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Commensal Rats and Humans: Integrating Rodent Phylogeography and Zooarchaeology to Highlight Connections between Human Societies

Emily E. Puckett,* David Orton, and Jason Munshi-South

Phylogeography and zooarchaeology are largely separate disciplines, yet each interrogates relationships between humans and commensal species. Knowledge gained about human history from studies of four commensal rats (*Rattus rattus*, *R. tanezumi*, *R. exulans*, and *R. norvegicus*) is outlined, and open questions about their spread alongside humans are identified. Limitations of phylogeographic and zooarchaeological studies are highlighted, then how integration would increase understanding of species' demographic histories and resultant inferences about human societies is discussed. How rat expansions have informed the understanding of human migration, urban settlements, trade networks, and intra- and interspecific competition is reviewed. Since each rat species is associated with different human societies, they identify unique ecological and historical/cultural conditions that influenced their expansion. Finally, priority research areas including nuclear genome based phylogeographies are identified using archaeological evidence to understand *R. norvegicus* expansion across China, multi-wave colonization of *R. rattus* across Europe, and competition between *R. rattus* and *R. norvegicus*.

1. Introduction

For centuries, rats have scurried across paintings, literature, film, and language, from the vernacular slight of the “rat race” to artistic embodiments such as the Rat King in Tchaikovsky’s *The*

Nutcracker ballet. While rats often have positive connotations in East Asian contexts, their cultural image in European and related traditions has been overwhelmingly negative, drawing moral associations of thievery, destructiveness, uncleanliness, and vice from the reality of rats’ diet, habitat, and fecundity. A common thread is the idea of rats as the shadow of humans: living alongside people while representing our own worst tendencies.^[1]

Rats’ life history influences these human perceptions. As commensals, rats live in proximity to people, using the food, water, and habitats that human societies provide; thus, their distribution and abundance reflect human societies. Their high birthrate (7–11 pups per litter), multi-annual breeding cycle, and hierarchical social structure aggregate rats into large and dynamic colonies, the proximity of which to humans encourages perceptions that

they steal food, breed uncontrollably, and are unsanitary. Rats also have real and perceived roles in transmitting zoonotic diseases,^[2] notably acting as reservoirs of plague, frequently implicated in the Eurasian and North African “second pandemic” from the mid-14th C AD.

The genus *Rattus* has 64 species,^[3] and biogeography is an open question. Within the genus, the deepest divergence occurred between the Asian and Australo-Papuan clades approximately 2.44 Mya, undergoing subsequent biogeographic structuring between New Guinea and Australia.^[4] To date, mitochondrial phylogenies have included 26 or fewer species,^[5] and comparisons between phylogenies with and without nuclear data identify mito-nuclear discordance for some species.^[4,6,7]

Humans primarily interact with four commensal species: the black (*R. rattus*), Asian house (*R. tanezumi*), Pacific (*R. exulans*), and brown (*R. norvegicus*) rat. Commensalism evolved at least three times (Figure 1a); however, the ability to use “artificial” habitat (which IUCN defines as croplands, rural gardens, and urban areas) was associated with 27 *Rattus* species.^[8] Whether species using artificial habitats are synanthropic (living in anthropogenic spaces) or anthrodependent (dependent on anthropogenic resources and habitats) needs further study of their natural history in both human dominated and wild environments.^[9] Below we outline current knowledge of the phylogeography and zooarchaeology of four commensal rats.

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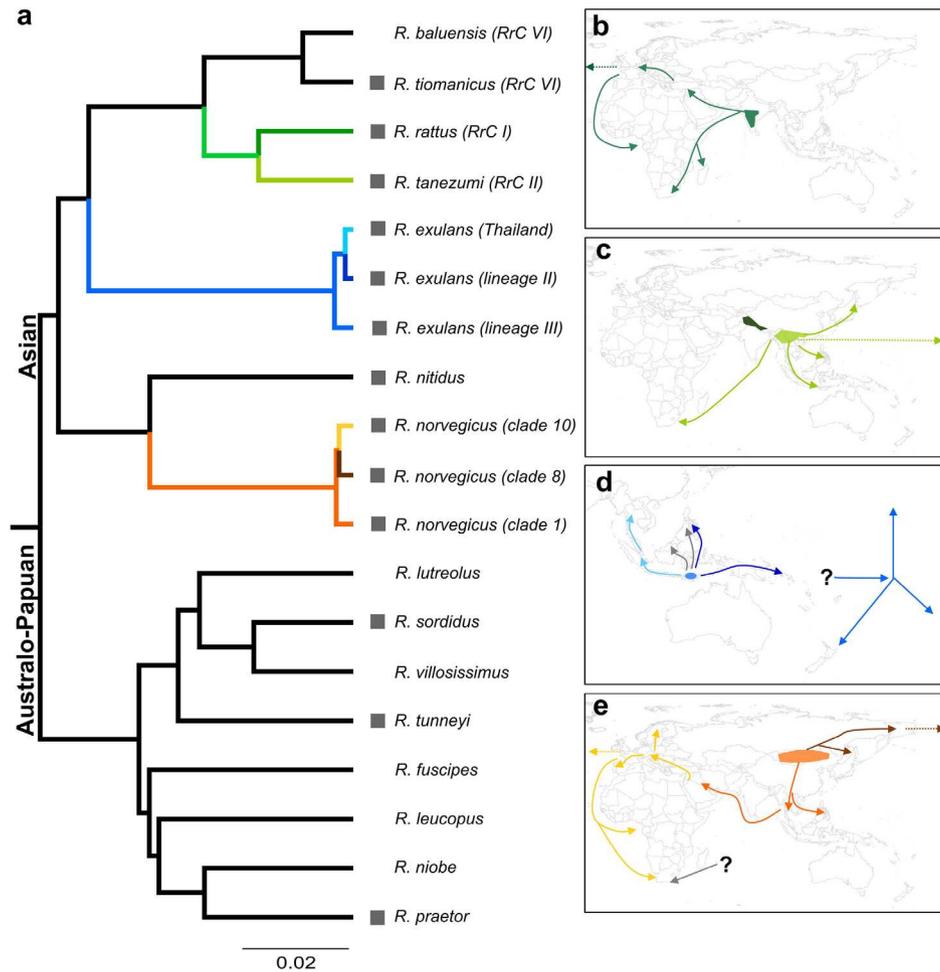


Figure 1. a) Neighbor-joining mitogenome phylogenetic tree ($n = 15$ *Rattus* species and one *Mus musculus* outgroup (not shown^[79]); NCBI accessions NC023347, NC029888, and those found within published papers^[26,80,81]) where interior colored branches denote possible evolution of commensalism, and grey squares indicate rat species able to live in artificial habitats (27 of 64 *Rattus* taxa listed by IUCN). We note identifiers of within species diversity in parentheses based on Aplin et al.^[10] for *R. rattus* complex (RrC), Robins et al.^[6] for *R. exulans*, and Puckett et al.^[81] for *R. norvegicus*. Inferred natal ranges (filled polygons) and range expansion routes for b) *R. rattus* (green); c) *R. tanezumi* RrC II (lime green) and RrC III (hunter green); d) *R. exulans* lineage I (grey; not shown in phylogeny), Thailand/mainland SEA (light blue), lineage II (dark blue), and lineage III (medium blue);^[23,26] and e) a distilled subset of *R. norvegicus* clades highlighting patterns from the nuclear genome.^[27] Dashed arrows in panels b, c, and e represent expansions to the western hemisphere.

1.1. *Rattus rattus* and *R. tanezumi*

Aplin et al.^[10] identified six mitochondrial clades within the *R. rattus* native range that they described as a species complex (RrC). Based upon these results, the authors recommended collapsing *R. rattus* (RrC I) and *R. tanezumi* (RrC II [southeast Asian clade], III [Himalayan clade], and IV) into a single species, but also suggested that RrC IV may be a separate species. This interpretation presents a challenge in that species delimitation based solely on mitochondrial sequence is limited in the coalescent history analyzed and maternal inheritance of the mitogenome, thus using nuclear genome sequence would increase the robustness of inference.^[11] We treat *R. rattus* and *R. tanezumi* as separate species in our discussion both due to divergent mitochondrial clades and differences in chromosome number (*R. rattus* $2n = 38$, although with geographic variation for 40 or 42 chromosomes; *R. tanezumi* $2n = 42$ ^[12]).

The original global population structure analysis for black rats using mitochondrial haplotypes resulted in a polytomy in the phylogeny,^[10] indicative of rapid expansion (or alternatively of limited informativeness of the marker). Expanded sampling within India revealed multiple clades of diversity in RrC I and suggested that the west coast and Western Ghats Mountain range served as source populations for the global expansion.^[13] The global samples are in a unique and recently derived clade suggesting diversification after expansion (Figure 1b), and possible back-migration to India.

The earliest firm evidence for commensal *R. rattus* outside its native range in southern India comes from third millennium BC proto-urban settlements in the Indus valley and Mesopotamia, though there is disputed subfossil evidence of a free-living Levantine population in the early Holocene.^[14] Populations on Mediterranean islands are confirmed by the late first millennium BC, while rats subsequently spread through the

Roman Empire, particularly along major communication routes, and were widespread throughout Europe by the thirteenth century AD.^[15,16] The earliest sub-Saharan African zooarchaeological finds, from seventh to eighth century AD Zanzibar and Pemba islands, coincide with the emergence of long-range trade networks around the Indian Ocean.^[17] This may have led to the high frequency mitochondrial haplotypes found along the eastern African coast and Madagascar, which contrast with west African haplotypes more closely associated with the Arabian peninsula.^[13,18]

In contrast RrC II is thought to have expanded from modern Myanmar and Thailand eastward to China and into Japan (Figure 1c), while RrC IV native to modern day Cambodia and Vietnam expanded southward to the Indonesian Peninsula based on mitochondrial phylogeographies.^[10] Although RrC III was identified as a unique mitochondrial clade,^[10,19] nuclear and morphometric analyses group it with RrC II^[20] Pacific house rats have been found in North America^[21] and South Africa;^[22] however, lack of phylogeographic resolution prevents identification of source populations. (Aplin et al., 2011). Zooarchaeological evidence for commensal rats and their dispersal in southern and eastern Asia is problematic due to the presence of multiple species with similar morphologies, although recent advances in molecular and morphometric identification are likely to improve the situation.

1.2. *Rattus exulans*

The location of the natal range of *R. exulans* is an open question, although hypothesized to be the island of Flores due to high mitochondrial diversity^[23] (yet secondary contact is an alternative hypothesis). Four mitogenome lineages have been identified and are used to infer the timing and routes of the peopling of Near and Far Oceania.^[24,25] In Pacific rats, lineage II is found in the Philippines, New Guinea, and Santa Cruz Island, while lineage III extends throughout Far Oceania including New Zealand, Hawaiian Islands, and Easter Island.^[24,26] Finally, lineage I and an un-numbered clade expanded to Borneo and the Philippines, and southeast Asia (SEA), respectively (Figure 1d),^[23,26] under the hypothesis that Flores is the ancestral range.

1.3. *Rattus norvegicus*

In contrast to the other commensal lineages that originated in southern Asia, brown rats are thought to be from northern China and Mongolia (and possibly into southeast Siberia as the natal range extent is an open question), thus their tolerance of temperate and cold environments. This northern origin may explain the late start (thirteenth century AD) of global range expansion (Figure 1e);^[27] first toward SEA and coastal ports, then into the Middle East and Europe via trade networks, and finally globally to western Africa, eastern North America, South America, and New Zealand.^[28,29] Rats also expanded from the ancestral range eastward into China, Russia, and eventually to western North America.^[28,30] Analyses from South Africa have identified multiple introductions, both from European^[22] and an unknown source population.^[31]

The global spread of *R. norvegicus* has seen little zooarchaeological study due to challenges with species identification and dating; thus, documentary evidence of brown rat in Europe from the 18th C AD represents a terminus ante quem for its presence.^[32] Attribution of most earlier zooarchaeological finds to *R. rattus* may represent confirmation bias, given that postcranial specimens of the two species cannot be reliably distinguished morphologically.^[33]

1.4. Linking Rodent and Human Demography

Though subject to far less historical and archaeological attention than domestic species, commensals are a near-ubiquitous element of human existence, with profound impacts on health, subsistence, and day-to-day life. At the same time, humans have inadvertently influenced these species' evolution and distribution, creating new niches and enabling colonization beyond native ranges.^[34] The resulting dependency on humans makes these animals powerful but largely untapped proxies for human processes including sedentism, settlement development/urbanism, migration, and trade.

The evolution of commensalism in different species is tied to characteristics of human societies, most obviously sedentism, which appears to underlie the emergence of commensal *Mus musculus* in the Levant c.13 000 BC, shortly before the development of agriculture.^[35] Size and form of settlements may also be prerequisites for commensal populations: western house mouse (*M. m. domesticus*) spread rapidly alongside farming around parts of the eastern Mediterranean characterized by large, dense, long-lived early farming settlements, but not into the western Mediterranean or temperate Europe, where early settlements were typically smaller and more dispersed.^[36]

Colonization histories of commensals may shed light on timing and routes of human migrations, such as with the Pacific rat. Likewise, human-mediated dispersals can elucidate contacts between regions and societies that might otherwise be obscure. *Microtus arvalis*—unknown in mainland Britain, and not generally considered commensal—reached Orkney with or shortly after agriculture in the fourth millennium BC, indicating significant maritime contact between the archipelago and continental Europe during the Neolithic period.^[37] The dispersal of black rat from India to the Mediterranean and Africa, meanwhile, probably owes more to trade networks than to human population movements.^[17,38] Combining these geographically separate events for expansion of commensals builds an underlying picture of which human societies were connecting with each other and when; and different species identify unique connections based on their natal ranges.

2. Phylogeography and Zooarchaeology Offer Different Insights on Range Expansions, but a Complete Picture When Integrated

Where phylogeography provides a broad picture of geographic patterns of diversity and timing of range expansions, (sub)fossil evidence can refine timescales and reveal past colonization events of extirpated populations. For commensal and domestic

species, such evidence derives primarily from zooarchaeology. Notably, population genomic studies of single sites can contribute to temporal inference particularly when using coalescent approaches to estimate parameters including time since founding or change in population size.^[39] Using individual population histories may provide context for understanding variability in environment related to commensal rodent presence.^[40] We detail limitations of both phylogeography and zooarchaeology, then consider how an integrated perspective would bolster inference specifically related to commensal rats.

2.1. Limitations of Phylogeography

Phylogeographic studies elucidate the geographic ranges of within species lineages and allow inference of the directionality from source to newly established populations; yet we note three limitations. Mito-nuclear discordance is one of the most consequential limitations in phylogeography. As phylogeographic studies have transitioned to investigating both cytoplasmic and nuclear genomes, a high prevalence of mito-nuclear discordance has been observed across taxa.^[20,41] Thus, studies that only investigate mitochondrial patterns of geographic variation may infer incorrect range extents for lineages and either under- or overestimate diversity in secondary contact zones. Without information from the nuclear genome, those patterns cannot be elucidated nor the specific evolutionary mechanism that led to mito-nuclear discordance inferred. A further weakness of mitochondrial-only phylogeography is the presence of a single high-frequency haplotype across broad geographic areas, resulting in little to no data for fine-scale inference particularly when compared to using a population genomics approach.

Phylogeographic studies perform poorly at elucidating temporal change within a geographic site. Extirpated populations represent an extreme case where contemporary samples would not exist, thus there could be no inference that a species or lineage was ever present. Population replacement may or may not leave a genetic signature depending on how the succession occurred. A scenario where a geographic site was occupied, extirpated, then recolonized would have a true history of a longer-term presence of a species than a demographic model would estimate. Additionally, the lineages that re-colonized the site may differ from the original. By contrast, if there was gene flow during population replacement, we may observe admixture, introgression, or mito-nuclear discordance. With specific respect to anthropogenic movement of commensal species, phylogeography necessarily misses lineages transported by humans that did not establish populations or contribute to gene flow at a geographic site particularly due to competition with conspecifics.^[42]

Phylogeographic inference does not necessitate continuous sampling across the range, which generally is a strength. However, unsampled populations may lead to erroneous inference, and this is especially problematic when ancestral range populations are not sampled, although inclusion of “ghost” populations in coalescent models may aid in demographic inference.^[43] Conversely, uneven geographic sampling may also lead to incorrect inference. While rarefaction analyses of diversity estimates aid interpretation,^[44] they may be insufficient in secondary contact zones or regions of back migrations.

2.2. Limitations of Zooarchaeology

Zooarchaeology can provide direct rather than inferred evidence for the presence of a species in a given time and place, including extirpated or replaced populations. This comes with significant challenges in terms of dating and species identification, exacerbated by variable preservation and recovery. Confident morphological identification of *Rattus* species is typically limited to cranial elements;^[33] size is a poor criterion even where skeletally mature specimens are available, given overlapping size distributions^[45] and marked variation through time and space. For example, some past populations of *R. rattus* were much larger than known today.^[38,46] Recent development of low-cost, minimally destructive collagen fingerprinting (“ZooMS”; **Figure 2**) mitigates this problem, allowing distinction between *R. rattus*, *R. norvegicus*, and *R. exulans*, at least.^[17,47] Confident dating can be problematic due to bioturbation and to the burrowing behaviors of rats, potentially allowing recent remains to penetrate earlier deposits. Direct radiocarbon dating is thus invaluable, and is now possible on very small samples,^[48] although its utility is limited by the shape of the calibration curve—notably for the eighteenth to early twentieth centuries (**Figure 3**)—and by carbon reservoir effects where rats consumed food from aquatic ecosystems.^[49] Finally, recovery of small mammal bones is highly dependent on excavation strategies that vary between archaeological traditions, potentially introducing systematic geotemporal biases.

2.3. Integrating the Disciplines

The spatial and temporal nature of samples links these disciplines; yet the power of an integrated approach comes from what we learn about humans by studying commensals through different lenses. Spatial inference goes beyond geographic coordinates to include important information about habitat. We recognize that biases in contemporary and historic sampling related to ease of site access and to wider research/development agendas that determine excavation priorities, respectively, will influence our understanding of the niche and interactions with humans. The temporal link comes from combining estimates of lineage divergence times from coalescent analyses of gene trees, with estimated age ranges of individual archaeological contexts which should be similar. Incomplete sampling within either subdiscipline would still allow inference from the other.

2.3.1. Zooarchaeological Samples as a Source of aDNA

Genetic analysis of zooarchaeological specimens can be a powerful tool, specifically for identifying partial or full population replacement over time.^[50] Beyond identifying temporal stability, aDNA samples also contribute to estimates of changing effective population size, and may identify extinct clades of genetic diversity. Further, analysis of pathogen aDNA from commensal fauna may elucidate the phylogeography of zoonotic diseases such as plague^[51] and leprosy.^[52]

The initial challenges associated with DNA extraction, sequencing, and GC conversion have largely been overcome for ancient samples.^[53] Further, *R. norvegicus* has an annotated

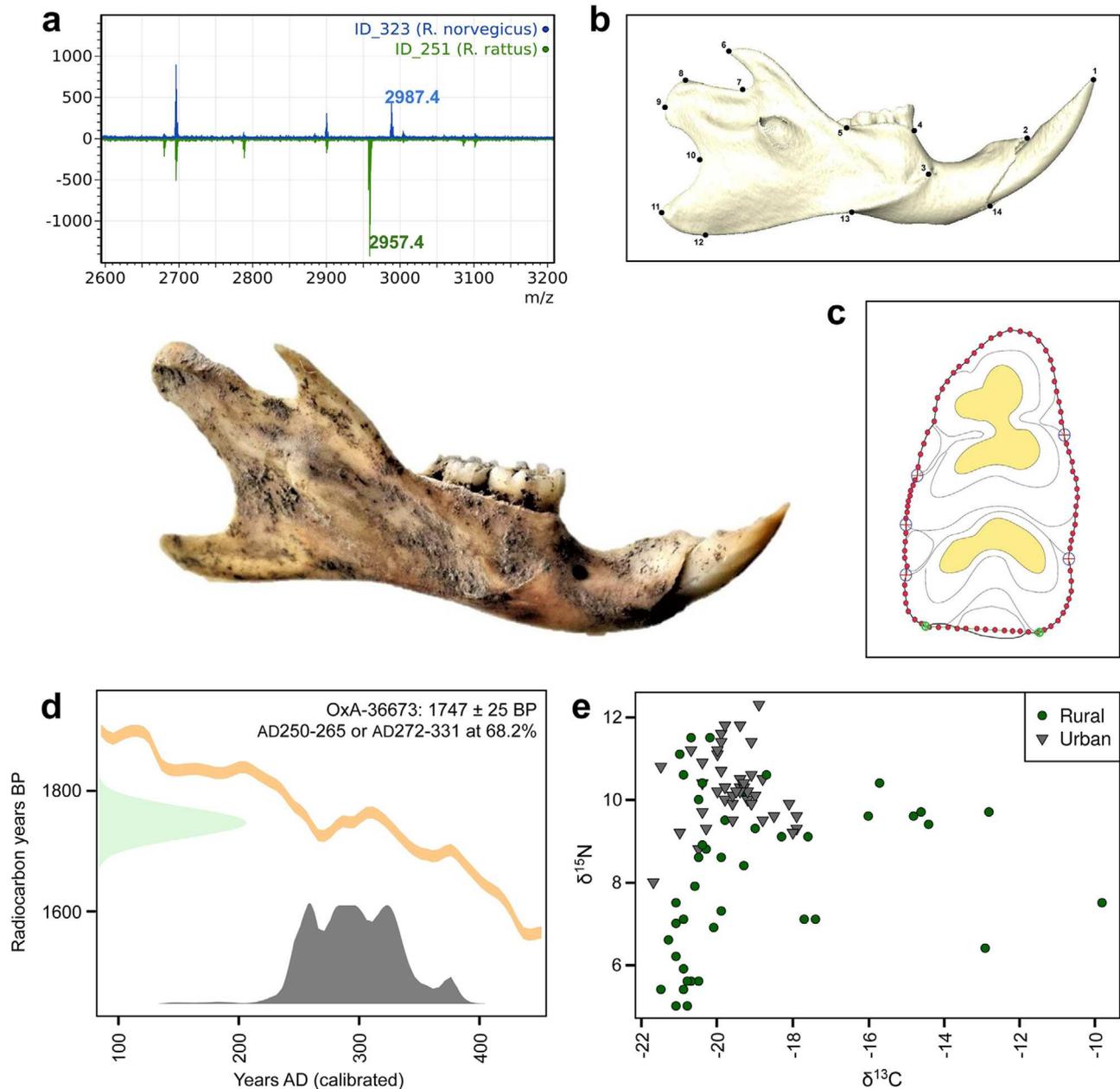


Figure 2. Archaeological *R. rattus* mandible (image: Ewan Chipping), showing examples of further morphological and molecular analyses: a) taxonomic identification of post-medieval Dutch rats via ZooMS collagen fingerprinting;^[47] b) geometric morphometric (GMM) analysis of functional variation in mandibular shape (image: Phil Cox); c) GMM analysis of first molar shape for phylogenetic signal (image: Arden Hulme–Beaman c) Reproduced under the terms and conditions of the Creative Commons Attribution 4.0 International License.^[61a] Copyright 2018, the Authors.); d) calibrated radiocarbon date on *R. rattus* bone from Roman Portugal (made with *rcarbon*^[82]); e) dietary isotopic analysis of *R. norvegicus* bones from nineteenth century Ontario.^[65]

reference genome (Rnor_6.0^[54]) allowing whole genome resequencing reads to be mapped for identification of variants and ancestral states for brown rats and other *Rattus* species. Mirroring broader trends in evolutionary genetics, analysis of aDNA has transitioned from single or few gene analyses (sometimes only using the mitochondrion) to resequencing the nuclear genome. Thus, contemporary challenges lie within the data analysis, particularly developing new methods that explicitly incorporate spatio-temporal variation.^[55]

Incorporation of genotypes from aDNA remains expensive and relatively inaccessible, requiring first expertise on, and access to, sites/samples pertinent to the phylogeographic questions; and second laboratory facilities with clean rooms and specialized bioinformatic expertise. The destructive nature of genetic analysis raises ethical issues given the scarcity and irreplaceability of archaeological samples,^[56] and this is exacerbated by success rates that can be low depending on age, climate, and burial environment. When dealing with small mammals it is

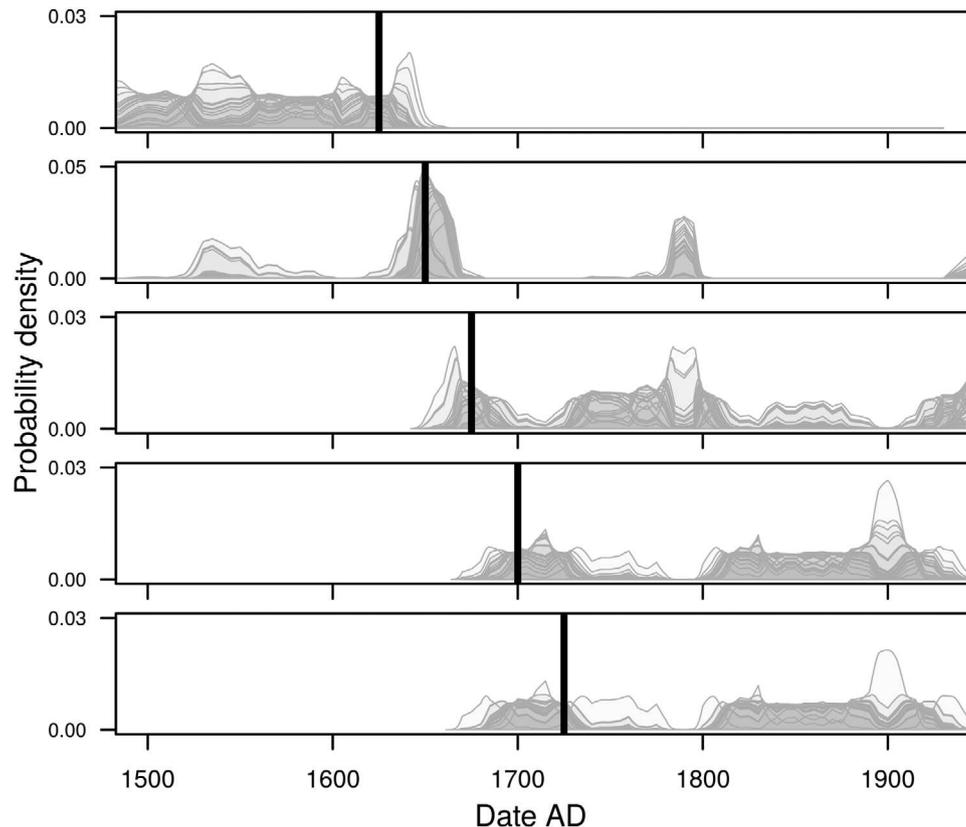


Figure 3. Simulated radiocarbon dates for hypothetical samples at 25-year intervals from AD 1625–1725, produced using *rcarbon*.^[82] Each pane shows the superimposed calibrated probability distributions for 20 simulated radiocarbon dates corresponding to a single calendar year, indicated by the vertical line, assuming 100% terrestrial diet and an error of ± 20 years. Samples from earlier than c. 1650 are likely to stand out as pre-dating the assumed eighteenth century date for *R. norvegicus* colonization of Europe, but may appear earlier than they really are; later samples can only be dated as c. 1650–1950, precluding refinement of the colonization chronology within the accepted range.

often necessary to destroy substantial portions or even entire specimens, heightening ethical concerns and precluding re-analysis of failed samples; by contrast larger taxa may be subsampled with minimal loss of potential for further research. Micromammal aDNA studies have thus lagged behind other taxa, largely concentrating on cave sites where preservation conditions are typically stable and sample sizes often large.^[57] While population-level analyses are the goal, avoiding repeat sampling of individuals may reduce sample sizes to as little as one in the smaller micromammal assemblages typical of settlement sites. Notably, genomic scale analyses are better able to utilize a single sample than mitochondrial-only analyses.

2.3.2. Zooarchaeological Data on Commensal–Human Relationships

Apart from ground-truthing and refining molecular chronologies, zooarchaeological remains can potentially reveal past dispersals and extirpations. They may also provide minimal dates for commensalism, for example, placing the origins of house mice at c. 13 000 BC in the Levant.^[35] Regular presence of a given small mammal species in anthropogenic contexts may indicate colonization of a commensal niche, where understanding of

deposit formation rules out other explanations, such as raptor activity in disused buildings^[58] or exploitation as human food.^[59] Firmer evidence comes with dispersal beyond the species' native range, while presence/absence in particular site types may provide evidence for the degree of anthrodependency. In Roman Europe, *R. rattus* finds are most common in urban settlements but also occur in villas (i.e., small, high-status rural settlements)^[45] and forts, suggesting that connectivity of settlements may have been as important as their size—although cities are likely to have been critical at a meta-population level. Such insights can be especially valuable given the impact of more recent dispersals: in Europe, zooarchaeology provides the only glimpse at the commensal ecology of *R. rattus* prior to arrival of *R. norvegicus*. If we can link commensal taxa to settlement conditions then we can also apply this in reverse, using their presence in poorly understood sites as a proxy for those conditions. One complication is the varying degree to which different species may become "feral" or revert to a wildtype independent of human settlements. If such a phenomenon is widespread then it may be difficult to use some species as proxies of human activity. Apparent extirpation of *R. rattus* from Britain at the end of the Roman period^[60] supports the argument that rats were indeed dependent on particular settlement types in this specific case, but in other contexts zooarchaeological evidence for anthrodependency may be less

clear-cut. Commensal *Rattus* and *Mus* are well-known to colonize islands free of human settlements, but these ecological situations are also usually free of many mammalian competitors or predators. The extent of reversion of anthrodependent populations to non-commensal wildtypes should be considered an open question of interest.

Bones and teeth from archaeological sites permit further inference (Figure 2). Where remains are more-or-less intact, Geometric Morphometric Methods (GMM) permit quantification of fine-scale shape variation. GMM has been applied to murine molar teeth to identify (sub)species^[61] and to detect finer-scale structuring, either alongside aDNA or alone as a phylogenetic proxy.^[62] By contrast, mandibular shape is highly plastic with regard to dietary and environmental factors,^[63] potentially showing adaptive signals even over short timescales.^[64] Stable isotope analysis of bone collagen also provides dietary information for commensal fauna in relation to humans and to settlement context, for example, showing differences between rural and urban *R. norvegicus* in nineteenth century Ontario.^[65] Where human bones are not available or cannot be sampled, commensal rats arguably represent a better proxy for human diet than dogs, the conventional choice.^[66] Isotopic analysis of *R. exulans* has also been used as a proxy for landscape change following human colonization of Pacific islands.^[67]

3. Open Questions toward Understanding Commensal *Rattus*

3.1. *R. rattus* and *R. tanezumi*

Taxonomy of the RrC is unresolved and development of diagnostic markers is most needed, particularly that distinguish lineages, hybrids, and within-lineage diversity. Even without taxonomic resolution, *R. rattus* and *R. tanezumi* expanded in different directions and appear to compete and/or hybridize with each other in portions of the introduced ranges.^[10,21] Given that most previous work on these species relied heavily on mitochondrial DNA analyses, it is premature to delineate specific hypotheses about invasion histories before preliminary nuclear genomic analyses are completed.

A robust nuclear phylogeographic analysis for black rats would aid in understanding the source populations and routes of dispersal into Europe both in the early first millennium AD then again in the ninth century AD. The presence of *R. rattus* throughout the Roman Empire, and its near-total absence in Europe or Africa beyond the frontier, suggest that it depended upon the urbanism and high-volume bulk trade of the Roman economic system. Following the break-up of the western Empire from the fifth century AD, rats were seemingly extirpated from the northern and western provinces,^[38] then reappeared in key Viking Age trading centers around the North Sea and—for the first time—Baltic littorals, again indicating a reliance on connectivity and (nascent) urbanism.^[15] Phylogeography and zooarchaeology may help elucidate the route of this (re)colonization, which is potentially highly significant for medieval economic history,^[15] and also interrogate whether refugial populations from the first wave served as a source for the second colonization.

3.2. *R. exulans*

Pacific rat lineage III may have diverged early (Figure 1a), where this sample was collected in Far Oceania^[26] yet the center of diversity was described westward on Flores.^[23] While competitive exclusion in Near Oceania of lineage III haplotypes may explain their Far Oceania distribution, it is unsatisfying that the pre-expansion range remains unknown. A nuclear phylogeographic analysis would add resolution to understanding both the movement of rats and people into the Pacific Ocean, and is particularly important given findings that the mitochondrial control region has low resolution in this species.^[26]

3.3. *R. norvegicus*

We outline five pressing phylogeographic questions. First, what was the extent of the natal range? Climatic tolerance,^[68] and mitochondrial and nuclear phylogeographies^[27,69] suggest northern China as the natal range, yet the extent into the Mongolian steppe and southeastern Siberia remains unknown. Second, brown rats may have been present in the Japanese archipelago before humans, but little genomic information or subfossil remains are available to examine whether ancient diversity persists. Non-commensal rats are still present on some Japanese islands, and are known to burrow near the sea where they feed primarily on fish and mollusks.^[70] Third, what were the source populations and timing for eastward expansion of the Asian lineage to the west coast of North America?^[28] Given climatic constraints, it is unlikely that brown rats crossed the land bridge before or with humans that colonized North America. Dense sampling around the northern Pacific Rim will be needed for a regional phylogeography; and zooarchaeological remains in North America may dramatically change hypotheses.

Fourth, the hypothesis that brown rats spread southward in coastal China with developing urbanization could be tested using dense sampling of the genomic diversity within China to refine our understanding of centers of diversity and patterns of movement. Although high mitochondrial diversity within China strongly suggests a Chinese center of origin, the identification of a north versus south China origin is less clear.^[69] Figure 1 in Song et al.^[69] indicates slightly higher haplotype diversity in the northeast versus south of China. The tree topology in Figure 1A of Zeng et al.^[71] and the demographic model in Puckett & Munshi-South^[27] further support a northern center of origin followed by southern expansion. Dated subfossil remains from Chinese archaeological sites might be even more informative given that contemporary multidirectional gene flow may have occurred. A related question is why brown rats seem to have not expanded into SEA more than a millennium ago,^[27] despite the establishment of economic ties between China and SEA well before this time period. One possibility is that climatic conditions (e.g., sub-optimal tropical climate and/or Medieval Climate Anomaly) and other factors prevented early cities in southern China and SEA from reaching levels of human activity that would support commensal brown rats in an otherwise suboptimal tropical environment.

Fifth, the specific routes and timing of westward migration from SEA and entrance into Europe have not been resolved.

Several possible routes exist, but none is clearly supported by the evidence. The Silk Road connected northern China to western Asia for centuries before brown rat arrival in Europe, raising the question of why rats did not arrive earlier. These trade routes travelled through arid, sparsely populated areas that may not have supported overland rat migrations. Alternatively, brown rats could have followed coastal trade routes around SEA and India that ultimately landed in the Middle East and Caucasus. European colonial shipping may also have allowed long-distance maritime movements directly from east Asia and SEA to Europe.^[72] Thus, both contemporary genomic data and confirmed zooarchaeological data (i.e., supported by molecular identifications and direct dating) are needed from ports and settlements along these possible routes.

3.4. All Commensal Rats

Commensal rodents show both inter-^[73] and intra-specific^[74] competition that may limit their distributions. Black rat populations in Europe declined or disappeared from many locations following brown rat invasion.^[75] Although both species rely heavily on human sources of food, their ecology and behavior vary, as the brown rat is geotropic, and the black rat adept at using vegetation, trees, and the upper reaches of buildings. Brown rats may also exclude black rats from ground-level habitat through aggressive interactions.^[76] One hypothesis is that the brown rat is larger and more aggressive than the black rat, and thus a better competitor for human food. However, both species coexist in subtropical and tropical environments, as well as in temperate locations with mild winters such as the west coast of North America. Thus, it is likely that the superior competitive ability of brown rats is contingent on climate and/or habitat type, although brown rats also thrive in tropical cities. Other factors, such as the spread of parasites or disease from one species to the other, may have also played a role^[77] in the displacement of black by brown rats. Almost no research effort has been put forth toward understanding where, and under what conditions, these species or other commensal *Rattus* coexist as invasive species. One potential path forward may be to characterize the fundamental and realized niches of both species in isolation and in coexistence scenarios, while trying to control for climate, habitat type, and other factors such as first arrival, which phylogeography or zooarchaeology may contribute to identifying. As with native commensal rodents in Niger, these two *Rattus* species may be spatially segregated in their use of habitat within invaded regions,^[78] or perhaps microhabitats on a scale heretofore unexamined.

Other priority research will focus on identifying tipping points needed for commensal range expansions. These could be due to landscape level variation in settlement type and density, to biotic variation in either rat or human density, or initiation of new societal connections.

4. Conclusions and Outlook

The integration of phylogeography and zooarchaeology offers immense promise to elucidate how urbanism and human communication and migration facilitated range expansions of

commensal *Rattus*. Answering open questions regarding *Rattus* species delimitation,^[3,5] biogeography, and repeating phylogeographic analyses with nuclear data will provide a strong foundation toward understanding both the evolution of commensalism and human-commensal interactions. We see high value in taking a comparative approach between species to illuminate these processes. For example, comparing historic brown rat expansion within China to black rat expansion in the Roman Empire would further refine the necessary conditions for commensalism.

On a broader scale, such lines of thought raise the question of why all of our major commensal rodent species originated primarily in south and east Asia. For example, why did the diverse Mesoamerican and South American rodents not produce commensal species, despite agricultural societies and ancient cities that persisted for hundreds of years? The answers require greater comparative work, but levels of urbanization, human population density, and biological characteristics of the local rodent species pool likely must all converge to drive the evolution of commensalism.

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Conflict of Interest

The authors declare no conflict of interest.

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