Plague reservoir species throughout the world

Abstract.

Plague is known since ancient history, as a re-emerging infectious disease, causing considerable socioeconomic burden in regional hotspots. To better understand the epidemiological cycle of the causative agent of the plague, its potential occurrence and possible future dispersion, one must carefully consider the taxonomy, distribution, and ecological requirements of reservoir-species in relation either to natural or human driven changes (e.g. climate change, urbanization). In recent years, the depth of knowledge on species taxonomy and species composition in different landscapes has undergone a dramatic expansion, driven by modern taxonomic methods such as synthetic surveys that take into consideration morphology, genetics and the ecological setting of captured animals to establish their species identities. Here we consider the recent taxonomic changes of the rodent species in known plague reservoirs and detail their distribution across the world, with a particular focus on those rodents considered to be keystone host species. A complete checklist of all known plague-infectable vertebrates living in plague reservoirs is provided as an appendix.

Key words: Plague, reservoirs, mammals, rodents, taxonomy

Introduction

Zoonotic diseases surveillance always benefits much from precise taxonomy of the reservoirs/vectors. With a deep taxonomic knowledge on *Anopheles gambiae* complex species, the main vector for malaria with significant human health burden, control measures have been slanted towards on human-specific malarial vectors (Besansky 1999; Bickford *et al.* 2007). Adequate treatment for man suffering from Leishmaniases, and effective control measures need an update taxonomy for parasites and the reservoirs (Ramírez *et al.* 2016). We will make the case that a similar improvement in the taxonomy of plague-infected small mammal species, as presented here, offers similar opportunities. We will first present an overview of the relevant dynamics, small mammal species and human interactions of plague ecosystems.

Plague is a contagious disease caused by the gram-negative enterobacteria *Yersinia pestis*. This bacterium has been responsible for mass human mortality in Eurasia and Africa (Gage & Kosoy 2005). Particularly devastating was the Second Plague Pandemic known as ‘Black Death’ which started in Central Asia in 1346 and subsequently circulated across Eurasia and Africa until it transitioned into the Third Pandemic in the 18th century (DeWitte 2014; Sticker 1908; Benedict

1996; Green 2018; Chouin 2018). Plague however has been present in human population for much longer. The oldest DNA confirmed flea-borne bubonic strain of the pathogen is from ~3800-year-old skeletal remains (Spyrou *et al.* 2018), while less pathogenic lineages have been discovered as far back as 6000 years ago (Rasmussen *et al.* 2015; Rascovan *et al.* 2019). Plague is still found in many Asian, African and North and South American countries, and causes a modest number of fatal infections every year (Bertherat 2019). Since 1954 the number of annually reported infections with *Y. pestis* has fluctuated between ~100–3000 cases, with 100–200 fatalities (Bertherat 2019).

Plague is a predominantly zoonotic disease circulated in natural plague foci as the rodent host - flea vector-*Y. pestis* system. Humans are an incidental and highly susceptible host at risk of infection particularly when the disease spills over during epizootic periods in wildlife plague reservoirs (Stenseth *et al.* 2008; Samia *et al.* 2011).

Current distribution of plague foci

Plague foci naturally occur in xeric regions between 49°-51° northern latitude and 34°-37° southern latitude (see Figure 1). The realized niche of plague foci has been strongly shaped by long-distance commercial trade across the centuries (Rascovan *et al.* 2019; Xu *et al.* 2019; Namouchi *et al.* 2018) and by landscape alterations (deforestation, desertification, overgrazing, and other agricultural activities) that brought humans and zoonoses reservoirs/vectors into close contact (Keesing *et al.* 2010; Lambin *et al.* 2010), and by large-scale interventions aimed at locally controlling or eradicating plague foci (Jones *et al.* 2019).

On a local scale, the realization of plague foci, and their dispersal on a more regional scale is associated with the biological (predators, vegetation, rodents, vectors, and the bacterium) and environmental factors (climate and elevation); such as the intensity of rodent migration during periods of overcrowding (McNeill 1979; Gage 2010), extended phenotype adaptation by the pathogen to a scarcity in vectors (Cui *et al.* 2020), and by the transport of the pathogen by predatory birds or mammals (Burdellov 1991; Poland & Barnes 1979). Human activity also plays a role on this regional scale of plague activity and dispersal. For instance, in Tanzania, the risk of plague infections among rodents is correlated to agricultural practices which affect reservoir density (McCauley *et al.* 2015).

Persistence of *Yersinia pestis* in natural foci

Plague foci can exist in a quiescent, enzoonotic, or epizootic state, depending on the host and flea vector species that occur in the ecosystem, their abundance, and other properties of the ecosystem itself. In the quiescent state, no cases are reported in humans and (providing the surveillance system exists) no cases are detected in rodents for an extended period of time. During the quiescent state, which can last decades, plague can be telluric (bacteria survive in the soil of the infected host burrows) (Baltazard *et al.* 1960; Boegler *et al.* 2012; Benavides-Montaña & Vadyvaloo 2017; Barbieri *et al.* 2020), or circulate in low intensity in small microfoci among "preserver" or "resistant" reservoir hosts. These microfoci are not picked up by chance or inaccessibility (Fedorov 1994; Stenseth *et al.* 2008; Ramasindrazana *et al.* 2017). The exact mechanism by which plague persists within preserver hosts during quiescent phase has not been fully elucidated. Several components are thought to be important, including a high resistance heterogeneity of the host (Eisen & Gage 2009), presence of a flea species which allows for the dormancy of plague within them (off-host fleas) (Gage & Kosoy 2005; Bazanova *et al.* 2007), and possibly also the ability of a reservoir species to reacquire the bacterium from plague-contaminated soil (Karimi 1963; Ayyadurai *et al.* 2008; Malek *et al.* 2017), when climatic conditions are favorable (Eisen *et al.* 2008a; Lowell *et al.* 2015).

A plague focus is in the enzoonotic phase when *Y. pestis* is regularly detected, but in low frequency (generally < 2% of rodents captured) (Davis *et al.* 2004; Xu *et al.* 2015). During the enzoonotic phase, plague is assumed to persist by being passed on between preserver hosts, or via meta-population turnover, where subpopulations replace one another during inter-epizootics periods (George *et al.* 2013). In other words, the role of an extirpated carrier can be assumed by another, hence ensuring the persistence of *Y. pestis* over extended periods. Whether a particular plague focus is classified as quiescent or as a low intensity enzoonotic phase is to some degree subjective and depends on the intensity of plague surveillance program.

The third stage is an epizootic cycle, i.e. an epidemic of plague among the rodents in the plague focus. Typically, there are three prerequisites for an epizootic cycle to occur. Firstly, the ecosystem needs to harbor a sufficient numbers of hosts that are highly sensitive to plague, which, when infected, generate a high levels of bacteremia in their blood. Secondly, a sufficient number of fleas must be present to transmit the infection between rodent hosts (Hinnebusch 2005, Reijnders *et al.* 2012). Finally, the plague bacterium should be in a non-telluric state, present in at least some of the rodent species in the ecosystem.

Three key roles of rodents within a plague focus

Yersinia pestis circulation within natural foci is thought to be guaranteed through three processes: preservation, accumulation, and dissemination (Burdellov 1991). Rodents are integral to all three of these processes. Preservation of the pathogen occurs through primary rodent hosts that are consistently present in the region, and generally experience low or heterogeneous levels of bacteremia when infected. Accumulation of the pathogen in the ecosystem occurs through secondary or tertiary rodent hosts which acquire *Y. pestis* from the primary or secondary hosts. The transmission is always mediated by fleas. The secondary and tertiary rodent hosts are typically highly sensitive to the pathogen and cause the disease to become more prevalent in the ecosystem. This creates a danger of spillover to other species (Gage 2010; Zeppelini *et al.* 2016). The dissemination happens particularly at times of rodent overcrowding, when the animals, especially the weaning juveniles, disperse towards vacant territories, providing the opportunity for spreading of the pathogen (Gage 2010). The burrow-dwelling infected fleas that remain active within a burrow after its rodent occupants have died, can convey the infection to its new dwellers. Plague-infected fleas can also be picked up by birds or mammals that prey on rodents may act as disseminator hosts, either by transporting plague-infected fleas to new regions, or by becoming infected themselves after consuming plague-infected prey (Burdellov 1991; Poland & Barnes 1979; Salkeld & Stapp 2006, Salkeld *et al.* 2007).

The interface between human communities and plague reservoirs can be permanent (like in synanthropic reservoirs- e.g. the epidemic in Madagascar in 2017), or dynamic- such as when plague reservoirs expand into urban communities or humans encroach upon existing wildlife reservoirs- (e.g. the plague outbreak in Los Angeles in 1924-1925 or the epidemic in Kurdistan (Iran) in the early 1940s which both were driven by infected rodents invaded to human communities) (Baltazard *et al.* 1960; Caten & Kartman 1968; Kool & Weinstein 2005; Randremanana *et al.* 2019).

The role of rodent taxonomy in understanding plague ecology

Three taxonomy-related factors play a particularly important role in understanding plague ecosystems – (1) the ecological and genetic characteristics of the present rodent host species, (2) species-tailored sampling and surveillance methodology, as well as (3) the impact of plague on conservation efforts on particular species.

First, a precise taxonomic identification based on systematic surveys (Zeppelini *et al.* 2016) is crucial to improve our ability to carefully extrapolate genetic and ecological traits of rodent species to for which we lack specific knowledge to closely related species which are better studied with regard to plague. This will allow us to understand the roles that different local rodent species may play (preserver, amplifier, disseminator) in a local plague ecosystem, evidence for plague resistance based on particular genes and gene families (Nilsson *et al.* 2020; Busch *et al.* 2013; Tollenaere *et al.* 2011; Andrianaivoarimanana *et al.* 2018), or the likelihood that the blood of a local rodent species is of the type that greatly facilitates the capacity of fleas to act as an efficient vector of plague (recent experimental work by Eisen *et al.* (2008b) and Bland *et al.* (2018), currently limited to only a few species). In all cases, having a taxonomically and genetically updated list of rodent hosts of plague ecosystems allows for careful extrapolation of these results across a wider range of species. Second, a more in-depth zoological knowledge of the reservoirs will affect sampling activities in foci during or after epizootics. Most plague surveillance done in urbanized areas employs methods that enhance the capture of certain taxa but exclude others (Moore *et al.* 2015; Zeppelini *et al.* 2016). A refined taxonomic list facilitates a more sound allocation of usually limited resources (Jones *et al.* 2019). Finally, the impact plague has on species which are of conservation concern is gaining attention (Biggins & Kosoy 2001a,b). For instance, plague epizootics cause significant reduction on the population size and heterogeneity of *Cynomys* spp., directly (cf. Trudeau *et al.* 2004), and on their key predator (*Mustela nigripes*) indirectly (Biggins & Godbey 2003; Matchett *et al.* 2010). Exact identification of hosts, their distribution and habitat demands is both a critical conservation objective and a public health priority.

Recent improvements in taxonomy

New and powerful techniques in taxonomy (e.g., single/multiple gene analyses, next generation sequencing (NGS), genome wide association studies (GWAS), ecological niche modeling (ENM), and geometric morphometrics) have led to considerable development in host and pathogen species delimitation, which altered their taxonomic ranks and exposed cryptic species richness (e.g. Lecompte *et al.* 2008 Pečnikar & Buzan 2014; Meinel *et al.* 2014; Bonnet *et al.* 2014; Purty & Chatterjee 2016; Fan *et al.* 2017; Colabella *et al.* 2018; Fan *et al.* 2018). Indeed, molecular techniques have profoundly changed our understanding of diversity by splitting species defined by morphology into several species with own evolutionary history (Zachos *et al.*

2013, 2020; Taylor *et al.* 2019). In a similar way, population genetic analyses of pathogen species are of prime importance in detecting possible cryptic species and revealing the processes that underline their evolution (Brown *et al.* 2013).

The management of many emerging infectious diseases will certainly facilitate by better understanding of the types of species form reservoirs (Plourde *et al.* 2017). The identification of sibling and cryptic species, as well as of molecular lineages and morphological variants which associate with zoonotic diseases is highly relevant for both wildlife conservation policy, management of host/pathogen populations. In a recent review of South American plague reservoirs, 22 of 50 rodent hosts of *Y. pestis* were found to have undergone taxonomic changes over the last 20 years (Bonvicino *et al.* 2015). Most recently, another contribution was also performed to associate previously published information of plague reservoirs and taxonomic dynamics in Brazilian foci (Fernandes *et al.* 2020). Such researches are highlighting the urgent need for a global update of the taxonomy of rodent species living in plague foci. Available lists are either limited in geographic scope (Bonvicino *et al.* 2015), taxonomically outdated (Pollitzer 1960; Gratz 1999), or incomplete in their description of the systematic methodology used (Sludskiy 2014b; Dubyanskiy & Yeszhanov 2016). Different species, as well as different populations of particular species show a variance in susceptibility, mortality, and life history, they might play a different role in plague epidemiological cycles. As a result, precise taxonomic identification is of the utmost importance and demands systematic surveys to avoid biases (Zeppelini *et al.* 2016).

In this study, we aim to update the current information on worldwide plague reservoirs in order to improve future plague preparedness and surveillance programs. For this purpose, we will provide a taxonomically updated global list of both the "preserver" rodent hosts living in plague foci, as well as all other plague-sensitive rodents living within these foci.

Materials and Methods

In this review, an up-to-date taxonomic list of the vertebrate fauna of the plague reservoirs are provided considering the available literature indexed in Google Scholar, NCBI's PubMed, Science Direct, World Health Organization manuals up to June 2020 (e.g. Davis 1953; Pollitzer 1960; Hudson *et al.* 1964; Marshall *et al.* 1967; Lechleitner *et al.* 1968; Warsawski *et al.* 1971; Klein *et al.* 1975; Turner *et al.* 1975; Twigg 1978; Nelson 1980; Clover *et al.* 1989; Henke *et al.* 1990; Dyer & Huffman 1999; Gratz 1999; Kozlov & Sultanov 2000; Fukushima *et al.* 2001;

Karimova & Neronov 2007; Salkeld *et al.* 2007; Edmunds *et al.* 2008; Chen *et al.* 2009; Riehm *et al.* 2011; Saraev & Sklyarenko 2012; Ziwa *et al.* 2013; Martin-Alonso *et al.* 2014; Sludskiy 2014a,b Bonvicino *et al.* 2015; Malek *et al.* 2016; Dubyanskiy & Yeszhanov 2016). Moreover, to cover all the related works properly, different combinations of keywords were used for our search such as "Wildlife Plague", "Plague, epizootic/enzootic periods", "Plague, Reservoirs, Rodents", "Plague, Reservoirs, Small mammals", "Plague History", "*Yersinia pestis*, Reservoirs, Wildlife", "Plague outbreaks", "Plague, Reservoirs, Taxonomy", "Rodent-borne Diseases, Reservoirs". The references found in the selected articles were studied to increase the scope of the search and cover as many articles as possible. The next step was a taxonomic update of the known species, taking into account the recent taxonomic dynamics in zoological literature. The "*Handbook of the Mammals of the World* (Wilson *et al.* 2016, 2017)" series were considered to be the principal foundations but compiled with the information available from the International Union for Conservation of Nature (IUCN), and the Integrated Taxonomic Information System (ITIS) (Tom & Dave 2019). Furthermore, recent changes in available publications up to June 2020 were screened (e.g. Miura *et al.* 2006; Kryštufek & Vohralik 2012; Kitchener *et al.* 2017; Lebedev *et al.* 2018; Bannikova *et al.* 2019; Mahmoudi *et al.* 2020). Finally, unintended spelling errors in previous lists (Sludskiy 2014b; Dubyanskiy & Yeszhanov 2016) were corrected. Extracted list of reservoirs were classified into their taxonomic orders, and a chi-squared test was performed between the observed distribution and the true distribution of species among mammalian orders to determine whether plague reservoir species are special or the infection has been taken erratically.

Finally, the distribution data of each species was collected from the range data on the website of IUCN Red List (<https://www.iucnredlist.org/>). Taking into account the *Handbook of the Mammals of the World* (Wilson *et al.* 2016, 2017) and recent taxonomic re-arrangements, several incorrect spellings and outdated taxonomy were observed for the reported reservoirs on the IUCN website (last updated November, 2019). For instance, *Pygerethmus platyurus*, emended to *Pygeretmus platyurus*; *Paradoxurus hermaphrodites* to *Paradoxurus hermaphroditus*, and *Cavia porcella* is corrected to *Cavia porcellus*. Species which were listed under their previous taxonomy on the IUCN website were also taken into consideration beneath their most current taxonomy. The global figure of plague reservoir species-richness was performed using the emended taxonomy presented in this manuscript (Figure 2).

Discussion

The list of reservoirs provided in the present study combined the assembled works by Sludskiy (2014b), Bonvicino *et al.* (2015), and Dubyanskiy & Yeszhanov (2016) with subsequent additions found in our extensive review of literature published up to June 2020 (see, Appendix Table). Compared to previous taxonomic collections of reservoir plague hosts, this work adds 15 species, thus resulting in a total of 351 species of mammals. We highlight ≥ 47 species (13.35%) that can act as known primary hosts of plague around the world; 25 among these species are resistant (such as *Meriones persicus* and *M. libycus* in Iranian-Kurdistan focus), while 22 are considered susceptible (such as *Meriones vinogradovi* and *M. tristrami* from the Pre-Araksinsky low mountain (Azerbaijan, Armenia) and Iranian Kurdistan foci, cf. Baltazard *et al.* 1960; Emelyanov 1974) (for a species richness map and complete list of resistant and susceptible reservoirs at the global scale cf. Table 2 and Figure 3). However, one should take into account that the list of preserver and amplifier hosts are not fully understood, and require further investigation (e.g. experimental inoculation). 108 taxonomic names were updated to their most current status (either synonymous alterations or inter-generic/family translocations) and 15 alternative/misspellings of species names were corrected. Taxonomic and distributional notes are linked to the host species with dynamic or uncertain affinity and questionable distributions (cf. Appendix).

Identified reservoir species belong to eleven orders: Scandentia (1 species), Hyracoidea (1 species), Afrosoricida (1 species), Didelphimorphia (2 species), Primates (2 species), Artiodactyla (7 species), Eulipotyphla (13 species), Lagomorpha (14 species), Carnivora (31 species), and Rodentia (279 species). Wild birds, order Passeriformes (3 species), can also be contaminated with plague. It is clear that the species living within plague reservoirs and infected by plague are heavily slanted towards the Rodentia, Lagomorpha, and Carnivora. Comparison of the observed and expected distribution of mammalian orders among reservoirs were statistically significant considering the number of species in each mammalian order (Pearson's chi-squared test, $\chi^2 = 27.042$, $p = 0.001$) (Table 1). This finding points on the characteristics of the plague reservoirs. Rodents and lagomorphs are usually the most specious and abundant in majority of ecosystems, their high birth rate yield a large number of naïve host individuals (Plourde *et al.* 2017). Other mammalian orders, mainly with slower life history, low reproduction output and species composition, are either absent from plague foci, less effective as reservoirs or carriers, or

simply understudied. Carnivores are exception, as they are highly mobile, consume mainly small mammals (e.g. rodents and lagomorphs) which put them at high risk for the infection. Most birds, reptiles, and amphibians are thought to be resistant to *Y. pestis* infection (Gage & Kosoy 2005), limiting plague predominantly to mammalian hosts and their ectoparasites.

Virtually any mammal can be infected by *Y. pestis* and may take part in the dynamic of infection between wildlife and humans, either as the main or incidental host of plague. However, the major vertebrate hosts in most primary foci are certain rodents (Table 2). Actually, it seems that diseases reservoirs are special in many aspects (cf. Plourde *et al.* 2017). Rodents are the most successful of all mammalian orders in terms of species number, have a worldwide distribution (excluding Antarctica), and are major components of nearly every terrestrial fauna (Kryštufek *et al.* 2005). They encompass 2552 extant species, i.e. 39.3% of the mammalian total species richness (Burgin *et al.* 2018). Their adaptability to a wide variety of lifestyles (e.g. arboreal, subterranean, semi-aquatic etc.), environments (e.g. urban, desert, and sylvatic biotopes), their high reproductive output and rapid population turnover render them highly permissible amplification agents of zoonotic pathogens (Han *et al.* 2015). Mammals are considered the main source of novel human pathogens, and rodents are the mammalian order from which the highest number of known pathogen species have thus far been isolated (Woolhouse & Gaunt 2007; White & Razgour 2020). Indeed, fast-lived mammalian species tend to have higher reservoir competence for human pathogens (Brunner *et al.* 2008; Han *et al.* 2015). Rodents are by far the dominant carrier host of *Y. pestis*, alike for many other human pathogens (Plourde *et al.* 2017). As of now, 279 species of rodents have been identified as plague carriers, and the majority of them are from the superfamily Muroidea, specifically from the families Muridae and Cricetidae with 91 and 88 species, respectively. The complete list of the reservoirs and (a) related region(s) can be found in the Appendix.

A high level of rodent diversity within an ecosystem increases the translocation of plague between different reservoir hosts, prevents its local extinction, provides refuge for its survival, and facilitates pathogen dissemination (Ostfeld & Keesing 2000; Snall *et al.* 2008; Laudisoit *et al.* 2009; Dunn *et al.* 2010). For plague, we see a positive association between species richness with the occurrence of plague and the intensity of plague outbreaks (Bonvicino *et al.* 2015; Sun *et al.* 2019). Such a relationship with species richness appears to be a general feature of disease

ecology (Mollentze & Streicker 2020), and highlights the value of good regional taxonomic profiles in estimating outbreak risks.

Plotting ranges of the plague-infectable species on maps clearly shows that only the presence of plague-infectable hosts, regardless of whether they are reservoirs or potential carriers (cf. Figures 2 and 3) is not a good predictor of the global spread of plague foci. For example, the map on Figure 2 exposes a high concentration of potential reservoirs in Europe where no known plague foci currently exist, although they are speculated to have existed in the past, based on historical and phylogenetic analyses (Carmichael 2016; Bos *et al.* 2016). Other conditions are also needed for the pathogen to survive and effectively circulate in the ecosystem. These conditions have not yet been established, but possibly retained in the soil following the death of the infected hosts (Baltazard *et al.* 1960; Eisen *et al.* 2008) in which rodent burrows are being explored (Karimova & Neronov 2007; Malek *et al.* 2017; Spyrou *et al.* 2019; Barbieri *et al.* 2020). Species richness maps of potential hosts therefore should be considered with caution. The IUCN Red List, while frequently used (e.g. Han *et al.* 2015), is not of indispensable quality and gives an impression of the species richness distribution of plague hosts, rather than an absolute resource. For example, on the map, Madagascar lacks any plague hosts, while there are at least three species of rodents which have been experimentally confirmed to be plague-infected on the island (Rahelinirina *et al.* 2017). Furthermore, previous studies have already demonstrated that several other non-rodent species (*Setifer setosus*, *Tenrec ecaudatus* and *Hemicintetes* sp.) (Migliani *et al.* 2001; Richard *et al.* 2015) have been found seropositive or infected to plague on Madagascar, but their role in plague epidemiology are still under considerations through ongoing studies.

Conclusion

Recent developments in species delimitation and rearrangements of mammalian systematics have altered the taxonomic ranks of many groups. Cryptic species richness was exposed, previous morphospecies were split up into groups of closely related species, or were species moved from one taxonomic group to another (e.g. Lecompte *et al.* 2008; Zachos *et al.* 2013; Meinel *et al.* 2014; Bonnet *et al.* 2014; Pečnikar & Buzan 2014; Purty & Chatterjee 2016; Fan *et al.* 2017; Colabella *et al.* 2018; Fan *et al.* 2018; Taylor *et al.* 2019; Zachos *et al.* 2020). Such large taxonomic developments warrant a close re-examination of known plague reservoirs species (e.g. Bonvicino *et al.* 2015), particularly because –with few taxonomists involved in historic plague research–, plague host species have frequently been traditional identified only by

morphological traits. Such an approach may be misleading, especially in cases of sibling/cryptic/closely related species or different geographic lineages. Because different species might respond to control measures differently, a precise species identification (both for pathogens and host) is of fundamental importance in understanding zoonotic disease epidemiology, control practices, and prevention of outbreaks (Bickford *et al.* 2007). Our updated taxonomy of plague reservoir species integrates a large number of taxonomic changes and corrects earlier misclassified species among previously identified reservoirs. Such a curated list opens up the possibility for interdisciplinary researchers to combine genomic, laboratory and field observations of plague more effectively to understand the epidemiological cycle of plague, and to improve local surveillance based on the local species composition.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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Table 1. Observed representation of mammalian orders among reservoirs (in percentage) versus expected. The expected values represent the amount of species per order that would be identified as reservoirs if they were found as a reservoir host in the same proportions as they are all mammals. Positive residuals represent more reservoir species than expected by chance. Negative residuals represent fewer reservoir species than expected by chance.

Mammalian orders	No. of species	No. of identified reservoirs	Observed (%)	Expected (%)	Residuals (O-E)
Scandentia	24	1	0.2849003	0.505689001	-0.2208
Hyracoidea	5	1	0.2849003	0.105351875	0.1795
Afrosoricida	55	1	0.2849003	1.158870628	-0.8740
Didelphimorphia	111	2	0.56980057	2.338811631	-1.7690
Primates	518	2	0.56980057	10.91445428	-10.3447
Artiodactyla	551	7	1.994301994	11.60977665	-9.6155
Eulipotyphla	527	13	3.703703704	11.10408765	-7.4004
Lagomorpha	98	14	3.988603989	2.064896755	1.9237
Carnivora	305	31	8.831908832	6.426464391	2.4054
Rodentia	2552	279	79.48717949	53.77159713	25.7156
total	4746	351	100	100	0

Table 2. Main reservoir species in different foci worldwide. Reservoirs differ considerably from one focus to another. Resistant species are shown in **bold**.

Region	Reservoir species	Reference
Former Soviet Union:		
Pre-Caspian region	<i>Spermophilus pygmaeus</i>	Gratz (1999), Onishchenko &
Sandy areas	<i>Meriones meridianus</i> , <i>M. tamariscinus</i>	Kutyrev (2004)
Central Asian	<i>Rhombomys opimus</i> , <i>Meriones libycus</i>	
Central Asia highlands	<i>Marmota baibacina</i> , <i>M. caudata</i> , <i>Microtus juldaschi</i>	
Transcaucasian area	<i>Meriones libycus</i> , etc.	
High-mountain territories of Caucasus and Trans-Caucasia	<i>Spermophilus musicus</i> , <i>Microtus</i> cfr. <i>arvalis</i>	
Low-mountain Trans-Caucasia	<i>Meriones vinogradovi</i> , <i>M. libycus</i>	
Transbaikalia focus	<i>Marmota sibirica</i> , <i>Spermophilus dauricus</i>	
Altai highlands	<i>Marmota baibacina</i> , <i>Urocitellus undulatus</i> , <i>Ochotona pallasi</i>	
Southeast Asia and the western Pacific	<i>Bandicota bengalensis</i> , <i>Millardia meltada</i> , <i>Tatera indica</i> , <i>Rattus norvegicus</i> , <i>R. rattus</i> , <i>R. rattus diardii</i> , <i>Suncus murinus</i> , <i>Rattus exulans</i>	Pollitzer (1960), Gratz (1999), Sludskyi (2014b)
Plague foci of southwestern Asia:		
Iran	<i>Meriones persicus</i> , <i>M. libycus</i> , <i>M. tristrami</i> , <i>M. vinogradovi</i>	Baltazard <i>et al.</i> (1952, 1960), Gratz (1999)
Africa	<i>Arvicanthis</i> spp. (<i>A. niloticus</i>, etc.) ,	Pollitzer (1960), Gratz (1999),

		<i>Gerbilliscus brantsii</i> , <i>Otomys irroratus</i> , <i>Mastomys natalensis</i> , <i>Mastomys coucha</i> , <i>Rattus rattus</i> , <i>R. norvegicus</i> , <i>Meriones shawi</i> , <i>M. libycus</i> , <i>Suncus murinus</i>	Malek <i>et al.</i> (2016), Moore <i>et al.</i> (2015).
America:			
North (USA)	America	<i>Cynomys gunnisoni</i> , <i>Otospermophilus variegatus</i> , <i>Microtus californicus</i> , <i>Peromyscus</i> spp. (<i>P. californicus</i>, <i>P. maniculatus</i>, etc.)	Pollitzer (1960), Gratz (1999)
Mexico		<i>Cynomys mexicanus</i>	Pollitzer (1960)
South America		<i>Oligoryzomys</i> spp., <i>Calomys</i> spp., <i>Necromys lasiurus</i> , <i>Sciurus stramineus</i> , <i>Akodon orophilus</i> , <i>Aegialomys xanthaeolus</i> , <i>Sylvilagus brasiliensis</i> , <i>Rattus rattus</i> , <i>Galea spixii</i>	Pollitzer (1960), Bonvicino <i>et al.</i> (2015)
Pacific coast		<i>Otospermophilus beechey</i> , <i>Neotamias</i> spp., <i>Callospermophilus lateralis</i>	Gratz (1999)

Figure Caption:

Figure 1. Global distribution of natural plague foci as of March 2016, based on the historical data and current information (modified after the WHO 2016).

Figure 2. Geographic distribution of the number of plague hosts around the world at the spatial resolution of 0.5 arc degree and based on distributional ranges of 345 hosts in the IUCN Red List of Threatened Species. Maps for a further 10 species were not available at the desired resolution. For a complete list of 355 hosts see the Appendix.

Figure 3. Geographic distribution of the main reservoir species (~70 species) in different foci around the world at the spatial resolution of 0.5 arc degree.