the timing of and competitive interactions among mouse populations during one of the earliest processes of human-mediated biological invasion, which transpired among preagricultural societies. This study emphasizes the significance of human niche construction activities in sedentary settlements for commensal pathways to domestication (2, 3). The commensal nature of relationships between humans and mice through time, mouse behavioral flexibility, and morphological shifts also strengthen assertions that animal domestication may have relied to an important extent on indirect selection in the human niche, acting on existing variation and behavioral and phenotypic plasticity of target species (49).

Materials and Methods

Modern Referential Model. Ecological monitoring of small mammals and investigation of commensal use of settlements by local species of *Acomys* were conducted in six small-scale settlements of seasonally mobile Maasai herders in southern Kenya. These settlements were occupied for durations varying from 3 to 12 mo seasonally over 2–45 y. The study area is located within the administrative district of Kajiado in the Maasai locality of Eselenkei (50). Eselenkei is a semiarid region of southern Kenya characterized by average annual rainfall of 425–675 mm and dominated by *Acacia-Commiphora* bush that is associated with shallow red sandy substrates. Mobile pastoralism is the predominant land use in the study area, where rain-fed farming is not sustainable due to low and unpredictable rainfall. The different ages of six settlements selected for this study, from 2 to 45 y old, span the entire age range of Maasai settlements in the region (30).

We used a standard ecological field technique for studying small rodents and shrews, capture-mark-release trapping, which was used inside the six villages and in adjacent control sites of similar size. At each site, we deployed an orthogonal 25-trap (large folding aluminum Sherman live traps: 3 × 3.5 × 9 in) grid for a period of 5–7 d, and this trapping technique was repeated three more times to produce a total trapping effort of 7,350 trap days (number of traps × number of trapping days). Data on taxonomic identification and body measurements were taken for each trapped individual. Nine different taxa of small rodents and insectivores were documented in traps (*Acomys*, *Gerbillus*, *Mastomys*, *Elephantulus*, *Grammomys*, *Crocidura*, *Taterillus*, *Tatera*, and *Lemniscomys*), of which *Acomys* provided the most frequently trapped individuals across settlement and control sites. The presence of two species of *Acomys* in our trapping area accords with published measurements, which distinguish the species based on tail lengths (*A. wilsoni* is a ST species, and *A. ignitus* is a LT species; 3–5 cm and 5.5–9 cm, respectively) (table 1 in ref. 25), and with maps of species distribution in the International Union for Conservation of Nature Red List of Threatened Species (maps.iucnredlist.org). We note that the study was approved by the Animal Studies Committee of Washington University in St. Louis.

Rodent Samples and Geometric Morphometrics of Molar Form in Modern and Fossil Mice. Research focused on rodent mandibles. Samples were retrieved using flotation and were selected from well-stratified contexts, including at Ain Mallaha features, such as densely packed floors, walls, and pits. Architecture is reduced in the Late and Final Natufian phases (last 50 cm of a 3-m section), but distinct occupation lenses within floors provided sampling contexts. Taphonomic analysis investigated variation in fossilization and weathering patterns, finding no evidence for such variation.

Total sample sizes were 64 modern samples and 372 fossil samples. Geometric morphometrics provide a more accurate and reliable technique for specific and subspecific differentiation within the *Mus* group based on cranial remains than previously used linear morphometric methods. Improved accuracy in comparison to earlier studies of *Mus* fossil material in the Levant (20) is due to the use of high-resolution digitizing, quantification, and partitioning of shape and size information.

To compare modern and archaeological samples of mice, we used the first lower molar (M1) as a phenotypic marker and a geometric morphometric approach to quantify and analyze morphological variation (26). In this study, we captured the form of the M1 with a 2D outline of its crown in occlusal view. This technique employs 64 equidistant Cartesian coordinates starting from the apex of the M1 and digitized from photographs using tpsDig 2.12 (51). The starting point is considered a landmark (type 3), and the 63 other points are considered semilandmarks (52). To extract comparable shape variables out of these outlines, we used Procrustes superimposition based on a

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generalized least square approach, which aligns the outlines to remove size, position, and orientation components from the coordinates and to obtain a new set of coordinates called Procrustes coordinates or shape variables used in subsequent statistical analyses. Semilandmarks were aligned with a bending energy method (53). The centroid size (square root of the summed distances between each point and the outline centroid) is also computed after alignment and is used as a size variable for each specimen.

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