



Stowaways: Maritime ecology of the oldest commensal ship rats (*Rattus rattus*) found on a Mediterranean shipwreck

Sierra Harding^{a,b,*}, Madeline Tapson^c, Guy Bar-Oz^b, Deborah Cvikel^a, Nimrod Marom^b

^a Leon Recanati Institute for Maritime Studies, School of Archaeology and Maritime Cultures, University of Haifa, Abba Khushy Ave. 199, Haifa 3498838, Israel

^b Laboratory of Archaeozoology, School of Archaeology and Maritime Cultures, University of Haifa, Abba Khushy Ave. 199, Haifa 3498838, Israel

^c McMaster Ancient DNA Centre, Department of Anthropology, McMaster University, 1280 Main St W, Hamilton, ON L8S 4L8, Canada

ARTICLE INFO

Keywords:

aDNA
Ecology
Island rule
Ma'agan Mikhael B
Plague
Shipwreck
Ship rats

ABSTRACT

Ship rats (*Rattus rattus*) have successfully colonized six continents and 80% of islands worldwide by stowing-away on anthropogenic vessels. Numerous zooarchaeological and metagenomic studies have contributed to tracing the western dispersal of ship rats out of the Indian subcontinent and into the Mediterranean Basin, North Africa, and Europe. This has increased understanding of historical maritime mobility, trade contacts, and the spread of pandemic disease such as the plague. Moreover, considerable research has been conducted on the behavior, ecology, and population dynamics of ship rats in invaded areas, which supports conservation and eradication efforts. However, few studies have shed light on the mode of travel in between the geographic origins and destinations of ship rats, such as ships and boats, which act as mobile, commensal habitat for this cosmopolitan species. We address this lacuna here, by analyzing an assemblage of ship rat remains from an early Islamic period shipwreck, the Ma'agan Mikhael B, located on the Carmel coast of modern Israel. Using zooarchaeological, biometrical, and palaeogenetic (aDNA) methodologies, we investigated the maritime ecology of ship rats regarding dispersal behavior, habitat selection, source-sink dynamics, and relative body size. The results of this study suggest that ship rats actively inhabited the Ma'agan Mikhael B as part of their habitat selection processes, that conditions onboard provided high-quality habitat (adequate food and harborage, likely absence of predators and disease), and that they appear to have exhibited a degree of gigantism, possibly due to 'island rule'. This study has implications for future metapopulation genetic studies on ship rats, as well as shows the value of zooarchaeological analysis in understanding the ecological circumstances of the maritime mobility of ship rats in the Mediterranean region.

1. Introduction

As one of the world's most invasive species, the common black rat (also known as ship rat, house rat, roof rat, fruit rat, Alexandrine rat and *Rattus rattus* complex [RrC] Lineage 1 *sensu* [Aplin et al. \(2011\)](#)) has successfully colonized six continents and 80% of islands around the globe ([Cassaing et al., 2007](#); [Caut et al., 2008](#); [Feng and Himsworth, 2014](#); [Hooker and Innes, 1995](#); [Innes et al., 2001](#); [King et al., 2011, 2014](#); [Ventura and López Fuster, 2000](#)). This has been facilitated by their critical survival advantages of prolific reproduction biology, omnivory, and a remarkable adaptability to anthropogenic environments ([Innes et al., 2001](#); [King et al., 2011, 2014](#); [Puckett et al., 2020](#)). The extensive mobility of ship rats has been aided by stowing-away on human vessels

and vehicles, then subsequently establishing populations in areas outside of their native geographic range in South Asia ([Aplin et al., 2011](#); [Armitage, 2010](#); [Ervynck, 2002](#); [McCormick, 2003](#); [Rowe et al., 2011](#)).

The western dispersal of black rats along archaic land and sea trade routes out of the Indian subcontinent, through the Middle East and via the Persian Gulf, to the Levant, North Africa, and Europe has been revealed by zooarchaeological ([Armitage, 2010](#); [Ervynck, 2002](#); [Oueslati et al., 2020](#); [Panagiotakopulu, 2004](#); [Puckett et al., 2020](#); [Vigne and Valladas, 1996](#); [von den Driesch and Boessneck, 1983](#)) and metagenomic analyses ([Aplin et al., 2011](#); [Baig et al., 2019](#); [Cheylan et al., 1998](#); [Colangelo et al., 2015](#); [Yu et al., 2022](#)). The results of these studies have been utilized as a bio-proxy for historical maritime mobility, trade contacts, and pandemics—such as the plague—around the

Abbreviations: MMB, Ma'agan Mikhael B; RSI, Relative size index; TTL, Total length; CBL, Condylbasal length; ZYG, Zygomatic breadth; CTR, Cheektooth row.

* Corresponding author.

E-mail address: sharding@campus.haifa.ac.il (S. Harding).

<https://doi.org/10.1016/j.jasrep.2023.103947>

Received 18 September 2022; Received in revised form 25 February 2023; Accepted 8 March 2023

2352-409X/© 2023 Elsevier Ltd. All rights reserved.

Mediterranean Basin and on the Eurasian continent (Armitage, 2010; Armitage et al., 1984; Audoin-Rouzeau, 1999; Audoin-Rouzeau and Vigne, 1994, 1997; McCormick, 2003; Panagiotakopulu, 2004; Puckett et al., 2020). Other investigations into black rat phylogeography, behavior, and ecology have been geared toward eradication efforts in invaded areas, especially in the New World (Abdelkarim et al., 2005; Caut et al., 2008; Escoriza, 2020; Ewer, 1971; Feng and Himsworth, 2014; Granjon and Cheylan, 1990b, 1990a; Hooker and Innes, 1995; Innes et al., 2001; King et al., 2014, 2011; Wilmshurst et al., 2021). These previous works have illuminated many themes relating to the ‘who’, ‘what’, ‘where’, and ‘when’ of near-global ship rat invasions throughout time. Fewer studies have addressed the mechanics of ‘why’ and ‘how’ these commensal rodents occupy carts, river boats, and sea-going ships (Armitage, 1993, 1995, 2013; McCormick, 2003; Williams, 1932).

Ship rat infestations on large ships traversing the world’s oceans have been known historically to reach such epic proportions that states-of-emergency were declared by captains (Armitage, 1993, 2013) and large-scale eradication efforts ensued at ports-of-call (Williams, 1932). Armitage (1995) noted that some early modern ships supported entire colonies of rats; many of these individuals spent their entire lives aboard, and there were established, core populations evidenced by the presence of both sexes and the spectrum of age classes (very young–mature). Yet, the concept of ships as a mobile, semi-insular, commensal habitat for rats has not been thoroughly explored in the literature, probably due to the paucity of rodent remains recovered from ancient Mediterranean (Cucchi, 2008; Vigne and Villié, 1995) and early modern New World shipwrecks (Armitage, 1989, 1993, 1995, 2013). As a result, several questions remain unanswered regarding the ecology of rodent populations on ships. Some unresolved queries on this topic include: which environmental cues could cause rats to board a ship at harbor? What conditions onboard would contribute to high-quality habitat for a black rat? Conversely, what ecological hazards, such as predators or pathogens, might render a ship habitat an ‘ecological trap’ which could cause individuals to make maladaptive selection decisions (Schlaepfer et al., 2002)? Would a rat colony inhabiting a ship be considered a source, sink, or pseudo-sink population? Being semi-insular—closed at sea, open at port—could a ship be considered analogous to a naturally fragmented landscape, i.e. a near-shore island habitat which is sometimes connected to the mainland due to tidal flows? If so, might black rat populations on ships exhibit a degree of gigantism, as explained by the ‘island rule’ in some cases?

There is a general assumption in the literature that ship rats appear passively on watercraft, transferred blindly along with large grain cargoes or food supplies (Armitage, 1993, 1995, 2010; McCormick, 2003). Though this is a viable circumstance (Williams, 1932), it does not account for the instinct-driven dispersal behavior in which black rats actively engage as part of their habitat selection processes (Stamps, 2008). In ecology, source populations are those which are self-sustaining, meaning reproduction exceeds mortality and immigration is lower than emigration (Furrer and Pasinelli, 2016; Pulliam, 1988). A sink population is one that is not self-sufficient and unviable in the absence of immigration, while a pseudo-sink is one that appears as nonviable due to depressed fecundity or increased mortality resulting from density dependence, but is in fact viable due to immigration of new individuals (Watkinson and Sutherland, 1995). Though it is common knowledge that the global mobility of black rats has been accomplished by stowing away on ships, dispersal mechanisms and source–sink fluctuations in metapopulations between harbors, ships, and islands are not currently well understood.

The ‘island rule’ has been used to explain the tendency for smaller animals on islands to exhibit gigantism, and conversely dwarfism in larger animals, compared to their nearest mainland counterparts (Foster, 1964; Van Valen, 1973). Although the island rule is controversial and contested for many species, rodents in the Muridae family, including ship rats, have been found to comply with it in general (Adler and

Levins, 1994; Lomolino, 2005, 1985; Meiri et al., 2008; Meiri et al., 2006; Russell et al., 2011). The island rule speaks to relative size differences in insular populations, while the term ‘island syndrome’ encompasses that phenomenon as well as a suite of behavioral adaptations and diversity in phenotypic traits that have been observed in island populations (Adler and Levins, 1994; Blondel, 2000; Cassaing et al., 2007; Granjon and Cheylan, 1990a; Juette et al., 2020; Russell et al., 2011). In the case of rodents, these traits include higher and more stable densities, longer life spans, increased body mass, as well as reduced aggressiveness, reproductive output, and dispersal ranges (Adler and Levins, 1994; Granjon and Cheylan, 1990a). Some driving factors behind this syndrome expressed in rodents include reduced predation stress, less inter- and intraspecific competition, and extension of ecological niche; the effects are not uniform, however, and also depend on island size, isolation, and trophic complexity (Adler and Levins, 1994; Juette et al., 2020; Russell et al., 2011). Gigantism has been previously observed in island populations of black rats in the Mediterranean Basin and east Atlantic (Granjon and Cheylan, 1990b; Ibrahim et al., 2017; Ramalhinho et al., 1996; Ventura and López Fuster, 2000). In this study, we limit our investigation to the island rule, and explore the possibility for a ship’s rat population to tend toward relatively larger body sizes than nearby mainland samples. We postulate that this could potentially be due to the ecological conditions of semi-insular, commensal habitats provided by large watercraft, which bear similarities to naturally fragmented landscapes in terms of intermittent barriers to dispersal, continuous migration processes, reduced trophic diversity, and varying degrees of isolation (Juette et al., 2020).

In the late antique Mediterranean Basin, perhaps the most prominent ecological hazard to black rats onboard a ship would have been the threat of plague, the effects of which were devastating to the surrounding regions. The first recorded plague pandemic, the Plague of Justinian, spread around the basin in cyclical outbreaks spanning two centuries between 541 and 750 CE (Little, 2006a). Modern plague research has focused largely on western European outbreaks, although historical records outline the repeated onslaught of plague reemergence throughout southwest Asia and north African regions (Little, 2006b). In late antiquity, the Plague of Justinian was documented in notable outbreaks by contemporary historians in surrounding regions such as Constantinople, Alexandria, and Syria (Little, 2006a; Morony, 2006; Stathakopoulos, 2006). Such records even suggest that plague was present in Gaza, the Negev, and regions surrounding Jerusalem, likely having been transported from Alexandria via ports in Gaza and Ashkelon in approximately 541 CE (Morony, 2006; Stathakopoulos, 2006).

Black rats, and their associated fleas (*Xenopsylla cheopis*), played a key role in plague persistence and reemergence (McCormick, 2003; Panagiotakopulu, 2004). Well-preserved black rat remains recovered from a ship which had been travelling near ports and regions afflicted with the Plague of Justinian in late antiquity present an interesting opportunity to not only explore the ecological ramifications of these occurrences on ship rat populations at sea, but also to expand our understanding of past plague outbreaks by screening ancient rodent remains contemporary with this historical pandemic for the presence of the bacteria *Yersinia pestis*, the causative agent of plague (Harbeck et al., 2013; Wagner et al., 2014; Wiechmann and Grupe, 2005). Although the exact mechanisms of these dynamics in historical contexts are still not completely understood, we can gain valuable insights by expanding our research efforts to focus on regions around the Mediterranean Basin known to have been afflicted by cyclical periods of historic plague outbreaks.

Considering the ecological dynamics outlined above, the current study aims to address these open questions by analyzing an assemblage of ship rat remains found during underwater excavations of the early Islamic period shipwreck Ma’agan Mikhael B discovered on the Carmel coast of modern Israel. The methods employed to analyze this assemblage include zooarchaeological, biometric, and palaeogenetic ancient DNA (aDNA) techniques. Zooarchaeological data contributed to

understanding the number of individuals onboard and their osteological health, sex, and spatial distribution, which informs upon questions regarding dispersal behavior, habitat selection, and source-sink dynamics. Biometric methods were used to estimate the body size and age of the archaeological specimens, as well as any relative degree of size difference from samples of Mediterranean ship rats. The aDNA analysis tested for the presence of *Yersinia pestis*, the bacterium which causes plague. Presence or absence of this disease, and other osteological pathology such as rickets, has implications for the habitat quality of the ship and could contribute to a greater understanding of rodent-plague dynamics on board a ship that was likely travelling between regions struck by the Plague of Justinian. The results of these analyses were then synthesized and discussed in light of previous knowledge of the behavior, ecology, and population dynamics of invasive black rats in commensal and feral contexts. Increased understanding of ship rats' interactions with watercraft habitats will benefit future phylogenetic and morphometric research on their mobility, dispersion, and (re) colonization events in the premodern (before 1500 CE) Mediterranean region, with further potential applications beyond this zone. This study also adds to the corpus of knowledge regarding historical plague vectors, and offers a fresh perspective to the anthropocentric discourse on black rats in the literature, by attempting to see ships from a rat's point-of-view.

2. The finds

2.1. The shipwreck

The Ma'agan Mikhael B shipwreck is located on the Carmel coast of modern Israel (32°33'18.7"N/34°54'16.1"E), approximately 30 km south of Haifa, and 3.2 nautical miles north of the historic harbor at Caesarea-Maritima (Fig. 1 inset) (Cohen and Cvikel, 2019). It rests 70 m offshore, in 1.5 msw and under 1.5 m of sand. The study of the shipwreck and its artifacts are overseen by one of the co-authors (D.C.), under the auspices of the Leon Recanati Institute for Maritime Studies (RIMS) at the University of Haifa. Radiocarbon analysis of samples from the ship's timbers and other organic remains has dated the site to 648–740 CE (Cohen and Cvikel, 2019), which falls during the early Islamic period in the region (Avni, 2014; Constable, 2003; Fischer and Taxel, 2014; Walmsley, 2000; Whitcomb, 1995). The ship was most likely a merchantman conducting maritime trade, and its original dimensions are estimated at 25 m in length (stem to stern) by 7 m in breadth (Cohen and Cvikel, 2019). Based on CAD renderings, the internal volume has been estimated at 313.88 m³, and the internal area (stem to stern, floor to wales) at 220.27 m² (N. Helfman, pers. comm.). The ship's ceramic, faunal, botanical, and entomological assemblages suggest a sailing route and trade contacts around the shores of the eastern Mediterranean, including Turkey, Cyprus, Egypt, and the Levant (Cohen and Cvikel, 2019, 2020; Creisher et al., 2019; Friedman and Cohen, 2023; Harding, 2021; Harding et al., 2022).

Seven excavation seasons have been conducted between 2016 and 2021 (Fig. 2A). These missions have revealed a mostly intact and

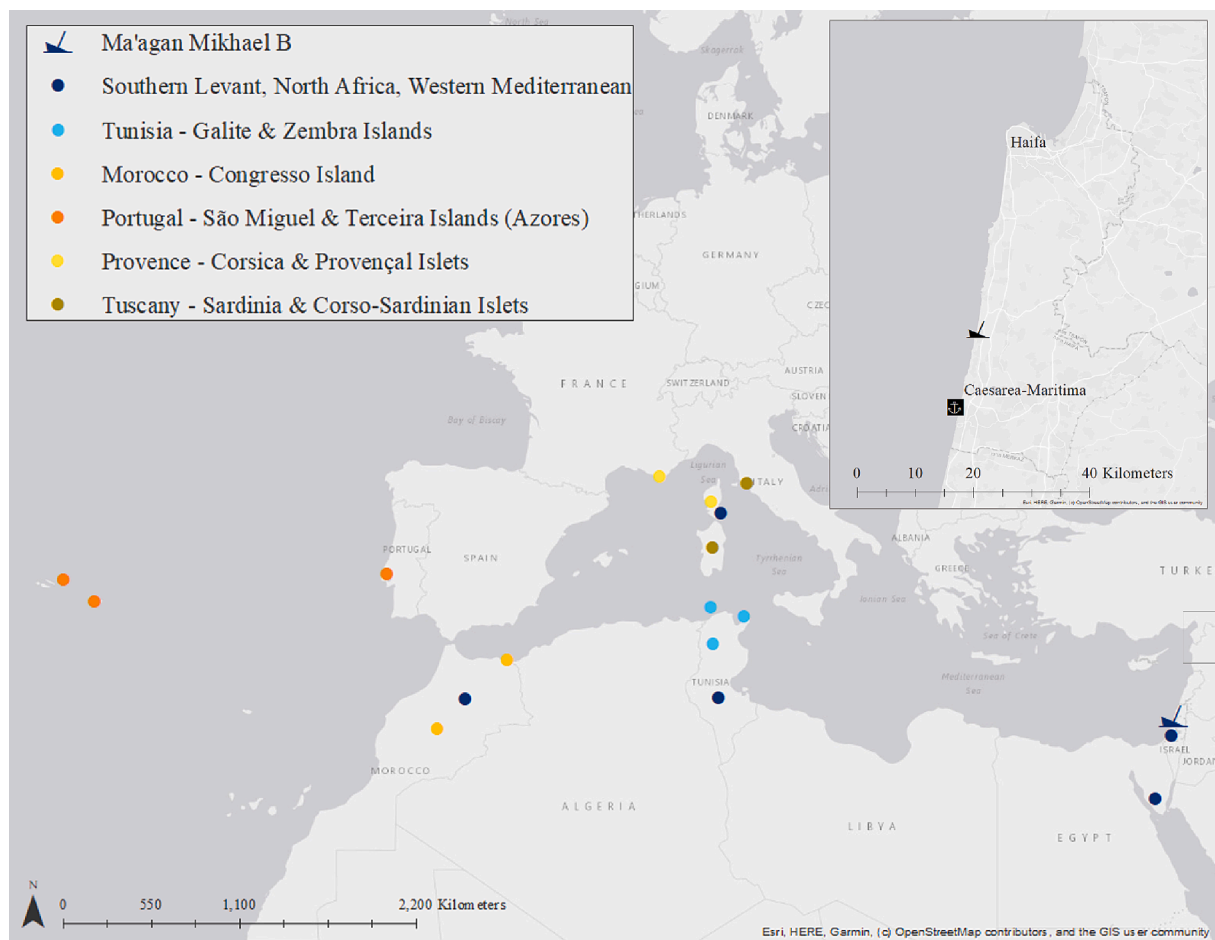


Fig. 1. Generalized geographic locations of comparative samples and datasets utilized throughout this study. Inset map shows the location of the Ma'agan Mikhael B shipwreck on the Carmel coast, not far from the historic harbor at Caesarea-Maritima and the city of Haifa. Map credit: S. Harding.

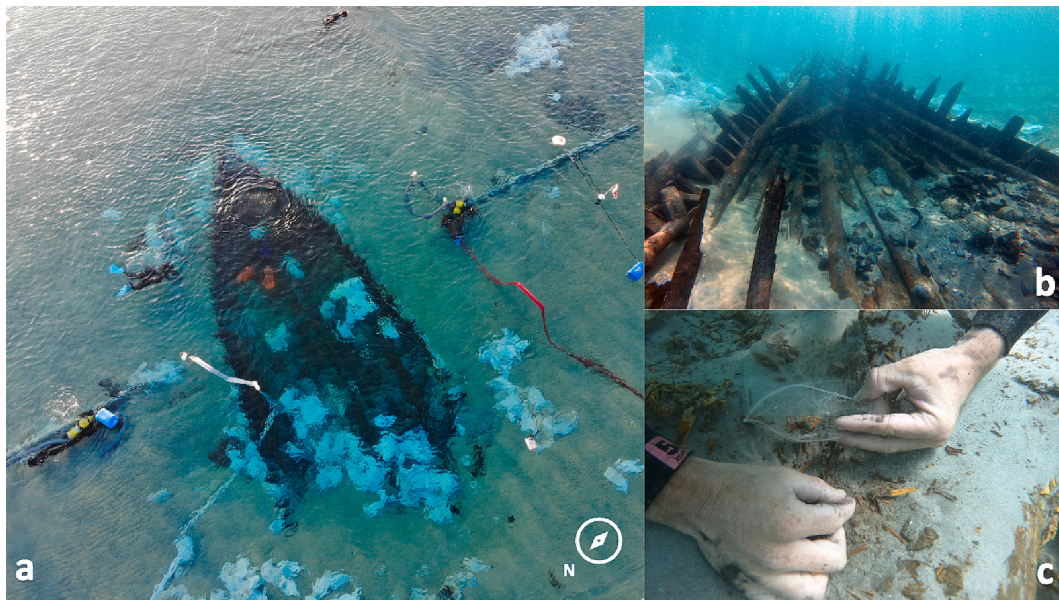


Fig. 2. A) Aerial view of the excavation of the bow area on the Ma'agan Mikhael B. Image credit: R. Levinson. B) Underwater view of the bow area where most ship rat remains were found. Image credit: A. Yurman. C) A diver collects ship rat bones during the underwater excavation. Image credit: A. Yurman.

extremely well-preserved hull (Fig. 2B), as well as significant assemblages of artifacts including ceramics, glass, coins, cordage, botanical, and faunal remains (Cohen and Cvikel, 2019, 2020; Creisher et al., 2019; Harding, 2021; Harding et al., 2022). The Ma'agan Mikhael B was heavily laden with a cargo of amphorae containing foodstuffs such as nuts, fruits, and olives (Cohen and Cvikel, 2019; Creisher et al., 2019). Cadelle beetles (*Tenebroides mauritanicus*) encased in the sealant of the ship's timbers suggested grain was among the crew's rations; however, pests such as wheat weevils (*Sitophilus granaries*), which could provide evidence for a large wheat shipment onboard, were absent (Friedman and Cohen, 2023). Diverse faunal remains were also identified, including domestic, wild, and commensal taxa (NISP = 256) and the bones of preserved fish within amphorae (NISP = 657) (Harding, 2021; Harding et al., 2022).

2.2. Rodent skeletal remains

The remains of small rodents were discovered during excavation, and retrieved by hand (Fig. 2C). The skeletal elements from each locus were placed in zip bags with seawater on-site, labeled and catalogued, then transferred to the Yaacov Yak Kahanov Laboratory for Ancient Ship Research at the University of Haifa for further analysis. In the laboratory, these specimens were removed from the zip bags and transferred to cardboard boxes. They were allowed to dry in refrigerated storage, and are conserved there at a stable temperature (5 °C). These skeletal elements were not desalinated prior to storage, in order to allow for advanced analyses including aDNA genomic testing.

3. Methods

3.1. Zooarchaeological identification

For all faunal remains recovered from the Ma'agan Mikhael B, species identification was conducted using the comparative collection at the Laboratory of Archaeozoology at the University of Haifa (Harding, 2021). Rodent skeletal element identification was aided by supporting literature (Armitage et al., 1984; Greene, 1935). Individual specimens were identified to taxon and skeletal element, assigned a catalogue number, and recorded in a database. Additional data per element was collected, including side, part, epiphyseal fusion status, and the tooth

wear stage (TWS) of the maxillary molar row (M^1 – M^3) after Armitage in Morales and Rodríguez (1997). Bone surface modifications were also observed and recorded, in order to further understand the peri- and postmortem histories of these faunal remains (Fernández-Jalvo and Andrews, 2016). Taphonomic factors included fragmentation, burning, coloration, sand abrasion stage, and marine corrosion level (see Supplement S1-2 for references, evaluation criteria, and target variables for each category (Harding and Tapson, 2023)).

3.2. Biometrics

Measurements were recorded in millimeters for the ship rat crania and mandibulae after the *Lepus* protocol in von den Driesch (1976: 50–51, 64, figs. 18a, 18b, 25). Specific definitions of these measurements are available in Supplement Tables S3-1, 2, 3, following von den Driesch (1976). Length and width measurements (greatest length [GL], greatest breadth [GB], proximal breadth [Bp], distal breadth [Bd]) of selected post-cranial bones were also noted; since there was no protocol specifically defined for rodent skeletons, we used the general guidance for mammal atlases and long bones (atlas, innominate, long bones, phalanges) (von den Driesch, 1976: 65–66). All measurements were taken by one of the co-authors (S.H.), using vernier calipers accurate to 0.01 mm.

Several biometric analyses in this study rely on comparative measurements of archaeological and modern black rats. Our null hypothesis was that there would be no statistically significant difference in cranial measurements of early Islamic period and modern black rats from the Mediterranean region, with an alpha level of significance at < 0.05 . If we could not reject the null hypothesis, then subsequent comparisons between the archaeological and modern datasets would be viable. To test this hypothesis, one of the co-authors (S.H.) collected cranial measurement data from samples of modern black rats derived from mainland populations in the Southern Levant (Israel and Sinai; $N = 76$) and North Africa (Morocco, Tunisia; $N = 32$), and island populations from the Western Mediterranean (Corsican islets of Porto Vecchio and Toro, Iles Cerbicales; $N = 29$) in (Table 1, Fig. 1) (see Supplement Table S1-1 for raw data, Figure S1-1 for geographic origins of individual specimens). These modern specimens were housed in mammalian collections at the Steinhardt Museum of Natural History (Tel Aviv) and the Muséum national d'Histoire naturelle (Paris). Only adult specimens were

Table 1

Number of specimens from each region and locale utilized to compare the Ma'agan Mikhael B ship rats to conspecifics from mainland and island sample populations from around the Mediterranean Basin.

Modern Sample Region (N)	Locale (N)	Collection
Southern Levant (N = 76)	Israel (N = 75), Sinai (N = 1)	Steinhardt Museum of Natural History
North Africa (N = 23)	Morocco (N = 17), Tunisia (N = 6)	Muséum national d'Histoire naturelle
Western Mediterranean (N = 29)	Corsican Islets: Porto-Vecchio & Toro, Iles Cerbicales (N = 29)	Muséum national d'Histoire naturelle

recorded. Because sexual size dimorphism has been shown to be minimal for black rats, we combined sexes in the biometric analysis (Faleh et al., 2012; Granjon and Cheylan, 1990b; Ibrahim et al., 2017; Mori et al. 2017; Ramalhinho et al., 1996; Russell et al., 2011; Ventura and López Fuster, 2000; Yom-Tov et al., 1999). We chose four cranial measurements that are often used in biometric studies on black rat crania (Granjon and Cheylan, 1990b; Ibrahim et al., 2017; Ramalhinho et al., 1996; Ventura and López Fuster, 2000), including the total skull length (TTL), condylobasal length (CBL), zygomatic breadth (ZYG), and the length of the cheek tooth row (CTR) preferring the right side when possible (Fig. 3A, Table 2). These correspond directly to the following cranial measurements as defined in the *Lepus* protocol by von den Driesch (1976: 50–51, fig. 18a and 18b): #1) Total length; #2) Condylobasal length; #9) Cheektooth Row; #16) Zygomatic Breadth. Summary statistics were produced for this dataset and are reported in the results.

To investigate any significant differences between the archaeological and modern specimens, we tested our hypothesis using Kruskal-Wallis tests on the four cranial measurements by region in the R software environment (v. 4.2.2, R Core Team, 2022). We used Kruskal-Wallis because the variances were not assumed to be equal among the groups. Effect size was reported as epsilon squared (ϵ^2) (Tomczak and Tomczak, 2014); magnitude of the effect is interpreted on a scale from 0.00 (negligible) – 1.00 (very strong) (Rea and Parker, 2014; Tomczak and Tomczak, 2014). A post-hoc Dunn's pair-wise test was performed on significant results from the Kruskal-Wallis test, with p-values adjusted by the Holm method. The following R packages were used in these analyses: 'rcompanion' (Mangiafico, 2021); 'stats' (R Core Team, 2022); 'tidyverse' (Wickham, 2019); 'dplyr' (Wickham et al., 2021a; Wickham et al., 2021b); 'FSA' (Ogle et al., 2021). Associated code is available in Supplement S6 (Harding, 2023) [dataset].

Premortem body size of the ship rats, as expressed by length of head and body (mm) and weight (g), were estimated following Morales and Rodríguez (1997). This method extrapolates the measurement of a mandibular dimension to approximate the body size of black rats using

Table 2

Definitions of the cranial measurements utilized throughout this study, following the *Lepus* protocol in von den Driesch (1976).

Cranial Measurement	Abbreviation	Definition
Total Length	TTL	#1) Total length: Akrokranium–Prosthion
Condylobasal Length	CBL	#2) Condylobasal length: alar border of the occipital condyles–Prosthion
Cheektooth Row	CTR	#9) Length of the cheektooth row measured along the alveoli on the buccal side
Zygomatic Breadth	ZYG	#16) Oral zygomatic breadth, greatest breadth across the oral part of the zygomatic arch

formulae for length and weight metrics (see Supplement S1-1 for equations and further details (Harding and Tapson, 2023) [dataset]). The formulae are based on the mandibular measurement from the symphysis to the alar end of the articular process (noted by Morales and Rodríguez as 'C4') (Fig. 3B). Approximating the weight of the archaeological specimens at the time of death allows for age estimations in conjunction with tooth wear stages.

To detect any degree of gigantism/dwarfism in the archaeological assemblage compared to mainland conspecifics, a relative size index (RSI) of body mass was calculated using the cubed condylobasal length (CBL³) of the cranium, following the method described by Lomolino (1985) (see Supplement S1-1 for equations and further details (Harding and Tapson, 2023)). We used the CBL cranial measurement for this analysis as this was the cranial metric most commonly available in both the archaeological and modern specimens, as well as previously published literature on black rat cranial morphometric studies from the Mediterranean and eastern Atlantic region (Granjon and Cheylan, 1990b; Ibrahim et al., 2017; Ramalhinho et al., 1996; Ventura and López Fuster, 2000) and other studies on mammalian orders and the island rule (Meiri et al., 2006).

Lomolino's (1985, 2005) method relies on dividing a measurement taken on an island population by the same metric of their nearest mainland counterparts; this simple fraction produces an index where values >1.0 express a degree of gigantism and values <1.0 express dwarfism. Lomolino's (1985) method prefers to compare body mass measurements; however, when those are not available, a length measurement can be cubed to approximate volume as a substitute for a mass measurement. We utilized the latter option because the archaeological specimens consisted only of skeletal remains, the individuals from the museum collections did not consistently have weights recorded, nor did the samples in previously published datasets. Thus, we predicted that we would have more informative results by comparing the CBL³ values across datasets, since that was the single most commonly recorded cranial metric reported. Since we do not know the exact provenance of the Ma'agan Mikhael B ship rats, three RSI values were calculated using the same samples of modern black rats from museum collections

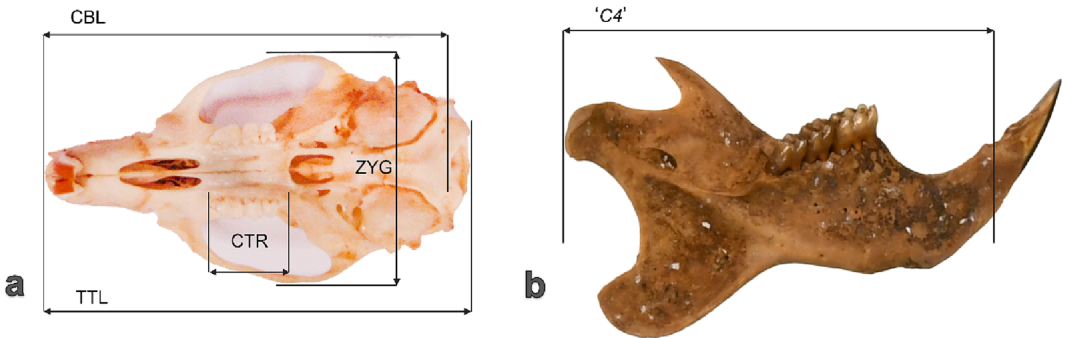


Fig. 3. A) Depictions of the four cranial measurements used to compare the Ma'agan Mikhael B ship rats to population samples from the Southern Levant, North Africa, and West Mediterranean. TTL = Total skull length; CBL = Condylobasal length; CTR = Cheektooth row; ZYG = Zygomatic breadth. B) Depiction of the mandibular measurement 'C4' utilized in formulae to estimate the body size and weight of the archaeological specimens.

described above (Mainland: Southern Levant, North Africa; Island: Western Mediterranean). These RSI values allow us to ascertain the archaeological sample's relative size in comparison to a range of Mediterranean locales. We expected the RSI values of the Ma'agan Mikhael B assemblage derived in comparison to the mainland samples (Southern Levant, North Africa) to be >1 , and the RSI value compared to the island samples (Western Mediterranean) to be ≤ 1 . We included an island sample as a sort of control, since we expected the shipwreck rats to be closer to their size than the mainland samples.

The RSI values of the archaeological dataset were then compared to RSI values calculated for nine island populations of black rats in the Mediterranean and eastern Atlantic in which gigantism attributed to the island rule has been identified in previously published studies (Fig. 1). These datasets include: the islands of (1) Galite and (2) Zembra off the northern coast of Tunisia (Ibrahim et al., 2017); (3) Congresso Island off the Mediterranean coast of Morocco (Ventura and López Fuster, 2000); the Azores islands of (4) São Miguel and (5) Terceira in the eastern Atlantic waters of Portugal (Ramalhinho et al., 1996); (6) Corsica Island and (7) Provençal Islets (Port-Cros, Bagaud) near Provence, France; and, (8) Sardinia and (9) Corso-Sardinian Islets (Santa Maria, Cavallo, Lavezzi, Gargalo, Piana, Ratino, Ilots Lavezzi) near Tuscany, Italy (Granjon and Cheylan, 1990b) (Table 3, Fig. 1). Using diverse statistical tests and methods, each of these previous studies found significant differences between island black rat samples and the nearest mainland populations' cranial dimensions; the majority of island population samples were significantly larger than their nearest mainland counterparts. We calculated these island populations' RSI values using the authors' published data. In the case of the Provençal and Corso-Sardinian Islets, we used a combined average of the published mean CBL values respectively, to increase sample size for these small and numerous islands (see Supplement Table S6-3 for original values as recorded in Granjon and Cheylan (1990b)). In Table 3, we have included some of the previously published summary statistics provided by the respective authors, including the number of observations (N), sample mean, and standard deviation (SD) for each locale. Raw numbers for these datasets were not published.

We preferred to use the RSI method to gauge degrees of gigantism/dwarfism in Mediterranean and east Atlantic island black rat

Table 3

Previously published datasets utilized in the relative size index (RSI) analysis. The mean condylobasal length (CBL) measurement for each locale is provided, along with the number of observations and the standard deviation as reported by the original authors.

Region	Locale	CBL (N)	CBL Mean	CBL SD	Reference
Tunisia	Galite Island	35	36.64	1.85	Ibrahim et al., 2017
	Zembra Island	35	36.91	2.56	
	Tunisia Mainland	35	35.12	1.49	
Morocco	Congresso Island	20	41.82	1.65	Ventura and López Fuster, 2000
	Morocco Mainland	9	39.15	1.73	
Portugal	Terceira Island	26	39.9	1.4	Ramalhinho et al., 1996
	São Miguel Island	33	40.29	1.28	
	Portugal Mainland	23	38.86	1.57	
Provence	Corsica Island	38	41.5	1.69	Granjon and Cheylan, 1990b
	Provençal Islets	39	45.65	1.16	
	Provence Mainland	20	42.6	1.9	
Tuscany	Sardinia Island	9	40.5	1.83	Granjon and Cheylan, 1990b
	Corso-Sardinian Islets	91	43.05	1.09	
	Tuscany Mainland	19	42.8	1.6	

populations for several reasons: the raw data collected in previously published studies was not available which obstructs recalculating statistics with additional, novel data and methods; the measurements and summary statistics from these studies were not always directly comparable to one another; to avoid problems with interoperator measurement error; and, to avoid problems with Type 1 errors when numerous hypotheses are tested simultaneously. We felt the RSI method was useful in providing a meaningful range of values expressing the range of gigantism/dwarfism present in island populations of black rats, which could also be more sensitive to weak or nuanced signals of size differences that may be overlooked by using standard alpha levels of statistical significance tests. We did not test for adherence to Bergman's rule because Rodentia have been found not comply with it, and therefore it is not valid for this taxonomic order (Meiri and Dayan, 2003).

3.3. aDNA laboratory procedures

Samples from two of the rodent crania from the Ma'agan Mikhael B were sent for aDNA analysis at the McMaster Ancient DNA Centre in Hamilton, Ontario, Canada (MMB 714: portion of maxilla and teeth; MMB 717: incisor and molar). The samples were assessed for the presence of *Yersinia pestis*. Multiple methods were performed in an effort to identify *Y. pestis* including a qPCR assay (Schuenemann et al., 2011), mapping to the *Y. pestis* CO92 whole genome (NC_003143.1), and assessing for classified reads through BLASTn. The details of the laboratory procedures and protocols are available in Supplement S1-3 (Harding and Tapson, 2023).

4. Results

4.1. Zooarchaeological analysis

The rodent specimens recovered from the Ma'agan Mikhael B were taxonomically identified as *Rattus rattus* based on cranial and dental morphology, which is supported by the aDNA analysis. The skeletal elements were represented by crania, mandibulae, and post-cranial bones (NISP = 115, Fig. 4, Supplement S2 (Harding, 2022c) [dataset]). The minimum number of individuals (MNI = 6) was based on the crania, three of which were mostly complete (Fig. 5) and three were fragmented. Inspection of the post-cranial elements confirmed the MNI. Individuals MMB 7008, MMB 762, and MMB 740 were represented by nearly complete skeletons, while MMB 714, MMB 717, and MMB 735 only presented cranial elements. The mandibular and post-cranial elements observed in loci MMB 746, MMB 754, MMB 6233, and MMB 769 did not increase the MNI. Dental elements were analyzed for tooth decay and skeletal elements were inspected for deformation caused by rickets, as these conditions have been shown archaeologically to affect ship rat populations on early modern vessels (Armitage, 1995). Dental and osteological pathologies were not observed in this assemblage (Supplement S7, Fig. S7-1–11 (Harding, 2022b) [dataset]).

Assigning sex to the archaeological specimens was accomplished by observing the morphology of the pelvis. The mensural method used to demonstrate bony pelvic sexual dimorphism in Muridae does not work for *Rattus* spp., and the innominates of male and female ship rats differ only very slightly in the shape of the posterior border of the ilium crest (Brown and Twigg, 1969: p. 6, Fig. 7). Based on this one morphological criterion, the pelvises from MMB 740 and MMB 7008 appear to be male (Table 7, Fig. 6).

The majority of ship rat remains were recovered from the bow area, near food storage amphorae and the proposed location of the galley (Cohen and Cvikel, 2019; Creisher et al., 2019) (Fig. 7). The location of the ship rat remains suggested that they had burrowed under the amphorae cargo, and between the stringers and hull planks. Very few of the ship rat skeletal elements were broken (N = 15/115, 13%), showing a minimal extent of fragmentation (Supplement S4 (Harding, 2022b) [dataset]). The intensity of fragmentation was also low, with the

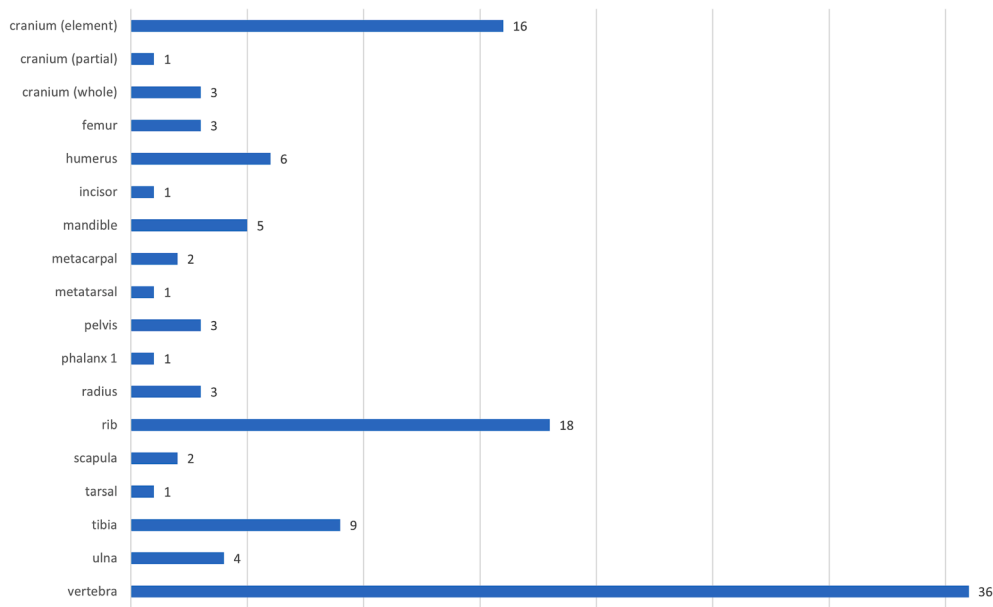


Fig. 4. Frequency distribution of black rat skeletal elements identified onboard the Ma'agan Mikhael B. Counts of each skeletal element are noted at the end of each bar.



Fig. 5. Examples of three ship rat crania recovered from the Ma'agan Mikhael B (left to right: MMB 735, MMB 762, MMB 740). Image credit: A. Efremov.

majority being complete (88.5%), and few nearly complete (8%) or broken in half (3.5%). The coloration of the bones ranged from pale brown to dark yellowish brown (see Supplement S4 for Munsell codes). Evidence for burning (carbonization, calcination) was not present. The sand abrasion stages were overall very low (Stage 1 = 57%; Stage 2 = 43%), indicating that these remains had been in place with very little movement since the time of the wrecking event. Environmental or digestive corrosion on these small skeletal elements was absent in the entire assemblage, which strongly suggests that these remains were not exposed to the open marine environment after being buried by sand within the shipwreck site. If digestive corrosion had been noted on the ship rat remains, it could have provided evidence for a small carnivore onboard. Domestic cats have been recorded in the historic and archaeological record as companions brought along on voyages to help control rat infestations on ships (Armitage, 1989, 2013), but feline remains were not identified among the diverse taxa ($N = 13$) within the faunal assemblage of this ship (Harding, 2021).

Although only six individuals were identified, there were likely many more ship rats aboard. Evidence for a widespread infestation was noted in the form of rodent incisor gnawing marks on food refuse bones

(Armitage, 2013), as seen on the pot-sized caprine rib shown in Fig. 8. Considering the bone surface modifications observed above, the location of the rat remains found within the hull, and the fact that these rodents are known to be good swimmers (Badou et al., 2021; Wilmshurst et al., 2021), it is most likely that the individuals recovered during excavation did not have time to escape their burrows before the ship sank (Armitage, 1995, 2013).

4.2. Biometric analysis

Measurements for all cranial, mandibular, and post-cranial elements are available in Supplement S3 Tables S3-1, S3-2, and S3-3 (Harding, 2022a) [dataset]. Approximately half of all the long bone epiphyses were unfused in the assemblage (see Supplement S4), yet all were adult-sized in comparison with the reference collection. Epiphyseal fusion schedules for ship rats were not available in the literature, probably due to the relatively short life span of rats averaging 1–2 years in the wild (Innes et al., 2001; Morales and Rodríguez, 1997; Wilmshurst et al., 2021).

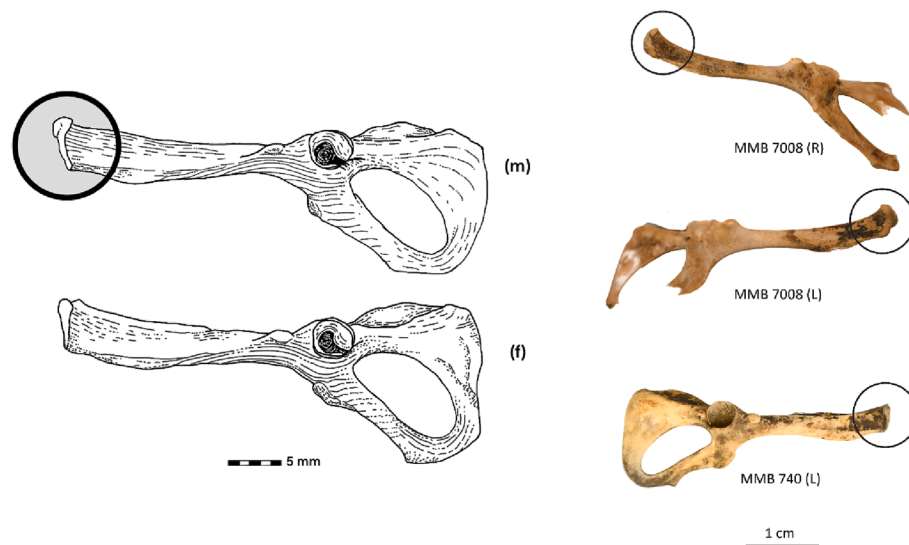


Fig. 6. Morphology of male and female ship rat pelvises redrawn from Brown & Twigg (1969: p. 6, Fig. 7), c.f. MMB 740 and MMB 7008. Illustration redrawn by A. Marck, photo credit to R. Shaffir, adapted by S. Harding.

4.2.1. Summary statistics of cranial measurements

Summary statistics were calculated for the archaeological and modern specimens from the Southern Levant, North Africa, and the Western Mediterranean as recorded in this study; these include the number of observations per metric and group, mean, median, minimum, maximum, and standard deviation (Table 4). Based on the results of the Kruskal-Wallis tests, we could not reject the null hypothesis for three of the cranial measurements (TTL, ZYG, CTR); however, a significant difference (p -value = 0.004, ϵ^2 = 0.0988) was found between the groups for the CBL measurement (Table 5). A post-hoc Dunn's test on the CBL results revealed that the only significant differences among the pair-wise comparisons were between Southern Levant–West Mediterranean (P . adj = 0.028), and North Africa–West Mediterranean (P .adj = 0.003); the rest of the adjusted p -values were not statistically significant (Table 6). We interpret these results to mean that the archaeological specimens in our dataset are not significantly different in size than modern populations of black rats in the Mediterranean region, and we may proceed with the subsequent comparative analyses. The significant difference found between the Southern Levant, North Africa and Western Mediterranean groups is very interesting, and we plan to address it in a future geometric morphometric study on the same dataset that is already underway.

4.2.2. Body size and age estimation

The tooth wear stages (TWS) observed in the six individuals from the Ma'agan Mikhael B were 'C' (N = 3) and 'D' (N = 3) (Table 7, Fig. S7–11). These are considered to be in the sub-adult–young adult range according to the schedule devised by Armitage in Morales and Rodríguez (1997) during their work on archaeological black rat assemblages in mainland Portugal. Ship rats continue to grow throughout life, so body weight has been used to estimate age (Morales and Rodríguez, 1997). Sexual maturity is reached between 8 and 12 weeks of life, and typically in the range of 80–90 g body weight. Young adults usually weigh 90–100 g, while adults weigh over 100 g; old adult rats (>400 days) can weigh upwards of 250 g (Morales and Rodríguez, 1997). By this schedule, we would expect the Ma'agan Mikhael B rats to weigh around 100 g each according to their TWS.

Based on the mandibular length measurement 'C4' sensu Morales and Rodríguez (1997), body weight and size at time of death were estimated for two individuals; MMB 7008 (TWS 'C') is estimated to have weighed 112.1 g and measured 168.1 mm long, and MMB 762 (TWS 'C') is estimated at 145.3 g and 184.6 mm (Table 7). According to Morales and

Rodríguez (1997), the estimated weights of the archaeological individuals supersede what would be expected from mainland Portuguese rats in the sub-adult–young adult range. However, they do fall within and even slightly beyond the expected range for rats of the same TWS on New Zealand. Armitage's TWS 'C' and 'D' approximately correspond to Age Class III and IV, respectively, from the schedule illustrated in Wilmshurst et al. (2021) and utilized by Innes et al. (2001) to estimate the relative ages of ship rats in New Zealand. This TWS age class schedule has not been calibrated to actual ages in ship rats, but according to their study on black rats from this oceanic island, weights in the range of 110–140 g corresponded to a mean TWS class of 3.4 (comparable to Armitage's TWS 'C'), and >141 g to a mean TWS class of 4.3 (comparable to Armitage's TWS 'D'). These weight ranges by TWS are 10–40 g higher than those proposed by Morales and Rodríguez (1997) for Portuguese mainland rats; this discrepancy can likely be explained by gigantism exhibited in New Zealand ship rats, likely due to the island rule (Wilmshurst et al., 2021; Yom-Tov et al., 1999). We do not propose that New Zealand nor Portugal was the origin of the Ma'agan Mikhael B ship rats; rather, we utilize this comparison to show that the estimated weights of the Ma'agan Mikhael B ship rats are larger than expected for mainland European rats and closer in size to rats from a remote oceanic island in which black rats have been found to comply with the island rule.

4.2.3. Relative size index

The relative size of the archaeological specimens from the Ma'agan Mikhael B was estimated from RSI calculations using mainland samples from the Southern Levant and North Africa, as well as an island sample from the Western Mediterranean (Table 8). The RSI values produced when compared to the mainland samples were both >1 (MMB/S. Levant = 1.07; MMB/N. Africa = 1.18). On the contrary, the RSI of the archaeological group was <1 when compared to the sample from Corsican islets (MMB/W. Mediterranean = 0.95). These RSI values suggest that the mean size of the black rats occupying the Ma'agan Mikhael was larger than their mainland counterparts along the southern and south-eastern boundaries of the Mediterranean Basin, and slightly smaller than black rats from small islets.

A previous study by Meiri et al. (2008) on the relative sizes of island mammalian orders found that all samples of Muridae species utilized in their analysis produced a mean RSI value of 1.07 ± 0.09 ($p < 0.001$); the mean RSI value of well-sampled ($N > 5$ island and mainland specimens) Muridae species increased to 1.14 ± 0.07 ($p < 0.001$). We interpret

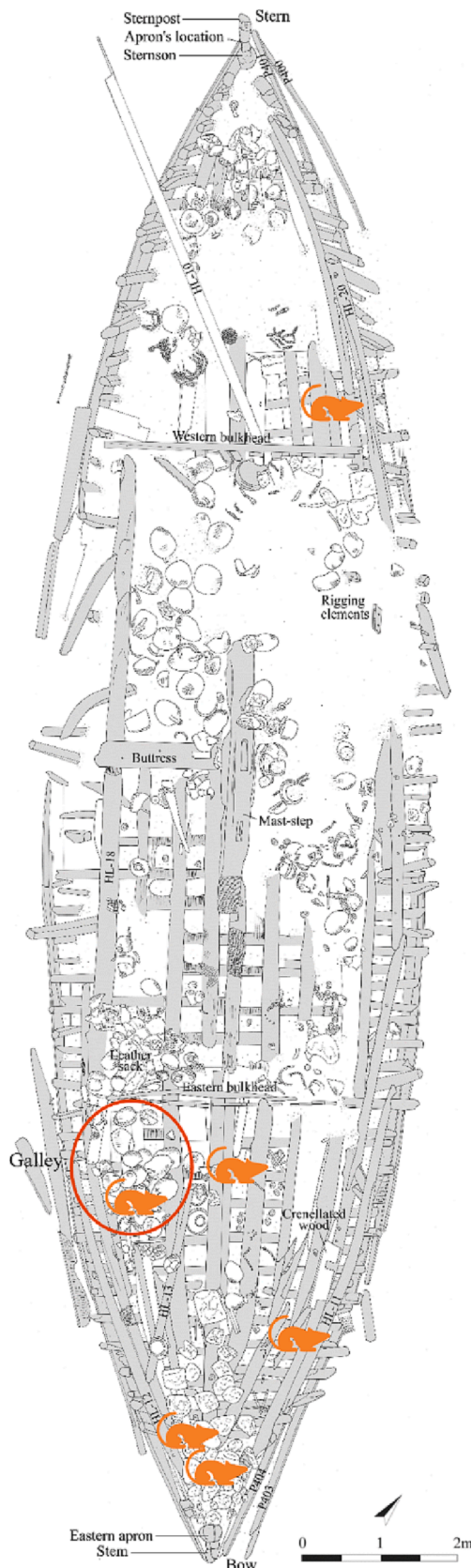


Fig. 7. Plan view of the Ma'agan Mikhael B with the locations of ship rat crania (MNI = 6) denoted with orange rat icons. The galley area is approximated with an orange oval. Illustration credit: P. Sibella, adapted by S. Harding. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 8. A) Rat gnawing marks on a pot-sized caprine rib fragment (MMB 778). B) Inset area from Fig. 7A, showing the gnawing marks in more detail. Image credit: S. Harding.

these previous findings in the context of this study to support the validity of our results. Although the Ma'agan Mikhael B ship rat's cranial measurements were not statistically significantly larger than the comparative mainland samples, the RSI values produced in comparison to a range of mainland Mediterranean locales agrees with Meiri et al.'s (2008) previous findings regarding the spectrum of gigantism exhibited by island populations of Muridae, a taxonomic family which includes ship rats.

Relative size calculations for other island populations of black rats from around the Mediterranean and east Atlantic produced a mean RSI of 1.08; the spectrum ranged from 0.85 to 1.23, with the vast majority (7 of 9) exhibiting values >1 (Table 9). The exceptions were the Mediterranean islands of Corsica (0.92 RSI) and Sardinia (0.85 RSI), which showed degrees of dwarfism relative to Provence and Tuscany, respectively. This was explained to be due to the trophic web of these large islands being more similar to nearby mainland ecosystems; black rat populations were not released from predation and competition pressures as they would be on smaller or more remote islands (Granjon and Cheylan, 1990b). These results suggest that the Ma'agan Mikhael B ship rats fall on the spectrum of gigantism exhibited by the majority of insular black rat island populations available for comparison in the region (Fig. 9). In Fig. 9, we have chosen to represent the RSI value of the Ma'agan Mikhael B ship rats relative to the Southern Levant sample because this was the most parsimonious option available based on the likely eastern Mediterranean sailing route as dictated by the other artifact assemblages under study.

4.3. aDNA analysis

We performed multiple methods in an effort to identify *Y. pestis* within individuals MMB 714 and MMB 717, such as a qPCR assay (Schuenemann et al., 2011), mapping to the *Y. pestis* CO92 whole genome (NC_003143.1), and assessing for reads classified to *Y. pestis* through BLASTn (Altschul et al., 1990) (see Supplement S5 for the detailed results of each method). None of these attempts were successful as neither individual had all four PCR replicates amplify indicating that the *pla* gene and thus the pPCP1 plasmid of *Y. pestis* was not present (Table S5-1), $<0.002\%$ of the total metagenomic dataset classified as *Y. Pestis* when run through BLASTn (Table S5-4), and $<0.0004\%$ of each successfully mapped to the *Y. Pestis* CO92 whole genome (Table S5-2). Although both MMB 714 and MMB 717 demonstrated good endogenous DNA preservation, the lack of success across all attempts to identify *Y. pestis* indicates that it was likely not present within these individuals.

Table 4

Summary statistics for the cranial measurements used to test the hypothesis that the modern and archaeological samples used in this study are comparable. TTL = Total Length of the Skull; CBL = Condylbasal Length; ZYG = Zygomatic Breadth; CTR = Cheektooth Row. The number of observations, mean, median, standard deviation (SD), minimum and maximum values of each measurement by region are reported.

Sample	Cranial Metric	N	Mean	Median	SD	Min	Max
MMB	TTL	1	39.98	39.98	–	39.98	39.98
MMB	CBL	4	37.05	37.00	1.22	35.70	38.50
MMB	ZYG	3	18.32	18.17	0.36	18.06	18.73
MMB	CTR	6	7.05	7.07	0.13	6.80	7.20
S. Levant	TTL	75	41.03	41.57	2.64	34.32	46.97
S. Levant	CBL	75	36.22	36.46	2.66	29.78	42.23
S. Levant	ZYG	71	17.99	17.88	1.49	15.14	24.64
S. Levant	CTR	76	6.99	6.88	0.70	6.18	11.97
N. Africa	TTL	23	40.27	40.58	2.52	33.77	43.95
N. Africa	CBL	23	35.31	35.64	2.39	28.41	39.22
N. Africa	ZYG	18	17.76	17.75	1.19	15.63	19.50
N. Africa	CTR	22	6.81	6.79	0.35	6.33	7.58
W. Mediterranean	TTL	28	42.20	41.78	1.53	39.73	45.26
W. Mediterranean	CBL	28	37.70	37.27	1.57	34.68	40.73
W. Mediterranean	ZYG	24	18.36	18.17	1.15	16.76	20.64
W. Mediterranean	CTR	28	6.99	6.99	0.30	6.6	7.91

Table 5

Results of the Kruskal-Wallis test on four cranial measurements by region. Statistically significant results are italicized.

Cranial Metric	Chi ²	DF	p-value	epsilon ²
TTL	7.8217	3	0.050	0.0588
CBL	13.138	3	<i>0.004</i>	0.0988
ZYG	2.457	3	0.483	0.0185
CTR	6.6618	3	0.083	0.0501

Table 6

Results of the Dunn's post-hoc pairwise test on the condylbasal length measurement, adjusted by the Holm method. Statistically significant results are italicized.

Dunn's Test Pair-Wise Comparison (CBL)	Z	P.unadj	P.adj
S. Levant–MMB	−0.6223005	0.5337442834	0.640
S. Levant–North Africa	1.7362128	0.086926697	0.174
MMB–North Africa	1.3533693	0.1759376809	0.264
S. Levant–West Med	−2.5977339	0.0093841197	<i>0.028</i>
MMB–West Med	−0.3123522	0.754772855	0.632
North Africa–West Med	−3.2400341	0.001195154	<i>0.003</i>

Table 7

Metrics and demographic data per individual ship rat identified on the Ma'agan Mikhael B. Condylbasal length (CBL) and mandibular measurement 'C4' are shown in millimeters. Estimated weight, body length, age, and sex profiles are reported. The tooth wear stage is based on the schedule by Armitage in [Morales and Rodríguez \(1997\)](#), which correspond to the age class schedule devised by Innes (2001).

Specimen	CBL (mm)	Mandible measurement 'C4' (mm)	Est. Weight (g)	Est. Length Head & Body (mm)	Tooth Wear Stage/Age Class	Age Cohort	Sex
MMB 714	35.7	–	–	–	D/IV	–	–
MMB 717	–	–	–	–	D/IV	–	–
MMB 735	38.5	–	–	–	C/III	–	–
MMB 740	36.5	–	–	–	D/IV	–	Male
MMB 762	37.5	24.3	145.3	184.6	C/III	Young Adult	–
MMB 7008	–	22.8	112.1	169.2	C/III	Young Adult	Male

Table 8

RSI values produced for the Ma'agan Mikhael B ship rats based on two mainland samples (Southern Levant, North Africa) and one island sample (West Mediterranean). The Ma'agan Mikhael B ship rats are slightly larger than the mainland samples, and slightly smaller than the island samples.

Shipwreck Sample	N	Mean CBL (mm)	Mean CBL ³	Comparative Sample	N	Mean CBL (mm)	Mean CBL ³	RSI
MMB	4	37.05	50858.63	S. Levant (Mainland)	75	36.22	47516.60	1.07
MMB	4	37.05	50858.63	North Africa (Mainland)	23	35.31	44024.37	1.18
MMB	4	37.05	50858.63	West Mediterranean (Island)	28	37.69	53540.01	0.95

5. Discussion & conclusion

At least six ship rats inhabited the Ma'agan Mikhael B when it sank. Two were likely male, and all appeared to be in the sub-adult–young adult age range based on their TWS. The estimated body size and weight at the time of death, as well as the RSI, suggest that this group of ship rats exhibited a degree of gigantism typical of island populations from Mediterranean and eastern Atlantic islands. It is unlikely that the individuals onboard carried plague, and evidence for other osteological pathology, such as rickets, was absent. These remains from an early Islamic period shipwreck on the southern Levantine coastline present the first and oldest direct evidence of a ship rat infestation on an antique sailing vessel in the premodern Mediterranean. The significance of this assemblage supersedes novelty, however, and allows for an opportunity to investigate the ecological circumstances of ship rats' maritime voyages in antiquity. This investigation also has implications for further understanding of the historical (re)colonization of the Mediterranean region by this invasive rodent.

Ship rats are driven to migrate by foraging instincts, mate-seeking, natal dispersion, or emigration from a home group in search of a higher quality, less competitive habitat ([Ewer, 1971](#); [Feng and Hims-worth, 2014](#)). Both male and female rats seek out food sources, sometimes outside the boundaries of their home ranges ([Ewer, 1971](#)). A fully stocked ship at harbor may appear as a high-quality habitat that offers a

Table 9

RSI data and computed values of comparative island populations relative to their nearest mainland counterparts from around the Mediterranean Basin and eastern Atlantic. The majority of island samples express a degree of gigantism compared to their associated mainland sample, on a spectrum of 0.85–1.23.

Island	N	Mean CBL (mm)	Mean CBL ³	Mainland	N	Mean CBL (mm)	Mean CBL ³	RSI
Provençal Islets	39	45.65	95131.06	Provence	20	42.6	77308.77	1.23
Congresso	20	41.82	73139.52	Morocco	9	39.15	60006.09	1.22
Zembra	35	36.91	50284.27	Tunisia	35	35.12	43317.51	1.16
Galite	35	36.64	49188.82	Tunisia	35	35.12	43317.51	1.14
São Miguel	33	40.29	65402.12	Portugal	23	38.36	58682.47	1.11
Terceira	26	39.9	63521.20	Portugal	23	38.36	58682.47	1.08
Corso-Sardinian Islets	91	43.08	79951.59	Tuscany	19	42.8	78402.75	1.02
Corsica	38	41.5	71473.38	Provence	20	42.6	77308.78	0.92
Sardinia	9	40.5	66430.13	Tuscany	19	42.8	78402.75	0.85

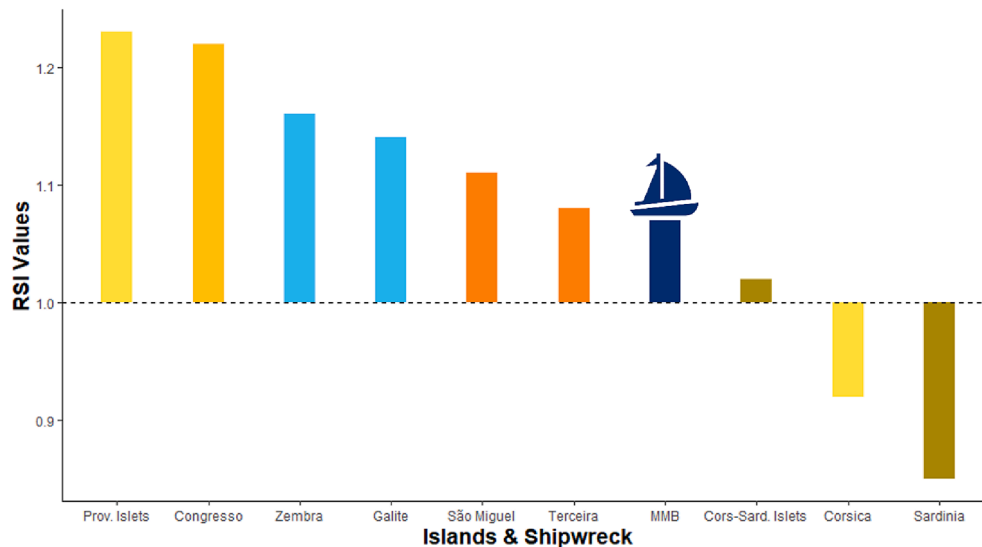


Fig. 9. Relative size index values of comparative island population samples from around the Mediterranean Basin and east Atlantic. The Ma'agan Mikhael B (MMB) is denoted with a ship icon.

competitive advantage in a heterogeneous urban landscape (Doligez and Bouludier, 2008; Stamps, 2008). Ship rats may use conspecifics, such as dominant males which often act as 'pioneers' for their home groups, as a source of information on habitat quality; this may help overcome natural neophobia of an unfamiliar habitat patch (Ewer, 1971; Feng and Himsworth, 2014; King et al., 2014; Stamps, 2008). Given the location of the ship rats aboard the Ma'agan Mikhael B near the food stores and galley, and the absence of evidence for a substantial grain shipment in which they could have been passively transferred, foraging may have been a prime motivating factor for boarding the ship. Moreover, black rats preferentially consume fruits, nuts, and seeds (Feng and Himsworth, 2014), which were among the contents of the amphorae on board (Cohen and Cvikel, 2019; Creisher et al., 2019). They also clearly enjoyed food scraps of the crew, as was seen on the caprine rib with gnawing marks; this aligns with ship rats' omnivory in commensal contexts.

Male ship rats of breeding age are also strongly driven by their instinct to search for mates, which could be an additional motivating factor for them to board watercraft (Ewer, 1971; Feng and Himsworth, 2014; King et al., 2014). This characteristic makes them extremely mobile, with evidence of high levels of landscape-scale movement (Innes et al., 2001; King et al., 2014; Wilmschurst et al., 2021). This seems to be an adaptive dispersal strategy to prevent mating with their own offspring which reach sexual maturity in 3–4 months, and increases their individual breeding success (King et al., 2014; Wilmschurst et al., 2021). Although male ship rats have a larger home range than females due to mate-seeking behavior, both sexes are highly mobile (up to 600 m per 2–3 days in open rural habitat) (King et al., 2011, 2014). These traits

suggest active colonization of ships such as the Ma'agan Mikhael B, driven by the same dispersal mechanisms that encourage rodents to invade other novel habitat patches i.e., near-shore archipelago islands which are intermittently connected to the mainland due to tidal ebbs and flows (Juette et al., 2020).

In addition to foraging and mate-seeking, factors that affect habitat selection include adequate nesting places and breeding opportunities (Doligez and Bouludier, 2008). Sufficient harborage determines whether an invasive rat population may become established in a habitat patch (Feng and Himsworth, 2014), and a ship or large boat could potentially offer such conditions. Although ship rats frequently reside in trees and rooftops, this behavior often abates in the absence of interspecific competition for lower altitude nesting space (Ewer, 1971; Innes et al., 2001; Milmore, 1943), as has been observed on invaded islands in the Mediterranean (Granjon and Cheylan, 1990a). Known to be excellent climbers, boarding a ship via ropes or cordage would not pose much of a challenge to black rats (Ewer, 1971; Feng and Himsworth, 2014). As extremely resourceful rodents with fairly plastic nesting site requirements, black rats have been noted to find harborage among the cargo and in protected corners of ships (Williams, 1932). Ship rats will make nests with virtually any materials available (Ewer, 1971), preferably as near as possible to a feeding place (Feng and Himsworth, 2014; LiphaTech, 2017). The Ma'agan Mikhael B surely offered ideal harborage for ship rats in-between the stringers and hull planks, which is where their skeletal remains were found during excavation. Nesting material could potentially have been made of gnawed ropes, baskets, or the pinecone (*Pinus pinea*) dunnage found around the amphorae cargo (Cohen and Cvikel, 2019).

Ship rats being panmictic with multiple paternity, a female might receive several males during her oestrous cycle (4–6 days) (King et al., 2014). With a short gestation period of just 20–22 days, a typical litter size of 3–10 pups, and sometimes delayed implantation, migrating pregnant females are capable of establishing a population in a new area with sufficient genetic variation to minimize bottleneck effect (Innes et al., 2001; King et al., 2014; Wilmshurst et al., 2021). Although research shows that pregnant females rarely migrate outside of their home zones (King et al., 2014), a few pregnant females in a mobile habitat—such as a ship—could potentially provide sufficient offspring to create a founder population at the next landfall. This breeding style also facilitates understanding how a small group of rats taken on at port could rapidly populate a ship at sea (Armitage, 1993, 1995; Williams, 1932). As for the Ma'agan Mikhael B, though female ship rats were not identified in the zooarchaeological analysis, it is quite possible that one or more may have been aboard. If so, this could have been a contributing factor to the attraction of males to the ship, as well as the potential for breeding onboard and subsequent natal dispersal at later landfalls.

Although ships could be considered somewhat ephemeral habitats for black rats, they are probably not any more so than any other habitat type in commensal or feral contexts due to rats' highly mobile dispersion instincts (Hooker and Innes, 1995; King et al., 2011). Black rat colonies are known to be extremely plastic, with a near constant exchange of new members fighting their way in and young or submissive members being driven out (Ewer, 1971; Feng and Himsworth, 2014); rats appear to be rather ephemeral creatures by nature. When a ship leaves a harbor, any rats onboard then have a significant barrier to movement and become insulated until the next landfall. This seems to us rather like the scenario in which rats invade nearshore islands and then become intermittently trapped as tidal flows disconnect and reconnect this habitat patch with the mainland (Juetten et al., 2020). Even small islands in the Mediterranean that are never connected to land seem to have a continuous flow of rats, as boating traffic acts as a bridge over the water barrier (Cheylan et al., 1998; Granjon and Cheylan, 1990a). As has been shown in the results of previous studies, gigantism in black rats has been observed in many Mediterranean and east Atlantic island populations which ostensibly experience a steady exchange of conspecifics, and yet the ephemeral nature of these habitat patches does not depress the island rule in this species under these circumstances. Therefore, we do not consider the ephemeral nature of a ship habitat to fundamentally negate the possibility of compliance with the island rule for black rats in this ecological context.

With respect to habitat selection factors, a medium to large-sized watercraft with abundant food stores, sufficient harborage, the presence of breeding age conspecifics, as well as the absence of small carnivores, predatory birds in the vicinity, and zoonotic diseases would appear to represent ideal habitat for ship rats. These conditions could potentially sustain a source population—much like the small islands and islets which black rats have successfully invaded in the Mediterranean and elsewhere around the world. Conversely, ships which lack some of these characteristics might act as ecological traps or attractive sinks, due to undetected risks of predation stress, disease, or poor breeding possibilities (Delibes et al., 2001; Schlaepfer et al., 2002). However, the populations of 'sink'-ships may become pseudo-sinks due to immigration of novel individuals during anchorage at subsequent ports-of-call. Therefore, depending on the conditions onboard, a population of rats on a ship could be considered a source, sink, or pseudo-sink under diverse circumstances (Furrer and Pasinelli, 2016).

Source-sink population dynamics are highly affected by available habitat quality, and selection processes must also take hazards into account (Doligez and Boulenger, 2008; Stamps, 2008). For ship rats these include the presence of predators, insufficient or unhealthy food resources, and lack of mates. A hazard that might not be perceptible for black rats infiltrating a ship would be the contraction of diseases from ectoparasites and conspecifics already in residence, such as plague (Panagiotakopulu, 2004), or being inflicted with rickets due to

nutritional deficiencies and an existence lived below decks away from sunlight (Armitage, 1995). Although black rats are able to withstand substantial concentrations of the plague bacillus in their blood, they can eventually die of the disease. The fleas which actually transmit plague (*X. cheopis*) must then jump to another host, thus maximizing the spread of the disease amongst the rodents—and humans—onboard a ship (McCormick, 2003; Panagiotakopulu, 2004). Another potential hazard could be the absence of the opposite sex with which to propagate; this may differentially affect males more than females as they are more likely to immigrate into novel areas in search of mates. The Ma'agan Mikhael B seems to have posed few hazards to the ship rats onboard—neither plague nor osteological pathologies were detected, no predators were identified, food resources appear to have been plentiful, and sufficient harborage seems to have existed for a small colony to be established.

Viewed through an ecological lens, the similarities between the habitats of ships and small islands are striking. A well-stocked ship resembles a floating island which transports black rats between source populations and connects a heterogeneous metapopulation dispersed over discontinuous patches of habitat over large geographical ranges i. e., the Mediterranean Basin. Albeit based on a small sample size, the evidence presented here suggests that the group of ship rats which inhabited the Ma'agan Mikhael B exhibited a larger mean body size than mainland populations in the Southern Levant and North Africa, to a degree which falls on the spectrum of gigantism observed on small islands and islets in the Mediterranean and east Atlantic. This increased body size in insular populations has been attributed to the island rule, the effects of which have been shown to vary based on island size and isolation with respect to trophic complexity, predator communities, and habitat quality (Adler and Levins, 1994; Juetten et al., 2020; Lomolino, 2005; Russell et al., 2011). Generally, the effects of the island rule on a rodent population are proportional to isolation and inversely proportional to area; larger, less isolated islands tend to have more predators and higher levels of interspecific competition which suppress compliance with the island rule, as was seen in the RSI values of Corsica and Sardinia. Although the mechanisms driving this trend are complex, we tentatively propose that black rat populations on ships could be affected by the island rule. We visualized this phenomenon on a continuum observed between the extremes of highly isolated oceanic islands (c.f. larger vessels undertaking trans-oceanic voyages during the Age of Sail) and more frequently connected coastal archipelagos (c.f. a ship conducting *cabotage* trade and making frequent landfalls). Ships may offer harborage, food, and mates, usually lack predators, and offer a less competitive environment compared to mainland commensal contexts—all factors that underlie the mechanisms which explain the island rule. Under this hypothesis, a merchantman like the Ma'agan Mikhael B would fall near the latter end of the continuum, which agrees with the degree of gigantism observed in the RSI value of the ship rat population onboard when compared with sample populations from around the Mediterranean Basin. Although limited to two specimens, the large, young adult male rats onboard also support this hypothesis, as they fit the profile for the most likely dispersers into a novel habitat patch in search of food and mates (Adler and Levins, 1994; Lomolino, 2005).

In summary, we suggest that ship rats may have actively dispersed onto ships in antiquity due to their instinctual habitat selection processes. The conditions onboard could cause a resident colony to fluctuate between source-sink, which has implications for metapopulation genetic studies on Mediterranean black rats. We cautiously propose that ships may be considered somewhat analogous to certain naturally fragmented landscape habitats, being semi-insular akin to coastal archipelagos intermittently connected to the mainland by tidal flows. This ecological similarity may influence the body size of resident ship rats, perhaps explained by the island rule. While firm conclusions about historic plague transmission and reemergence patterns cannot be drawn from the small sample size investigated here, the absence of evidence for plague on this early Islamic period vessel speaks not only to the habitat

quality of the ship, but also contributes to a better understanding of rodent population health on a ship in the eastern Mediterranean during a time when plague was believed by some to be frequently transported primarily via flea-infested ship rats. This work has shown the value of zooarchaeological analysis in understanding the ecological circumstances of the maritime mobility of ship rats in the premodern Mediterranean Basin. In light of the ideas put forth here, we hope future research will consider the agency of ship rats in their migrations around the globe.

Funding:

This work was supported by Israel Science Foundation under Grant #1891/16 and Grant #252/19, the European Union's Horizon 2020 Research and Innovation Program Grant #648427, and the Social Sciences and Humanities Research Council of Canada Grant #20008499.

Data availability statement:

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.7078843>, <https://doi.org/10.5281/zenodo.7078642>, <https://doi.org/10.5281/zenodo.7078688>, <https://doi.org/10.5281/zenodo.7078680>, and <https://doi.org/10.5281/zenodo.7059794>, under Creative Commons Attribution 4.0 International Public License.

CRedit authorship contribution statement

Sierra Harding: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Madeline Tapson:** Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Guy Bar-Oz:** Writing – review & editing, Funding acquisition. **Deborah Cvikel:** Resources, Writing – review & editing, Supervision, Funding acquisition. **Nimrod Marom:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that support the findings of this study are openly available in Zenodo under Creative Commons Attribution 4.0 International Public License. See reference list for DOI's.

Acknowledgements

The underwater excavations (IAA permits G-41/2016, G-40/2017, G-26/2018, G-34/2019, and G-42/2021) and research of the Ma'agan Mikhael B shipwreck are supported by the Israel Science Foundation (Grant #1891/16 to D.C.), the Honor Frost Foundation, the President and the Research Authority of the University of Haifa, the Sir Maurice and Lady Irene Hatter Research Grant, Kibbutz Ma'agan Mikhael, and anonymous donors, to whom the authors are grateful. The study of the ship rats was carried out as part of the Zooarchaeology of Southern Phoenicia research funded by the Israel Science Foundation (Grant #252/19 to N.M.). The genetic study of the rats commenced as part of the NEGEVBYZ ERC Project funded by the European Union's Horizon 2020 Research and Innovation Program (Grant #648427 to G.B.), and was also supported by the Social Sciences and Humanities Research Council of Canada by Grant #20008499 to Dr. Hendrik Poinar, McMaster Ancient DNA Centre, McMaster University. We thank Roe Shafir for his assistance in photographing the specimens. We appreciate access to the Steinhardt Museum of Natural History (Tel Aviv) and the Muséum national d'Histoire naturelle (Paris) mammal collections,

facilitated by Dr. Karin Tamar and Dr. Violaine Nicolas-Colin, respectively. Many thanks to Prof. Shai Meiri for his arguments on a previous version of this manuscript; the subsequent iterations were significantly bettered by them.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2023.103947>.

References

- Abdelkarim, J., Pascal, M., Samadi, S., 2005. Island colonization and founder effects: the invasion of the Guadeloupe islands by ship rats (*Rattus rattus*). *Mol. Ecol.* 14 (10), 2923–2931. <https://doi.org/10.1111/j.1365-294X.2005.02604.x>.
- Adler, G.H., Levins, R., 1994. The Island syndrome in rodent populations. *Q. Rev. Biol.* 69 (4), 473–490.
- Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J., 1990. Basic local alignment search tool. *J. Mol. Biol.* 215 (3), 403–410.
- Aplin, K.P., Suzuki, H., Chinen, A.A., Chessier, R.T., ten Have, J., Donnellan, S.C., Austin, J., Frost, A., Gonzalez, J.P., Herbreteau, V., Catzeffis, F., Soubrier, J., Fang, Y.-P., Robins, J., Matisoo-Smith, E., Bastos, A.D.S., Maryanto, I., Sinaga, M.H., Denys, C., Van Den Bussche, R.A., Conroy, C., Rowe, K., Cooper, A., Gilbert, M.T.P., 2011. Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS One* 6 (11), e26357.
- Armitage, P.L., 1989. Ship rats, salted meat and tortoises: selected aspects of maritime life in the "Great Age of Sail" (1500–1800's). *Bermuda Journal of Archaeology and Maritime History* 1, 143–159.
- Armitage, P.L., 1993. Commensal rats in the New World, 1492–1992. *Biologist: Journal of the Institute of Biology* 40 (4), 174–178.
- Armitage, P.L., 1995. Faunal Remains. In: Smith, R.C., Spirek, J., Bratten, J., Scott-Ireton, D. (Eds.), *The Emanuel Point Ship: Archaeological Investigations, 1992–1995*, Preliminary Report. Tallahassee: Bureau of Archaeological Research, Division of Historical Resources, Florida Dept. of State.
- Armitage, P.L., 2010. Unwelcome companions: ancient rats reviewed. *Antiquity* 68, 231–240. <https://doi.org/10.1109/MMM.2010.935773>.
- Armitage, P.L., 2013. The deep-sea Tortugas Shipwreck, Florida: *The Animal Bones*. *Odyssey Papers* 29.
- Armitage, P.L., West, B., Steedman, K., 1984. New evidence of black rat in Roman London. *London Archaeol.* 4 (14), 375–383.
- Audoin-Rouzeau, F., 1999. Le rat noir (*Rattus rattus*) et la peste dans l'occident antique et médiéval. *Bull. Soc. Pathol. Exotique* 92, 422–426.
- Audoin-Rouzeau, F., Vigne, J.-D., 1994. La colonisation de l'Europe par le rat noir (*Rattus rattus*). *Rev. Paleobiol.* 13 (1), 125–145.
- Audoin-Rouzeau, F., Vigne, J.-D., 1997. Le Rat Noir (*Rattus rattus*) en Europe Antique et Médiévale: Les Voies du Commerce et l'Expansion de la Peste. *Anthropozoologica* 25 (26), 399–404.
- Avni, G., 2014. *The Byzantine Islamic Transition in Palestine: An Archaeological Approach*. Oxford University Press, Oxford.
- Badou, S.A., Gauthier, P., Houemenou, G., Loiseau, A., Dossou, H.-J., Etougbetche, J., Dobigny, G., 2021. Population genetic structure of black rats in an urban environment: a case study in Cotonou, Benin. *Hystrix, Italian Journal of Mammalogy* 32 (2), 130–136. <https://doi.org/10.4404/hystrix>.
- Baig, M., Khan, S., Eager, H., Atkulwar, A., Searle, J.B., 2019. Phylogeography of the black rat (*Rattus rattus*) in India and the implications for its dispersal history in Eurasia. *Biol. Invasions* 21 (2), 417–433. <https://doi.org/10.1007/s10530-018-1830-0>.
- Blondel, J., 2000. Evolution and ecology of birds on islands: Trends and prospects. *Vie et Milieu* 50 (4), 205–220.
- Brown, J.C., Twigg, G.I., 1969. Studies on the pelvis in British Muridae and Cricetidae (Rodentia). *J. Zool., London* 158, 81–132.
- Cassaing, J., Derré, C., Moussa, I., Cheylan, G., 2007. Diet variability of Mediterranean insular populations of *Rattus rattus* studied by stable isotope analysis. *Isot. Environ. Health Stud.* 43 (3), 197–213. <https://doi.org/10.1080/10256010701562919>.
- Caut, S., Angulo, E., Courchamp, F., 2008. Dietary shift of an invasive predator: rats, seabirds and sea turtles. *J. Appl. Ecol.* 45 (2), 428–437. <https://doi.org/10.1111/j.1365-2664.2007.01438.x>.
- Cheylan, G., Granjon, L., Britton-Davidian, J., 1998. Distribution of genetic diversity within and between Western Mediterranean island populations of the black rat *Rattus rattus* (L. 1758). *Biol. J. Linn. Soc.* 63, 393–408.
- Cohen, M., Cvikel, D., 2019. Ma'agan Mikhael B, Israel: a preliminary report of a Late Byzantine-Early Islamic period shipwreck. *Int. J. Naut. Archaeol.* 48 (1), 189–207. <https://doi.org/10.1111/1095-9270.12331>.
- Cohen, M., Cvikel, D., 2020. Rigging of the Ma'agan Mikhael B shipwreck (7th–8th centuries AD): new finds. *Int. J. Naut. Archaeol.* 49 (2), 291–302.
- Colangelo, P., Abiadh, A., Aloise, G., Amori, G., Capizzi, D., Vasa, E., Annesi, F., Castiglia, R., 2015. Mitochondrial phylogeography of the black rat supports a single invasion of the western Mediterranean basin. *Biol. Invasions* 17 (6), 1859–1868.
- Constable, O.R., 2003. The transition from Byzantium to the Dar al-Islam. In: *Housing the stranger in the Mediterranean world: lodging, trade, and travel in late antiquity and the Middle Ages*. Cambridge University Press, Cambridge, pp. 40–67.

- Creisher, M., Goren, Y., Artzy, M., Cvikel, D., 2019. The amphorae of the Ma'agan Mikhael B shipwreck: preliminary report. *Levant* 51 (1), 105–120. <https://doi.org/10.1080/00758914.2020.1723355>.
- Cucchi, T., 2008. Uluburun shipwreck stowaway house mouse: molar shape analysis and indirect clues about the vessel's last journey. *J. Archaeol. Sci.* 35 (11), 2953–2959. <https://doi.org/10.1016/j.jas.2008.06.016>.
- Delibes, M., Ferreras, P., Gaona, P., 2001. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecol. Lett.* 4 (5), 401–403.
- Doligez, B., Boulonier, T., 2008. Habitat Selection and Habitat Suitability Preferences. In: Jorgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of Ecology*. Elsevier, Amsterdam, pp. 223–243. <https://doi.org/10.1016/B978-0-444-63768-0.00015-9>.
- Ervynck, A., 2002. Sedentism or urbanism? On the origin of the commensal black rat (*Rattus rattus*). In: Dobney, K., O'Connor, T. (Eds.), *Bones and the man. Studies in honour of Don Brothwell*. Oxbow, Oxford, pp. 95–109.
- Escoriza, D., 2020. Ship rats and island reptiles: Patterns of co-existence in the Mediterranean. *PeerJ* 8, e8821.
- Ewer, R.F., 1971. The biology and behaviour of a free-living population of black rats (*Rattus rattus*). *Anim. Behav. Monogr.* 4, 125–174. [https://doi.org/10.1016/S0066-1856\(71\)80002-x](https://doi.org/10.1016/S0066-1856(71)80002-x).
- Faleh, A.B., Annabi, A., Said, K., 2012. Morphometric variation in Black Rat *Rattus rattus* (Rodentia: Muridae) from Tunisia. *Acta Zoologica Bulgarica* 64 (4), 381–387.
- Feng, A.Y.T., Himsforth, C.G., 2014. The secret life of the city rat: a review of the ecology of urban Norway and black rats (*Rattus norvegicus* and *Rattus rattus*). *Urban Ecosystems* 17, 149–162. <https://doi.org/10.1007/s11252-013-0305-4>.
- Fernández-Jalvo, Y., Andrews, P., 2016. *Atlas of Taphonomic Identifications*. Springer Science + Business Media, Dordrecht.
- Fischer, M., Taxel, I., 2014. Yavneh-Yam in the Byzantine – Early Islamic transition: the archaeological remains and their socio-political implications. *Israel Explor. J.* 64 (2), 212–242.
- Foster, J.B., 1964. Evolution of mammals on islands. *Nature* 202 (4929), 234–235.
- Friedman, A.-L.-L., Cohen, M., 2023. Bugs onboard: Beetles and cockroaches from the Late Antiquity Ma'agan Mikhael B shipwreck, Israel. *J. Archaeol. Sci.: Rep.* 48, 103879.
- Furrer, R.D., Pasinelli, G., 2016. Empirical evidence for source-sink populations: a review on occurrence, assessments and implications: source-sink dynamics in animals. *Biol. Rev.* 91 (3), 782–795.
- Granjón, L., Cheylan, G., 1990a. Adaptations Comportementales des Rats Noirs *Rattus rattus* del Iles Ouest-Méditerranéennes. *Vie Milieu* 40 (2/3), 189–195.
- Granjón, L., Cheylan, G., 1990b. Différenciation biométrique des rats noirs (*Rattus rattus*) des îles ouest-méditerranéennes. *Mammalia* 54 (2), 213–231.
- Greene, E.C., 1935. *Anatomy of the Rat*. Transactions of the American Philosophical Society, vol. 27. The American Philosophical Society, Philadelphia.
- Harbeck, M., Seifert, L., Hänsch, S., Wagner, D.M., Birdsell, D., Parise, K.L., Wiechmann, I., Grupe, G., Thomas, A., Keim, P., Zöller, L., Bramanti, B., Riehm, J. M., Scholz, H.C., Besansky, N.J., 2013. *Yersinia pestis* DNA from skeletal remains from the 6th century AD reveals insights into JUSTINIANIC plague. *PLoS Pathog.* 9 (5), e1003349.
- Harding, S., 2021. Analysis of the Faunal Remains from the Ma'agan Mikhael B Shipwreck. University of Haifa. MA Thesis.
- Harding, S., 2022a. Stowaways Supplement S3: Ma'agan Mikhael B *Rattus rattus* cranial and post-cranial measurements datasheet. Zenodo. <https://doi.org/10.5281/ZENODO.7078642>.
- Harding, S., 2022b. Stowaways Supplement S7: supplemental figures. Zenodo. <https://doi.org/10.5281/ZENODO.7078843>.
- Harding, S., 2022c. Stowaways Supplement Table S2. Ma'agan Mikhael B *Rattus rattus* Skeletal Element Identification (NISP) Datasheet. Zenodo. <https://doi.org/10.5281/ZENODO.7078680>.
- Harding, S., 2023. Stowaways Supplement S6. Relative Size Index (RSI) Comparative Dataset & R Code for Mediterranean Ship Rats. Zenodo. <https://doi.org/10.5281/zenodo.7677467>.
- Harding, S., Lernau, O., Wouters, W., Marom, N., Cvikel, D., 2022. A tale of five fishes: first evidence of trade in Galilean salted fish on the Carmel coast in the early Islamic period. *Eur. J. Archaeol.* 1–21. <https://doi.org/10.1017/eea.2022.50>.
- Harding, S., Tapson, M., 2023. Stowaways supplement S1 methods & comparative materials. Zenodo. <https://doi.org/10.5281/zenodo.7677398>.
- Hooker, S., Innes, J., 1995. Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum. *N. Z. J. Zool.* 22 (3), 291–304. <https://doi.org/10.1080/03014223.1995.9518044>.
- Ibrahim, A.B., Salem, I.B., Chetoui, M., Nouria, S., 2017. Morpho-metric analysis of the insular and mainland *Rattus* in Tunisia. *Biologia* 72 (8), 927–934. <https://doi.org/10.1515/biolog-2017-0093>.
- Innes, J.G., King, C.M., Flux, M., Kimberley, M.O., 2001. Population biology of the ship rat and Norway rat in Pureora forest park, 1983–87. *N. Z. J. Zool.* 28 (1), 57–78. <https://doi.org/10.1080/03014223.2001.9518257>.
- Juette, T., Garant, D., Jameson, J.W., Réale, D., 2020. The island syndrome hypothesis is only partially validated in two rodent species in an inland-island system. *Oikos* 129 (11), 1739–1751. <https://doi.org/10.1111/oik.07249>.
- King, C.M., Innes, J.G., Gleeson, D., Fitzgerald, N., Winstanley, T., O'Brien, B., Bridgman, L., Cox, N., 2011. Reinvasion by ship rats (*Rattus rattus*) of forest fragments after eradication. *Biol. Invasions* 13 (10), 2391–2408.
- King, C.M., Winstanley, T., Innes, J., Glee, D., 2014. Multiple paternity and differential male breeding success in wild ship rats (*Rattus rattus*). *N. Z. J. Ecol.* 38 (1), 76–85.
- LiphaTech, 2017. Commensal Rodent Facts. Retrieved June 22, 2022, from <https://liphat.ech.com/>.
- Little, L.K., 2006a. Life and Afterlife of the First Plague Pandemic. In: Little, L.K. (Ed.), *Plague and the End of Antiquity: The Pandemic of 541–750*. Cambridge University Press, pp. 3–32.
- Little, L.K. (Ed.), 2006b. *Plague and the End of Antiquity: the Pandemic of 541–750*. Cambridge University Press, Cambridge. 10.1017/CBO9780511812934.
- Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* 32 (10), 1683–1699. <https://doi.org/10.1111/j.1365-2699.2005.01314.x>.
- Lomolino, M.V., 1985. Body size of mammals on islands: the island rule reexamined. *Am. Nat.* 125 (2), 310–316.
- Mangiafico, S., 2021. rcompanion: Functions to Support Extension Education Program Evaluation.
- McCormick, M., 2003. Rats, communications, and plague: toward an ecological history. *J. Interdiscip. Hist.* 34 (1), 1–25. <https://doi.org/10.1162/002219503322645439>.
- Meiri, S., Cooper, N., Purvis, A., 2008. The island rule: Made to be broken? *Proc. R. Soc. B Biol. Sci.* 275 (1631), 141–148. <https://doi.org/10.1098/rspb.2007.1056>.
- Meiri, S., Dayan, T., 2003. On the validity of Bergmann's rule. *J. Biogeogr.* 30 (3), 331–351. <https://doi.org/10.1046/j.1365-2699.2003.00837.x>.
- Meiri, S., Dayan, T., Simberloff, D., 2006. The generality of the island rule reexamined. *J. Biogeogr.* 33 (9), 1571–1577. <https://doi.org/10.1111/j.1365-2699.2006.01523.x>.
- Milmore, B.K., 1943. Harborage of *Rattus rattus Alexandrinus*. *Public Health Reports* (1896-1970), vol. 58. 10.2307/4584633.
- Morales, A., Rodríguez, J., 1997. Black rats (*Rattus rattus*) from medieval Mertola (Baixo Alentejo, Portugal). *J. Zool.* 241 (4), 623–642. <https://doi.org/10.1111/j.1469-7798.1997.tb05737.x>.
- Mori, E., Iacucci, A., Castiglia, R., Santini, L., 2017. Sexual-size dimorphism in two synanthropic rat species: comparison and eco-evolutionary perspectives. *Mamm. Biol.* 83, 78–80. <https://doi.org/10.1016/j.mambio.2016.12.002>.
- Morony, M.G., 2006. 'For whom does the writer write?': The first bubonic plague pandemic according to Syriac sources. In: Little, L.K. (Ed.), *Plague and the End of Antiquity: The Pandemic of 541–750*. Cambridge University Press, pp. 59–86.
- Ogle, D., Doll, J., Wheeler, P., Dinno, A., 2021. FSA: Fisheries Stock Analysis.
- Oueslati, T., Kbiri Alaoui, M., Ichkhakh, A., Callegarin, L., de Chazelle, C.A., Rocca, E., Carrato, et C., 2020. 1st century BCE occurrence of chicken, house mouse and black rat in Morocco: Socio-economic changes around the reign of Juba II on the site of Rirha. *J. Archaeol. Sci.: Rep.*, 29(July 2019), 1–10. 10.1016/j.jasrep.2019.102162.
- Panagiotakopulu, E., 2004. Pharaonic Egypt and the origins of plague. *J. Biogeogr.* 31 (2), 269–275. <https://doi.org/10.1046/j.0305-0270.2003.01009.x>.
- Puckett, E.E., Orton, D., Munshi-South, J., 2020. Commensal rats and humans: integrating rodent phylogeography and zooarchaeology to highlight connections between human societies. *Bioessays* 42 (5), 1–10. <https://doi.org/10.1002/bies.201900160>.
- Pulliam, H.R., 1988. Sources, sinks and population regulation. *Am. Nat.* 132 (5), 652–661.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramalhinho, M.G., Mathias, M.L., Santos-Reis, M., Libois, R., Fons, R., Petrucci-Fonseca, F., Collares-Pereira, M., 1996. First approach on the skull morphology of the black rat (*Rattus rattus*) from the Terceira and São Miguel Islands (Azores Archipelago). *Vie Milieu* 46 (3/4), 245–251.
- Rea, L., Parker, R., 2014. *Designing and Conducting Survey Research*, 4th ed. Jossey-Bass, San Francisco.
- Rowe, K.C., Aplin, K.P., Baverstock, P.R., Moritz, C., 2011. Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *System. Biol.* 60 (2), 188–203. <https://doi.org/10.1093/sysbio/syq092>.
- Russell, J.C., Ringler, D., Trombini, A., Le Corre, M., 2011. The island syndrome and population dynamics of introduced rats. *Oecologia* 167 (3), 667–676. <https://doi.org/10.1007/s00442-011-2031-z>.
- Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.* 17 (10), 474–480.
- Schuenemann, V.J., Bos, K., DeWitte, S., Schmedes, S., Jamieson, J., Mittnik, A., Forrest, S., Coombes, B.K., Wood, J.W., Earn, D.J.D., White, W., Krause, J., Poinar, H.N., 2011. Targeted enrichment of ancient pathogens yielding the pPCP1 plasmid of *Yersinia pestis* from victims of the Black Death. *Proc. Natl. Acad. Sci. U.S.A.* 108 (38).
- Stamps, J., 2008. Habitat. In: Jorgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of Ecology*. Elsevier, Amsterdam, pp. 1807–1810.
- Stathakopoulos, D., 2006. Crime and Punishment: The Plague in the Byzantine Empire, 541–749. In: Little, L.K. (Ed.), *Plague and the End of Antiquity: The Pandemic of 541–750*. Cambridge University Press, pp. 99–118.
- Tomczak, M., Tomczak, E., 2014. The need to report effect size estimates revisited. An overview of some recommended measures of effect size. *Trends Sport Sci.* 1 (21), 19–25.
- Van Valen, L., 1973. Pattern and the balance of nature. *Evolutionary Theory* 1, 31–49.
- Ventura, J., López Fuster, M., 2000. Morphometric analysis of the black rat, *Rattus rattus*, from Congreso Island (Chafarinas Archipelago, Spain). *Orsis* 15, 91–102.
- Vigne, J.D., Valladas, H., 1996. Small mammal fossil assemblages as indicators of environmental change in Northern Corsica during the last 2500 years. *J. Archaeol. Sci.* 23, 199–215.
- Vigne, J.D., Villié, P., 1995. Une preuve archéologique du transport d'animaux par bateau: le crâne du rat surmulot (*Rattus norvegicus*) de l'épave du "ça ira. In: *L'Homme Méditerranéen. Mélanges Offerts à Gabriel CAMPS Professeur. Émerite de l'Université de Provence. Publications de l'Université de Provence, Aix-En-Provence.*
- von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bull.* 1, 138.

- von den Driesch, A., Boessneck, J., 1983. A Roman cat skeleton from Quseir on the Red Sea coast. *J. Archaeol. Sci.* 10 (3), 205–211. [https://doi.org/10.1016/0305-4403\(83\)90003-1](https://doi.org/10.1016/0305-4403(83)90003-1).
- Wagner, D.M., Klunk, J., Harbeck, M., Devault, A., Wagglechner, N., Sahl, J.W., Enk, J., Birdsell, D.N., Kuch, M., Lumibao, C., Poinar, D., Pearson, T., Fourment, M., Golding, B., Riehm, J.M., Earn, D.J.D., DeWitte, S., Rouillard, J.-M., Grupe, G., Wiechmann, I., Bliska, J.B., Keim, P.S., Scholz, H.C., Holmes, E.C., Poinar, H., 2014. *Yersinia pestis* and the Plague of Justinian 541–543 AD: a genomic analysis. *Lancet Infect. Dis.* 14 (4), 319–326.
- Walmsley, A., 2000. Production, exchange, and regional trade in the Islamic East Mediterranean: old structures, new systems? In: Hansen, I.L., Wickham, C. (Eds.), *The Long Eighth Century*. Brill, Leiden, pp. 265–344.
- Watkinson, A.R., Sutherland, W.J., 1995. Sources, sinks and pseudo-sinks. *J. Anim. Ecol.* 64 (1), 126–130.
- Whitcomb, D., 1995. Islam and the socio-cultural transition of Palestine, early Islamic period (638–1099 C.E.). In: Levy, T.E. (Ed.), *The Archaeology of Society in the Holy Land*. Leicester University, London, pp. 488–501.
- Wickham, H., 2019. Welcome to the tidyverse. *J. Open Source Softw.* 4 (43), 1686.
- Wickham, H., François, R., Henry, L., & Müller, K., 2021. dplyr: A Grammar of Data Manipulation.
- Wickham, H., Girlich, M., Ruiz, E., 2021b. A “dplyr” Back End for Databases.
- Wiechmann, I., Grupe, G., 2005. Detection of *Yersinia pestis* DNA in two early medieval skeletal finds from Aschheim (Upper Bavaria, 6th century A.D.). *Am. J. Phys. Anthropol.* 126 (1), 48–55. <https://doi.org/10.1002/ajpa.10276>.
- Williams, C.L., 1932. Some Instances of Rapid Rat Infestation of Vessels. *Public Health Reports* (1896–1970), vol. 47.
- Wilmshurst, J.M., Ruscoe, W.A., Russell, J.C., Innes, J.G., Murphy, E.C., Nathan, H.W., 2021. Family Muridae. In: King, C.M., Forsyth, D.M. (Eds.), *The Handbook of New Zealand Mammals*. Otago University Press, Dunedin, pp. 161–240. [https://doi.org/10.1016/0006-3207\(92\)90720-8](https://doi.org/10.1016/0006-3207(92)90720-8).
- Yom-Tov, Y., Yom-Tov, S., Moller, H., 1999. Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *J. Biogeogr.* 26, 947–958.
- Yu, H.e., Jamieson, A., Hulme-Beaman, A., Conroy, C.J., Knight, B., Speller, C., Al-Jarah, H., Eager, H., Trinks, A., Adikari, G., Baron, H., Böhlendorf-Arslan, B., Bohingamuwa, W., Crowther, A., Cucchi, T., Esser, K., Fleisher, J., Gidney, L., Gladilina, E., Gol'din, P., Goodman, S.M., Hamilton-Dyer, S., Helm, R., Hillman, J.C., Kallala, N., Kivikero, H., Kovács, Z.E., Kunst, G.K., Kysely, R., Linderholm, A., Maraoui-Telmini, Bouthéina, Marković, N., Morales-Muñiz, A., Nabais, M., O'Connor, T., Oueslati, T., Quintana Morales, E.M., Pasda, K., Perera, J., Perera, N., Radbauer, S., Ramon, J., Rannamäe, E., Sanmartí Grego, J., Treasure, E., Valenzuela-Lamas, S., van der Jagt, I., Van Neer, W., Vigne, J.-D., Walker, T., Wynne-Jones, S., Zeiler, J., Dobney, K., Boivin, N., Searle, J.B., Krause-Kyora, B., Krause, J., Larson, G., Orton, D., 2022. Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European introductions associated with human economic history. *Nat. Commun.* 13 (1) <https://doi.org/10.1038/s41467-022-30009-z>.