Rodent trapping studies as an overlooked information source for understanding endemic and novel zoonotic spillover.

Rodent trapping to understand zoonotic spillover risk

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1. Abstract

Rodents are important globally distributed reservoirs of known and novel zoonotic pathogens. Ongoing anthropogenic land use change is altering the composition of host species assemblages and modifying the risk of zoonoses spillover events. These changes mean that an understanding of the current distribution of rodent species is vital for accurately describing disease hazard and managing risk. However, available species distribution and host-pathogen association datasets (e.g. IUCN, GBIF, CLOVER) are often taxonomically and spatially biased. Here, we synthesise data from West Africa from 127 rodent trapping studies, published between 1964-2022, as an additional source of information to characterise the range and presence of important zoonotic pathogen host species in this region. We identify that these rodent trapping studies, although biased towards human dominated landscapes across West Africa, can usefully complement current rodent species distribution datasets and we calculate the discrepancies between these datasets. For five regionally important zoonotic pathogens (Arenaviridae spp., Borrelia spp., *Lassa mammarenavirus*, Leptospira spp. and *Toxoplasma gondii*), we identify host-pathogen associations that have not been previously reported in host-association datasets. These omissions have the potential for biasing estimates of current risk and drivers of zoonoses. Finally, for these five pathogen groups, we find that the proportion of a rodent hosts range that has been sampled remains small with geographic clustering. A priority of future rodent trapping studies should be to sample rodent hosts across a greater geographic range to better characterise current and future risk of zoonotic spillover events. In the interim, future studies of spatial pathogen risk informed by rodent distributions must incorporate a measure of the current sampling biases. The current synthesis of contextually rich rodent trapping data

enriches available information from IUCN, GBIF and CLOVER which can support a more complete understanding of the hazard of zoonotic spillover events.

2. Author Summary

Emerging and endemic zoonotic diseases are projected to have increasing health impacts, particularly under changing climate and land-use scenarios. Rodents carry a disproportionate number of zoonotic pathogens and are abundant across West Africa, raising concerns about increasing outbreaks of endemic disease and the emergence of pandemics. Prior modelling studies rely on large, consolidated data sources which do not incorporate high resolution spatial and temporal data from rodent trapping studies. Here, we synthesise these studies to quantify the bias in the sampling of rodent hosts and their pathogens across West Africa. We find that rodent trapping studies are complementary to these datasets and can provide additional, high-resolution data on the distribution of hosts and their pathogens. Further, rodent trapping studies have identified additional potential host-pathogen associations than are recorded in consolidated host-pathogen association datasets. This can help to understand the risk of zoonotic diseases based on host distributions. Finally, we quantify the current extent of known rodent presence and pathogen sampling within a species range, highlighting that current knowledge is limited across much of the region. We hope that this will support work to study rodent hosts and their pathogens in currently under sampled regions to better understand the risk of emerging and endemic zoonoses in West Africa.

3. Introduction

There is increasing awareness of the global health and economic impacts of novel zoonotic pathogen spillover, driven by the ongoing SARS-CoV-2 pandemic and previous HIV/AIDs and Spanish Influenza pandemics [1]. The number of zoonotic disease spillover events and the frequency of the emergence of novel zoonotic pathogens from rodents are predicted to increase under intensifying anthropogenic pressure driven by increased human populations, urbanisation, intensification of agriculture, climate change and wildlife defaunation [2–5]. The impact of endemic zoonoses meanwhile remains underestimated [6]. Endemic zoonoses disproportionally affect those in the poorest sections of society, those living in close contact with their animals and those with limited access to healthcare [7–9].

Rodents along with bats contribute the greatest number of predicted novel zoonotic pathogens and known endemic zoonoses [10,11]. Of 2,220 extant rodent species, 244 (10.7%) are described as reservoirs of 85 zoonotic pathogens [10], although many species provide important and beneficial ecosystem services including pest regulation and seed dispersal [12]. Rodents typically demonstrate “fast” life histories [13] with traits such as early maturation and short gestation times (<4 days) further associated with being zoonotic reservoirs [10,14]. Rodent species with “fast” life histories thrive in human dominated landscapes, displacing species less likely to be reservoirs of zoonotic pathogens [15]. The widespread occurrence of reservoir species and their proximity to human activity make the description of rodent species assemblages and host-pathogen associations vitally important to understanding the hazard of zoonotic disease spillover and novel zoonotic pathogen emergence [16].

76 Despite the importance of understanding these complex systems, current evidence on host-
77 pathogen associations is considerably affected by taxonomic and geographical sampling biases
78 [11,17]. Curated biodiversity datasets such as the Global Biodiversity Information Facility
79 (GBIF) and resources produced by the International Union for Conservation of Nature (IUCN)
80 suffer from well described spatial and temporal sampling biases [18,19]. These sampling biases
81 can importantly distort produced species distribution models [20]. Datasets on host-pathogen
82 associations also can suffer from biases introduced from literature selection criteria and
83 taxonomic discrepancies. These biases are important because identification of potential
84 geographic hotspots of zoonotic disease spillover and novel pathogen emergence are often
85 produced from these types of host species distributions and host-pathogen associations
86 [21,22]. For example, systematically increased sampling, over-representation of certain
87 habitats and clustering around areas of high human population could lead to an apparent
88 association between locations and hazard that is driven by these factors rather than underlying
89 host-pathogen associations [11,23,24]. Predictions of zoonotic disease spillover and novel
90 zoonotic pathogen emergence must account for these biases to understand the future hazard of
91 zoonotic diseases [22].

92 West Africa has been identified as a region at increased risk for rodent-borne zoonotic disease
93 spillover events, the probability of these events are predicted to increase under different
94 projected future land-use change scenarios [4,25]. Currently within West Africa, rodents are
95 involved in the transmission of multiple endemic zoonoses with large burdens on human
96 health, these pathogens include Lassa fever, Schistosomiasis, Leptospirosis and Toxoplasmosis
97 [26,27]. Understanding of the distribution of these zoonoses are limited by biases in
98 consolidated datasets. Rodent trapping studies provide contextually rich information on when,

where and under what conditions rodents were trapped, potentially enriching consolidated datasets [28]. Studies have been conducted in West Africa to investigate the distribution of rodent species, their species assemblages, the prevalence of endemic zoonoses within rodent hosts (e.g., Lassa fever, Schistosomiasis) and to identify emerging and novel zoonotic pathogens [29–31]. However, individual level data from these studies have not previously been synthesised for inclusion in assessments of zoonotic disease spillover and novel zoonotic pathogen emergence.

Here, we synthesise rodent trapping studies conducted across West Africa published between 1964-2022. First, we use this dataset to investigate the geographic sampling biases in relation to human population density and land use classification. Second, we compare this to curated host datasets (IUCN and GBIF) to understand differences in reported host geographic distributions. Third, we compare identified host-pathogen associations with a consolidated dataset (CLOVER) to explore discrepancies in rodent host-pathogen associations and report the proportion of positive assays for pathogens of interest. Finally, within our dataset we investigate the spatial extent of current host-pathogen sampling to identify areas of sparse sampling of pathogens within their host ranges. We expect that rodent trapping studies provide an important additional source of high-resolution data that can be used to enrich available consolidated datasets to better understand the hazard of zoonotic disease spillover and novel zoonotic pathogen emergence across West Africa.

4. Methods

4.1. Data sources

4.1.1. Host and pathogen trapping data

To identify relevant literature, we conducted a search in Ovid MEDLINE, Web of Science (Core collection and Zoological Record), JSTOR, BioOne, African Journals Online, Global Health and the pre-print servers, BioRxiv and EcoEvoRxiv for the following terms as exploded keywords: (1) Rodent OR Rodent trap* AND (2) West Africa, no date limits were set. We also searched other resources including the UN Official Documents System, Open Grey, AGRIS FAO and Google Scholar using combinations of the above terms. Searches were run on 2022-05-01, and returned studies conducted between 1964-2021.

We included studies for further analysis if they met all of the following inclusion criteria; i) reported findings from trapping studies where the target was a small mammal, ii) described the type of trap used or the length of trapping activity or the location of the trapping activity, iii) included trapping activity from at least one West African country, iv) recorded the genus or species of trapped individuals, and v) were published in a peer-reviewed journal or as a pre-print on a digital platform or as a report by a credible organisation. We excluded studies if they met any of the following exclusion criteria: i) reported data that were duplicated from a previously included study, ii) no full text available, iii) not available in English. One author screened titles, abstracts and full texts against the inclusion and exclusion criteria. At each stage; title screening, abstract screening and full text review, a random subset (10%) was reviewed by a second author.

139 We extracted data from eligible studies using a standardised tool that was piloted on 5 studies
140 (Supplementary Table 1.). Data was abstracted into a Google Sheets document, which was
141 archived on completion of data extraction [32]. We identified the aims of included studies, for
142 example, whether it was conducted as a survey of small mammal species or specifically to
143 assess the risk of zoonotic disease spillover. we extracted data on study methodology, such as,
144 the number of trap nights, the type of traps used and whether the study attempted to estimate
145 abundance. For studies not reporting number of trap nights we used imputation based on the
146 number of trapped individuals, stratified by the habitat type from which they were obtained.
147 This was performed by multiplying the total number of trapped individuals within that study
148 site by the median trap success for study sites with the same reported habitat type.
149 Stratification was used as trap success varied importantly between traps placed in or around
150 buildings (13%, IQR 6-24%) compared with other habitats (3%, IQR 1-9%)

151 We also recorded how species were identified within a study and species identification was
152 assumed to be accurate. The number of individuals of these species or genera was extracted
153 with taxanomic names mapped to GBIF taxonomy [33]. We expanded species detection and
154 non-detection records by explicitly specifying non-detection at a trap site if a species was
155 recorded as detected at other trapping locations within the same study.

156 Geographic locations of trapping studies were extracted using GPS locations for the most
157 precise location presented. Missing locations were found using the National Geospatial-
158 Intelligence Agency GEOnet Names Server [34] based on placenames and maps presented in the
159 study. All locations were converted to decimal degrees. The year of rodent trapping was
160 extracted alongside the length of the trapping activity to understand seasonal
161 representativeness of trapping activity. The habitats of trapping sites were mapped to the IUCN

162 Habitat Classification Scheme (Version 3.1). For studies reporting multiple habitat types for a
163 single trap, trap-line or trapping grid, a higher order classification of habitat type was recorded.

164 For relevant studies we extracted data on all microorganisms and zoonotic pathogens tested
165 and the method used (e.g., molecular or serological diagnosis). Where assays were able to
166 identify the microorganism to species level this was recorded, non-specific assays higher order
167 attribution was used (e.g. to family level). We recorded the species of rodent host tested, the
168 number of individuals tested and the number of positive and negative results. For studies
169 reporting summary results all testing data were extracted, this may introduce double counting
170 of individual rodents, for example, if a single rodent was tested using both molecular and
171 serological assays. Where studies reported indeterminate results, these were also recorded.

172 Out of 4,692 relevant citations, we identified 127 rodent trapping studies (Supplementary
173 Table 2.). The earliest trapping studies were conducted in 1964, with a trend of increasing
174 numbers of studies being performed annually since 2000. The median year of first trapping
175 activity was 2007, with the median length of trapping activity being 1 year (IQR 0-2 years)
176 (Supplementary Fig 1.). Studies were conducted in 14 West African countries, with no studies
177 reported from The Gambia or Togo, at 1,611 trap sites (Fig 1A.).

178 Included studies explicitly reported on 601,184 trap nights, a further 341,445 trap nights were
179 imputed from studies with no recording of trapping effort based on trap success, leading to an
180 estimate of 942,629 trap nights (Fig 1B.). A minority of studies trapped at a single study site
181 (30, 24%), with 46 (36%) trapping at between two and five sites, the remaining 51 studies
182 (40%) trapped at between six and 93 study sites.

183 In total 76,275 small mammals were trapped with 65,628 (90%) identified to species level and
184 7,439 (10%) identified to genus, with the remaining classified to higher taxonomic level. The
185 majority of the 132 identified species were Rodentia (102, 78%), of which Muridae (73, 72%)
186 were the most common family. Soricomorpha were the second most identified order of small
187 mammals (28, 21%). 57 studies tested for 32 microorganisms, defined to species or genus level
188 that are known or potential pathogens. Most studies tested for a single microorganism (48,
189 84%). The most frequently assayed microorganisms were *Lassa mammarenavirus* or
190 Arenaviridae (21, 37%), *Borrelia sp.* (9, 16%), *Bartonella sp.* (4, 7%) and *Toxoplasma gondii* (4,
191 7%). Most studies used Polymerase Chain Reaction (PCR) to detect microorganisms (37, 65%),
192 with fewer studies using serology-based tests (11, 19%) or histological or direct visualisation
193 assays (11, 21%). From 32,920 individual rodent samples we produced 351 host-pathogen
194 pairs. With *Rattus rattus*, *Mus musculus*, *Mastomys erythroleucus*, *Mastomys natalensis* and
195 *Arvicanthis niloticus* being assayed for at least 18 microorganisms.

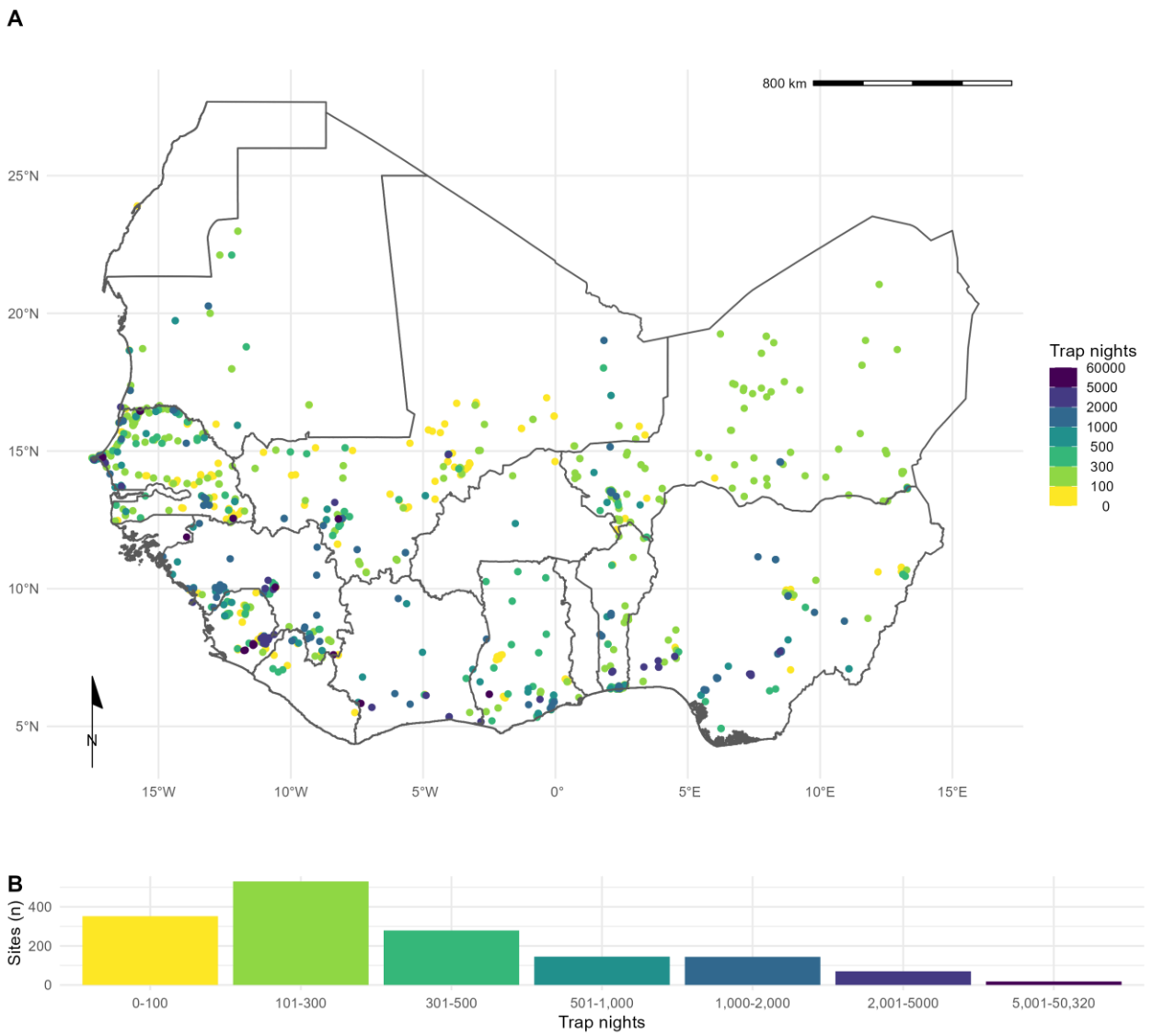


Fig 1: Rodent trapping sites across West Africa. A) The location of trapping sites in West Africa. No sites were recorded from Togo or The Gambia. Heterogeneity is observed in the coverage of each country by trap night (colour) and location of sites. For example, Senegal, Mali and Sierra Leone have generally good coverage compared to Guinea and Burkina Faso. B) Histogram of trap nights performed at each study site, a median of 248 trap nights (IQR 116-500) was performed at each site

4.2. Analysis

4.2.1. What is the extent of spatial bias in the rodent trapping data?

To investigate the extent of spatial bias in the rodent trapping data, we calculated trap-night (TN) density within each West African level-2 administrative region. The `sf` package in the R statistical language (R version 4.1.2) was used to manipulate geographic data, administrative boundaries were obtained from GADM 4.0.4 [35–37]. Trap-night density ($TN_{density}$) was calculated by dividing the number of trap nights by the area of a level-2 administrative area (R_{area}). For studies not reporting trap nights, imputation was used as previously described. Human population density was obtained for the closest year (2005) to the median year of trapping (2007) from Socioeconomic Data and Applications Center (SEDAC) gridded population of the world v4 at ~ 1km resolution ($P_{density}$) [38]. Median population density was then calculated for each level-2 administrative region. Land cover classification was obtained from the Copernicus climate change service at ~300m resolution [39]. The proportion of cropland, shrubland, tree cover (ψ_{tree}) and urban land cover (ψ_{urban}) within a level-2 administrative region in 2005 was calculated.

We investigated the association between relative trapping effort, measured as TN density, and the proportion of urban, cropland, tree cover and human population density using Generalised Additive Models (GAM) incorporating a spatial interaction term (longitude and latitude) [40]. The models were constructed in the `mgcv` package [41]. Selection of the most parsimonious model was based on Deviance explained and the Akaike Information Criterion for each model (Equations 1-5 below). Relative trapping effort was then predicted across West Africa using these covariates. We performed two sensitivity analyses, first, by removing sites with imputed

trapping effort, second, by associating trap locations to ~1km pixels rather than level-2 administrative areas.

$$\mathrm{TN}_{\mathrm{density}} \sim \mathrm{Tweedie}(X * Y) \tag{1}$$

$$\mathrm{TN}_{\mathrm{density}} \sim \mathrm{Tweedie}\left(\mathrm{P}_{\mathrm{density}} + (X * Y)\right) \tag{2}$$

$$\mathrm{TN}_{\mathrm{density}} \sim \mathrm{Tweedie}\left(\mathrm{P}_{\mathrm{density}} + \mathrm{R}_{\mathrm{area}} + (X * Y)\right) \tag{3}$$

$$\mathrm{TN}_{\mathrm{density}} \sim \mathrm{Tweedie}\left(\mathrm{P}_{\mathrm{density}} + \psi_{\mathrm{tree}} + \psi_{\mathrm{urban}} + (X * Y)\right) \tag{4}$$

$$\mathrm{TN}_{\mathrm{density}} \sim \mathrm{Tweedie}\left(\mathrm{P}_{\mathrm{density}} + \mathrm{R}_{\mathrm{area}} + \psi_{\mathrm{urban}} + (X * Y)\right) \tag{5}$$

4.2.2. What is the difference in rodent host distributions between curated datasets and rodent trapping studies?

We assessed the concordance of curated rodent host distributions from IUCN and GBIF with observed rodent detection and non-detection from rodent trapping studies for seven species with the most trap locations (*M. natalensis*, *R. rattus*, *M. erythroleucus*, *M. musculus*, *A. niloticus*, *Praomys daltoni* and *Cricetomys gambianus*). We obtained rodent species distribution maps as shapefiles from the IUCN red list and translated these to a ~20km resolution raster [42]. Distributions were cropped to the study region for globally distributed rodent species. We obtained rodent presence locations from GBIF as point data limited to the study region [43]. Presence locations were associated to cells of raster with a ~20km resolution produced for the study region.

244 For each of the seven species, we first calculated the area of the IUCN expected range, and then
245 the percentage of this range covered by presence detections in GBIF, and from detections in the
246 rodent trapping data. We then calculated the area of both types of both GBIF and rodent
247 trapping detections outside of the IUCN expected range. For rodent trapping data, we
248 additionally calculated the area of non-detections within the IUCN expected area. Finally, we
249 calculated the combined area of detection from both GBIF and rodent trapping data.

250 4.2.3. Are rodent trapping derived host-pathogen associations present in a 251 consolidated zoonoses dataset?

252 To examine the usefulness of rodent trapping studies as an additional source of data we
253 compared identified host-pathogen associations from trapping studies investigating zoonoses
254 with a consolidated zoonoses dataset (CLOVER) [11,44]. CLOVER is a synthesis of four host-
255 pathogen datasets (GMPD2, EID2, HP3 and Shaw, 2020) and was released in 2021, it contains
256 more than 25,000 host-pathogen associations for Bacteria, Viruses, Helminth, Protozoa and
257 Fungi. We compared the host-pathogen networks across the two datasets, where the CLOVER
258 data was subset for host species present in the rodent trapping data.

259 For host-pathogen pairs with assay results consistent with acute or prior infection, we
260 calculated the proportion positive and identify those absent from CLOVER. We expand the
261 analysis to host-pathogen pairs with pathogens identified to genus level in Supplementary Fig
262 4.

4.2.4. What is the spatial extent of pathogen testing within host ranges?

We use the sampled area of three pathogen groups and two pathogens (Arenaviridae, Borreliaceae, Leptospiraceae, *Lassa mammarenavirus* and *Toxoplasma gondii*) to quantify the bias of sampling within their hosts ranges. For each pathogen, we first describe the number of host species assayed, for the five most commonly tested species we associate the locations of sampled individuals to ~20km pixels and calculate the proportion of the IUCN range of the host in which sampling has occurred. We compare this figure to the total area in which the host has been detected to produce a measure of relative completeness of sampling within the included rodent trapping studies.

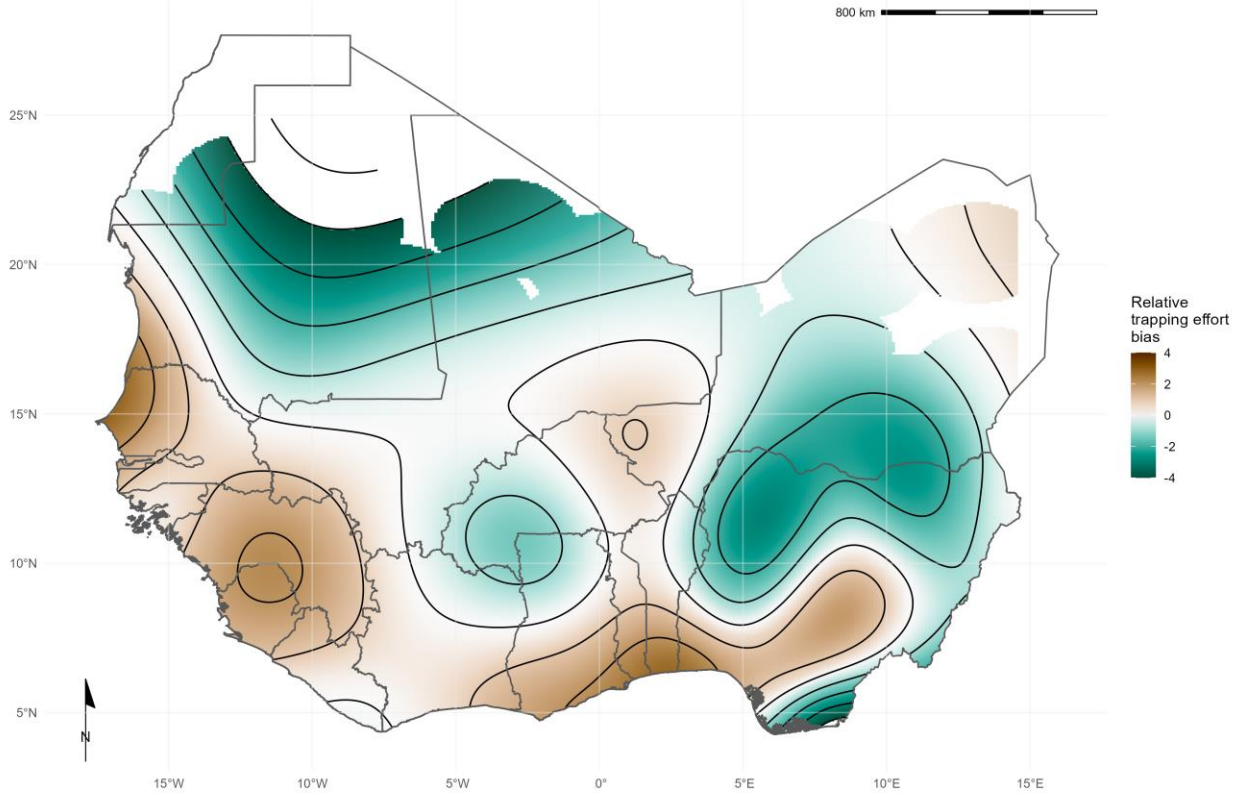
Data and code to reproduce all analyses are available in an archived Zenodo repository [32].

5. Results

5.1. What is the extent of spatial bias in the rodent trapping data?

We found non-random, spatial clustering of rodent trapping locations across the study region, suggestive of underlying bias in the sampling or rodents across West Africa. Trap sites were situated in 256 of 1,450 (17.6%) level-2 administrative regions in 14 West African nations. The regions with the highest TN density included the capitals and large cities of Niger (Niamey), Nigeria (Ibadan), Ghana (Accra), Senegal (Dakar), Ghana (Accra) and Benin (Cotonou). Outside of these cities, regions in, Northern Senegal, Southern Guinea, Edo and Ogun States in Nigeria and Eastern Sierra Leone had the greatest TN density (Fig 1A.).

The most parsimonious GAM model (adjusted R2 = 0.3, Deviance explained = 48.7%) reported significant non-linear associations between relative trapping effort bias and human population densities (Effective Degrees of Freedom (EDF) = 7.13, $p < 0.001$), proportion of urban landscape (EDF = 1.92, $p < 0.002$) and region area (EDF = 3.63, $p < 0.001$), alongside significant spatial associations (EDF = 27.3, $p < 0.001$) (Supplementary table 3.1). Greatest trapping effort bias peaked at population densities between 5,000-7,500 individuals/km^2, proportion of urban landscape >10% and region areas < 1,000km^2. Increased trapping effort was found in North West Senegal, North and East Sierra Leone, Central Guinea and coastal regions of Nigeria, Benin and Ghana; in contrast South East Nigeria, Northern Nigeria and Burkina Faso had an observed bias towards a reduced trapping effort (Fig 2). In sensitivity analysis, excluding sites with imputed trap nights, Mauritania, Northern Senegal and Sierra Leone remained as regions trapped at higher rates, with Nigeria being trapped at lower than expected rates (Supplementary Fig 3a.). In pixel-based sensitivity analysis spatial coverage was reduced with similar patterns of bias observed to the primary analysis (Supplementary Fig 3b.).



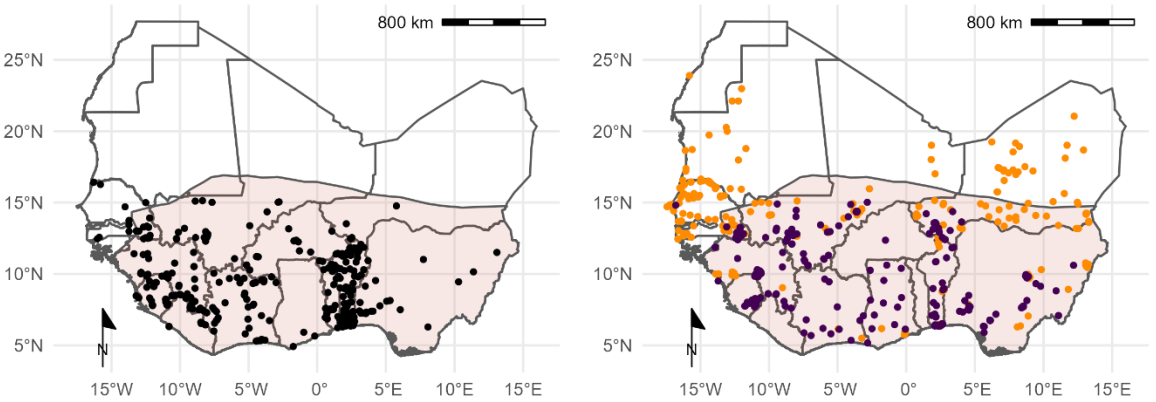
296

297 **Fig 2. Relative trapping effort bias across West Africa.** Modelled relative trapping effort bias
298 adjusted for human population density, proportion urban land cover and area of the
299 administrative region. Brown regions represent areas with a bias towards increased trapping
300 effort (e.g., North West Senegal), Green regions represent areas with a bias towards reduced
301 trapping effort (e.g., Northern Nigeria).

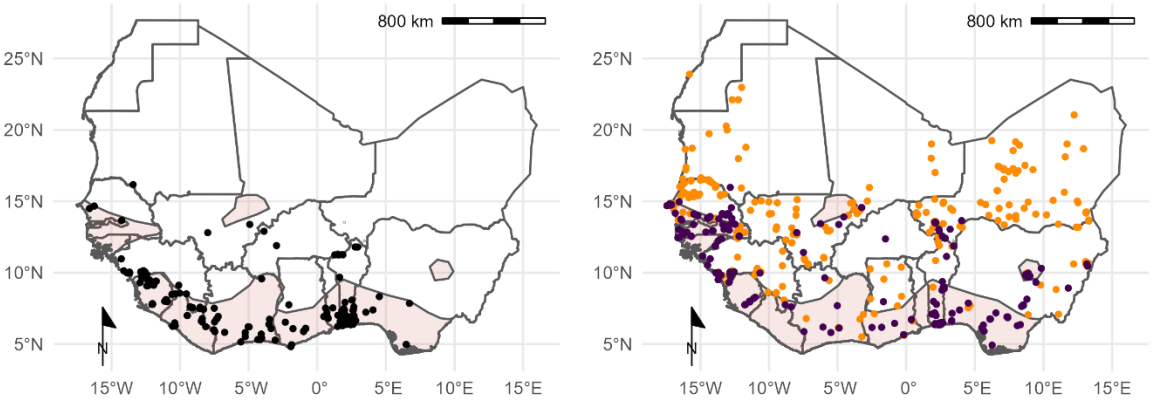
302 ## 5.2. What is the difference in rodent host distributions between
303 curated datasets and rodent trapping studies?

304 We found that for six of the seven most detected rodent species (*M. natalensis*, *R. rattus*, *M.*
305 *erythroleucus*, *M. musculus*, *A. niloticus* and *P. daltoni*), trapping studies provided more distinct
306 locations of detection and non-detection than were available from GBIF. For the endemic
307 rodent species (*M. natalensis*, *M. erythroleucus*, *A. niloticus*, *P. daltoni* and *C. gambianus*) IUCN
308 ranges had good concordance to both trapping studies and GBIF, however, individuals of *A.*
309 *niloticus* and *P. daltoni* were detected outside of IUCN ranges. In contrast, the non-native
310 species *R. rattus* and *M. musculus* were detected across much greater ranges than were
311 expected from IUCN distributions. Comparisons for *M. natalensis*, *R. rattus* and *M. musculus* are
312 shown in Fig 3, the remaining species are shown in Supplementary Fig 4.

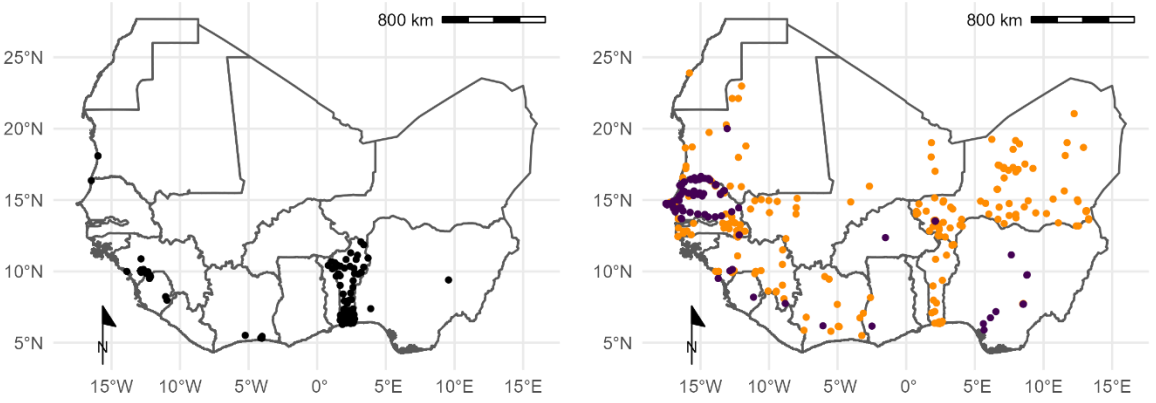
Mastomys natalensis



Rattus rattus



Mus musculus



Detection/Non-detection ● Detection ● Non-detection

313

314 **Fig 3. Locations of detection and non-detection sites for rodent species in West Africa**

315 Each row corresponds to a single rodent species. L) Presence recorded in GBIF (black points)
316 overlaid on IUCN species range (red-shaded area). R) Detection (purple) and non-detection
317 (orange) from rodent trapping studies overlaid on IUCN species ranges. M. musculus has no
318 IUCN West African range.

319 Comparison of the proportion of a species IUCN range in which detections and non-detections
320 occurred showed that sampling locations of these seven species within GBIF covered between
321 0.09-0.26% of expected ranges (Table 1.), compared to 0.03-0.24% for rodent trapping data.
322 Detections occurred outside IUCN ranges for all species in both the GBIF and rodent trapping
323 data, most noticeably for *A. niloticus* and *R. rattus*. Combining GBIF and rodent trapping data
324 increased the sampled area by a mean of 1.6 times compared to the GBIF area alone,
325 demonstrating limited overlap between the locations providing information to either dataset.
326 Non-detection of a species occurred across species ranges (mean = 0.11%, SD = 0.03%),
327 suggestive of spatial heterogeneity of presence within IUCN ranges.

Table 1: Comparison of IUCN, GBIF and rodent trapping ranges for the 7 most detected rodent species.

	IUCN	GBIF		Trapping studies			Combined
Species	Range (1,000 km^2)	Area inside range (1,000 km^2) (% of IUCN)	Area outside range (1,000 km^2)	Detection area inside range (1,000 km^2) (% of IUCN)	Area outside range (1,000 km^2) (% of IUCN)	Non-detection area inside range (1,000 km^2) (% of IUCN)	Detection area (1,000 km^2) (% of IUCN)
Mastomys natalensis	3,257	6.83 (0.21%)	0.19	4.4 (0.14%)	0.17	3.12 (0.1%)	10.66 (0.33%)
Rattus rattus	1,019	2.61 (0.26%)	0.52	2.42 (0.24%)	1.21	1.3 (0.13%)	4.88 (0.48%)
Mastomys erythroleucus	3,735	4.48 (0.12%)	0.04	3.24 (0.09%)	0.12	4.35 (0.12%)	7.5 (0.2%)
Mus musculus			2.15		1.85		3.94
Arvicanthis niloticus	1,829	1.69 (0.09%)	2.41	1.98 (0.11%)	0.34	3.09 (0.17%)	3.59 (0.2%)
Praomys daltoni	2,658	4.03 (0.15%)	0.29	2.03 (0.08%)	0.15	2.78 (0.1%)	5.83 (0.22%)
Cricetomys gambianus	2,476	5 (0.2%)	0.17	0.75 (0.03%)	0.06	2.99 (0.12%)	5.69 (0.23%)

5.3. Are rodent trapping derived host-pathogen associations present in a consolidated zoonoses dataset?

We found potentially important differences between the host-pathogen networks produced from included rodent trapping studies and the consolidated CLOVER dataset. When limited to taxonomic classification of both pathogen and host to species level we identified 25 host-pathogen pairs among 14 rodent and 6 pathogen species (Fig 4. and Fig 5.). We identified

negative associations (non-detection through specific assays) for 45 host-pathogen pairs among 35 rodent and 7 pathogen species. CLOVER contained 10 (40%) of our identified host-pathogen associations, the remaining 15 (60%) were not found to be present in CLOVER, additionally CLOVER recorded positive associations for 4 (9%) of the negative associations produced from the rodent trapping data.

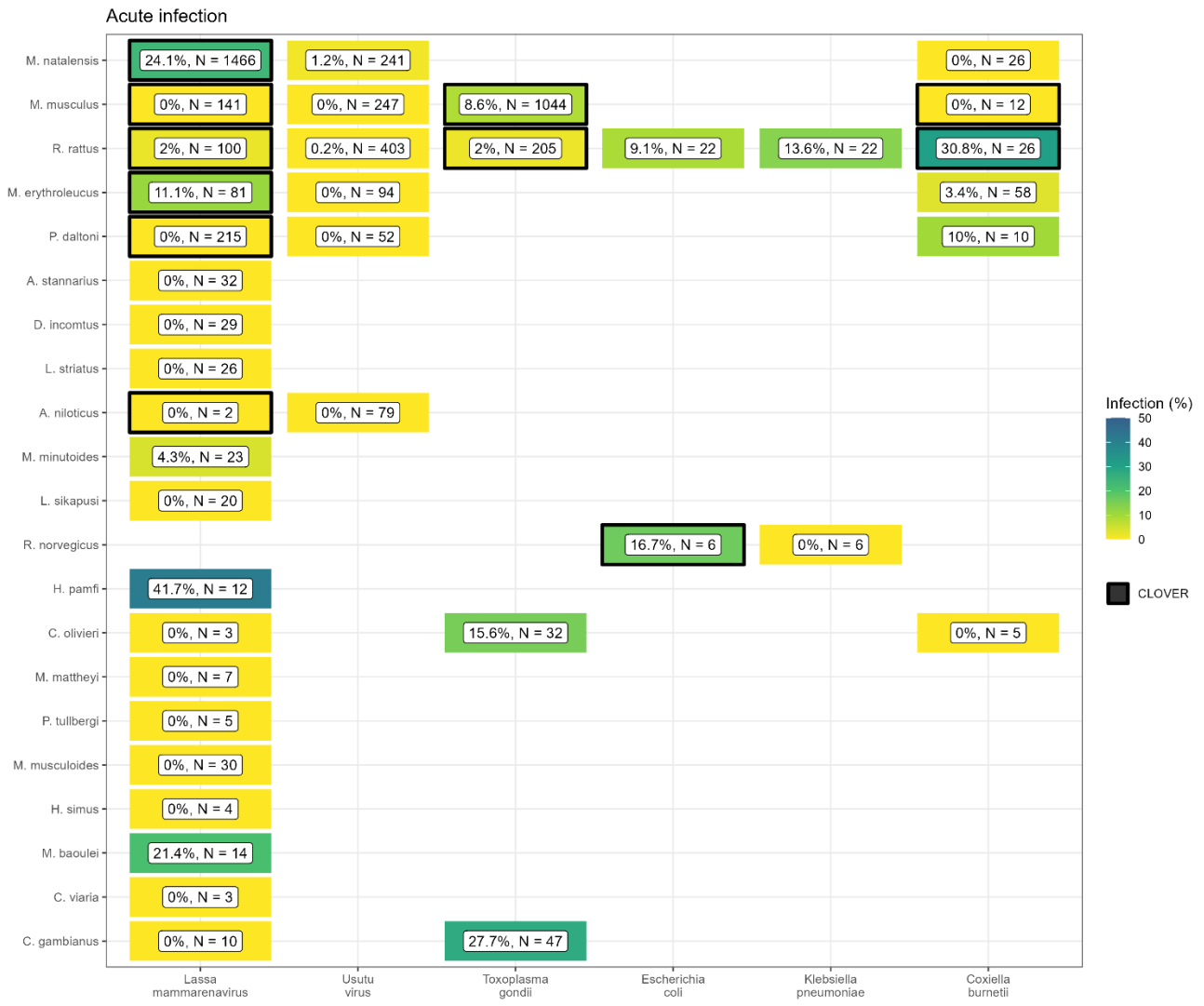
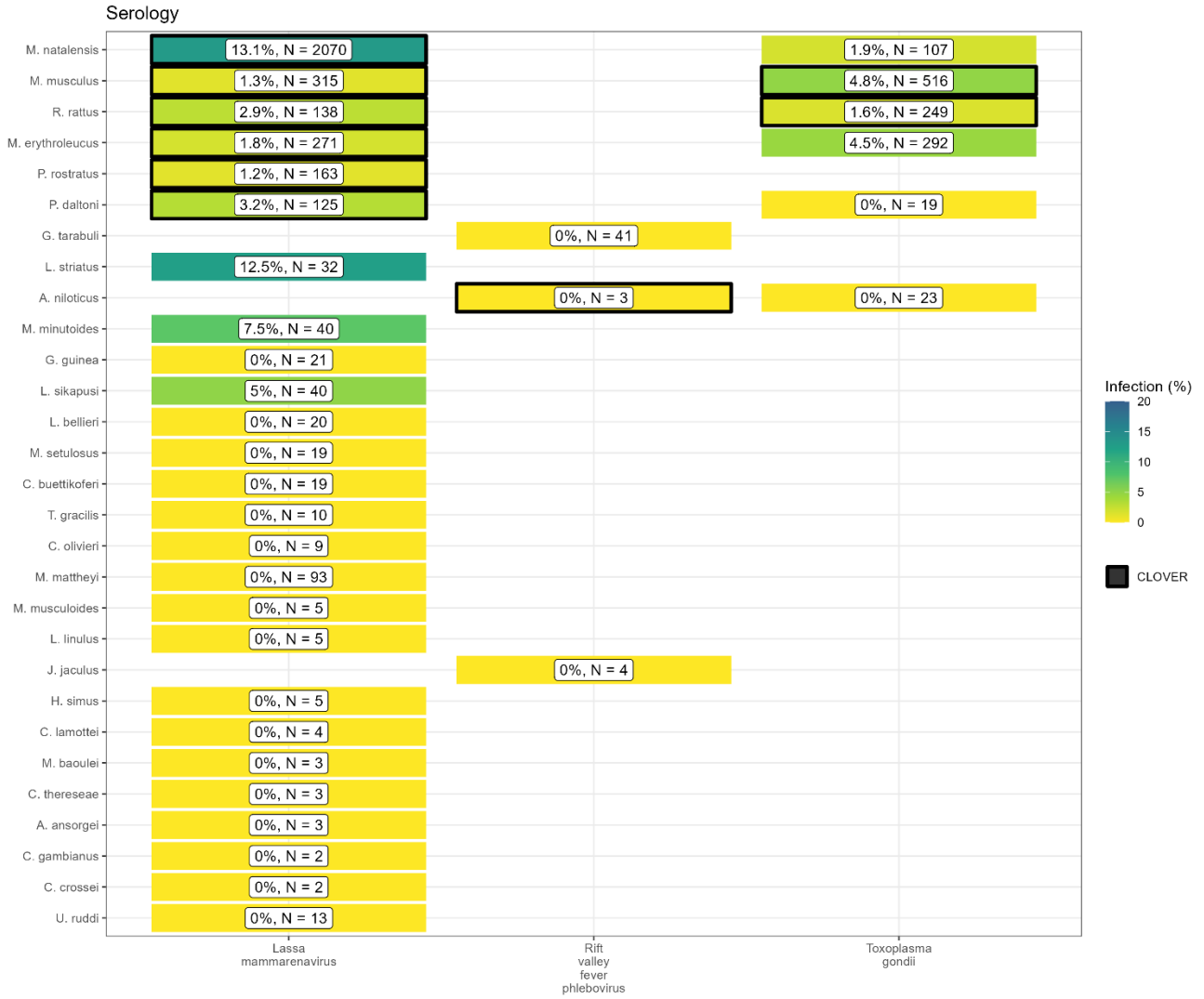


Fig 4. Host-Pathogen associations detected through acute infection. A) Identified species level host-pathogen associations through detection of acute infection (i.e. PCR, culture). Percentages and colour relate to the proportion of all assays that were positive, the number of

345 individuals tested for the pathogen is labelled N. Associations with a black border are present in

346 the CLOVER dataset.



347

348 **Fig 5. Host-Pathogen associations detected through evidence of prior infection.** B)

349 Identified species level host-pathogen associations through serological assays (i.e. ELISA).

350 Percentages and colour relate to the proportion of all assays that were positive, the number of

351 individuals tested for the pathogen is labelled N. Associations with a black border are present in

352 the CLOVER dataset.

353 CLOVER included an additional 492 host-pathogen associations we do not observe in rodent
354 trapping studies. The majority of these 392 (80%) pairs are from species with global
355 distributions (*M. musculus*, *R. rattus* and *R. norvegicus*), or from those with wide ranging
356 distributions in sub-Saharan Africa (38, 8%) (i.e., *A. niloticus*, *M. natalensis* and *Atelerix*
357 *albiventris*).

358 For pathogens not identified to species level (i.e. family or higher taxa only), we identified 148
359 host-pathogen pairs among 32 rodent species and 25 pathogen families (Supplementary Fig 4.),
360 with CLOVER containing 66 (45%) of these associations.

361 Rodent trapping studies identified additional rodent host species for six pathogens; *Lassa*
362 *mammarenavirus* (5), *Toxoplasma gondii* (4), Usutu virus (2), *Coxiella burnetii* (2), *Escherichia*
363 *coli* and *Klebsiella pneumoniae* (both 1), that were not present in this consolidated host-
364 pathogen association dataset.

365 5.4. What is the spatial extent of pathogen testing within a host's 366 range?

367 The five most widely sampled pathogen species/families in included studies were Arenaviridae,
368 Borreliaceae, *Lassa mammarenavirus*, Leptospiraceae and *Toxoplasma gondii* (Table 2.). Assays
369 to identify Arenaviridae infection were performed in 44 rodent species with evidence of viral
370 infection in 15 species. *Lassa mammarenavirus* was specifically tested for in 43 species with 10
371 showing evidence of viral infection. The most commonly infected species for both Arenaviridae,
372 generally, and *Lassa mammarenavirus* specifically, were *M. natalensis* and *M. erythroleucus*.

373 These species were assayed across between 10-20% of their trapped area, equating to ~0.02%
374 of their IUCN range (Table 2.).

375 Infection with species of Borreliaceae was assessed in 42 species, with evidence of infection in
376 17 rodent species. The greatest rates of infection were among *A. niloticus* (16%), *Mastomys*
377 *huberti* (11%) and *M. erythroleucus* (9%). Testing was more widespread than for Arenviruses
378 with coverage between 15-34% of their trapped area, however, this remains a small area in
379 relation to their IUCN ranges (<0.05%). Leptospiraceae and *Toxoplasma gondii* was assessed in
380 8 species, with evidence of infection in 5 and 6 rodent species respectively. The spatial coverage
381 of testing for these pathogens was more limited within IUCN host species ranges (~0.01%).

382

Table 2: Comparison of pathogen sampling ranges for the 5 most widely sampled pathogens and the 5 most sampled rodent host species (* no IUCN range in West African).

Pathogen	Species	Tested	Positive	Pathogen testing area (1,000 km^2)	Pathogen testing area within trapped area (%)	Pathogen testing area within IUCN range (%)
Arenaviridae sp.						
	Mastomys natalensis	2,841	104 (4%)	0.61	13.45%	0.02%
	Praomys daltoni	854	6 (1%)	0.42	19.43%	0.02%
	Mastomys erythroleucus	398	20 (5%)	0.40	11.97%	0.01%
	Rattus rattus	396	4 (1%)	0.38	10.5%	0.04%
	Praomys rostratus	310	5 (2%)	0.13	12.53%	0.02%
Borrelia sp.						
	Mastomys erythroleucus	1,586	140 (9%)	1.14	33.94%	0.03%
	Arvicanthis niloticus	1,551	253 (16%)	0.66	28.48%	0.03%
	Mastomys natalensis	733	54 (7%)	0.69	15.08%	0.02%
	Mastomys huberti	731	83 (11%)	0.23	29.83%	0.04%
	Mus musculus	686	26 (4%)	0.45	24.54%	*
Lassa mammarenavirus						
	Mastomys natalensis	3,199	580 (18%)	1.03	22.65%	0.03%
	Mastomys erythroleucus	352	14 (4%)	0.36	10.63%	0.01%
	Rattus rattus	177	2 (1%)	0.34	9.26%	0.03%
	Praomys rostratus	163	2 (1%)	0.27	27.02%	0.04%
	Mus musculus	147	0 (0%)	0.04	2.29%	*
Leptospira sp.						
	Rattus rattus	646	65 (10%)	0.40	11.1%	0.04%
	Arvicanthis niloticus	221	10 (5%)	0.02	0.9%	<0.01%
	Crocidura olivieri	141	14 (10%)	0.34	25.16%	*
	Mastomys natalensis	136	26 (19%)	0.36	7.91%	0.01%
	Rattus norvegicus	79	19 (24%)	0.21	40.08%	*
Toxoplasma gondii						

Pathogen	Species	Tested	Positive	Pathogen testing area (1,000 km^2)	Pathogen testing area within trapped area (%)	Pathogen testing area within IUCN range (%)
	Mus musculus	1,548	115 (7%)	0.62	33.64%	*
	Rattus rattus	428	8 (2%)	0.36	9.77%	0.03%
	Mastomys erythroleucus	292	13 (4%)	0.37	11.06%	0.01%
	Mastomys natalensis	107	2 (2%)	0.08	1.83%	<0.01%
	Cricetomys gambianus	47	13 (28%)	0.06	7.6%	<0.01%

6. Discussion

Endemic rodent zoonoses and novel pathogen emergence from rodent hosts are predicted to have an increasing burden in West Africa and globally [10]. Here we have synthesised data from 126 rodent trapping studies containing information on more than 72,000 rodents across 1,611 trap sites producing an estimated 942,669 trap nights across 14 West African countries. Locations studied are complementary to curated datasets (e.g. IUCN, GBIF), incorporation of our synthesised dataset when assessing zoonosis risk based on host distributions could counteract some of the biases inherent to these curated datasets [18]. We identified 25 host-pathogen pairs reported from included studies, 15 of these were not included in a consolidated host-pathogen dataset. Generally, the number of different species tested for a pathogen and the spatial extent of these sampling locations were limited. These findings highlight a number of sampling bias, supporting calls for further pathogen sampling across diverse species in zoonotic hotspots [45].

We found that rodent trapping data, like biodiversity data, showed important spatial biases [20]. Relative trapping effort bias was greater in Benin, Guinea, Senegal and Sierra Leone driven by long-standing research collaborations investigating the invasion non-native rodent species

401 (*M. musculus* and *R. rattus*) and the hazard of endemic zoonosis outbreaks (e.g., *Lassa*
402 *mammarenavirus*). Much of the region remains relatively under sampled, particularly Burkina
403 Faso, Côte d'Ivoire, Ghana and Nigeria, despite these countries facing many of the same
404 challenges. For example, annual outbreaks of Lassa fever are reported in Nigeria and there are
405 potentially 60,000 unrecognised cases of Lassa fever every year in Côte d'Ivoire and Ghana
406 [46]. Rodent sampling should be targeted towards currently under sampled regions to reduce
407 the potential impact of this bias and improve our understanding of both the distribution of
408 rodent hosts and the prevalence of pathogens within their populations. This will allow for
409 better estimation of risk from endemic and novel zoonoses.

410 Rodent trapping studies provide geographic and temporally contextualised data on both
411 species detection and non-detection which are not available from curated datasets. Non-
412 detection data can improve models of species distributions, unfortunately, high levels of
413 missing data on trapping effort will continue to confound the allocations of non-detections as
414 true absences [47]. Models of host species occurrence and abundance, improved by
415 incorporating species absence, are important to assess the effect of land use and climate change
416 on endemic zoonosis spillover to human populations and direct limited public health resources
417 towards regions at greatest risk [48,49].

418 Currently available consolidated datasets on host-pathogen associations (e.g. CLOVER, EID2
419 and GMPD2) do not include spatial or temporal components [50]. The current synthesis of
420 rodent trapping studies has highlighted that pathogens have been sparsely sampled within a
421 host's range. Current zoonosis risk models dependent on these sources of data are therefore
422 not able to incorporate spatial heterogeneity in pathogen prevalence across the host range.
423 Additional uncertainty in current models of zoonotic disease risk arises from host-pathogen

424 associations that have not been reported in these consolidated datasets. For example,
425 *Hylomyscus pamfi* infected with *Lassa mammarenavirus* and *R. rattus* infected with *Coxiella*
426 *burnetii*, will not be included when solely based on consolidated host-pathogen datasets.
427 Further, detection of zoonotic pathogens in multiple co-occurring host species supports the
428 adoption of multi-species to better understand the potential range of endemic zoonoses [51].

429 Few studies stratified detection and non-detection of hosts or pathogen prevalence by time,
430 therefore limiting inference of changes in host and pathogen dynamics. This limitation prevents
431 calculation of incidence of infection and the abundance of infectious rodents which potentially
432 varies by both time and space [52]. Understanding of temporal changes in viral burden and
433 shedding for endemic zoonoses is required to accurately predict current and future risk of
434 pathogen spillover.

435 Finally, due to data sparsity, we were unable to account for temporal change over the six
436 decades of rodent trapping studies. Land use change and population density have changed
437 dramatically over this period in West Africa [53]. We attempted to mitigate against this by
438 using the median year of trapping to understand the spatial and land use biases in trapping
439 activity. It is possible that land use and population density at trapping sites varied importantly
440 between when rodent trapping was conducted and the conditions in 2005. Despite this
441 limitation, the finding that trapping is biased towards high density, human dominated
442 landscapes is unlikely to substantially change.

443 We have shown that synthesis of rodent trapping studies to supplement curated rodent
444 distributions can counteract some of the inherent biases in these data and that they can add
445 further contextual data to host-pathogen association data. Together this supports their
446 inclusion in efforts to model endemic zoonotic risk and novel pathogen emergence.

Contribution of rodent trapping studies as data sources can be improved by adopting reporting standards and practices consistent with Open Science, namely sharing of disaggregated datasets alongside publication [54].

Future rodent trapping studies should be targeted towards regions that are currently under-studied. Further information on rodent presence and abundance across West Africa will aid the modelling of changing endemic zoonosis risk and the potential for novel pathogen emergence. Sharing of disaggregated data alongside research publications should be promoted with adoption of data standards to support ongoing data synthesis. Specifically, inclusion of exact locations of trapping sites, trapping effort and the dates at which trapping occurred would support more detailed inference of the spatio-temporal dynamics of host populations and the risk of endemic zoonosis spillover events. Despite these challenges we propose that rodent trapping studies can provide an important source of data to supplement curated datasets on rodent distributions to quantify the risk of endemic zoonosis spillover events and the hazard of novel pathogen emergence.

7. Author contributions

DS – Conceptualisation, Data Curation, Formal Analysis, Writing

LAA - Data Curation, Validation, Writing – Review and Editing

KEJ – Conceptualisation, Supervision, Writing – Review and Editing

DWJ & RK – Supervision, Funding Acquisition, Writing – Review and Editing

8. Data availability

All data and code to reproduce this analysis is available in an archived Zenodo repository [32].

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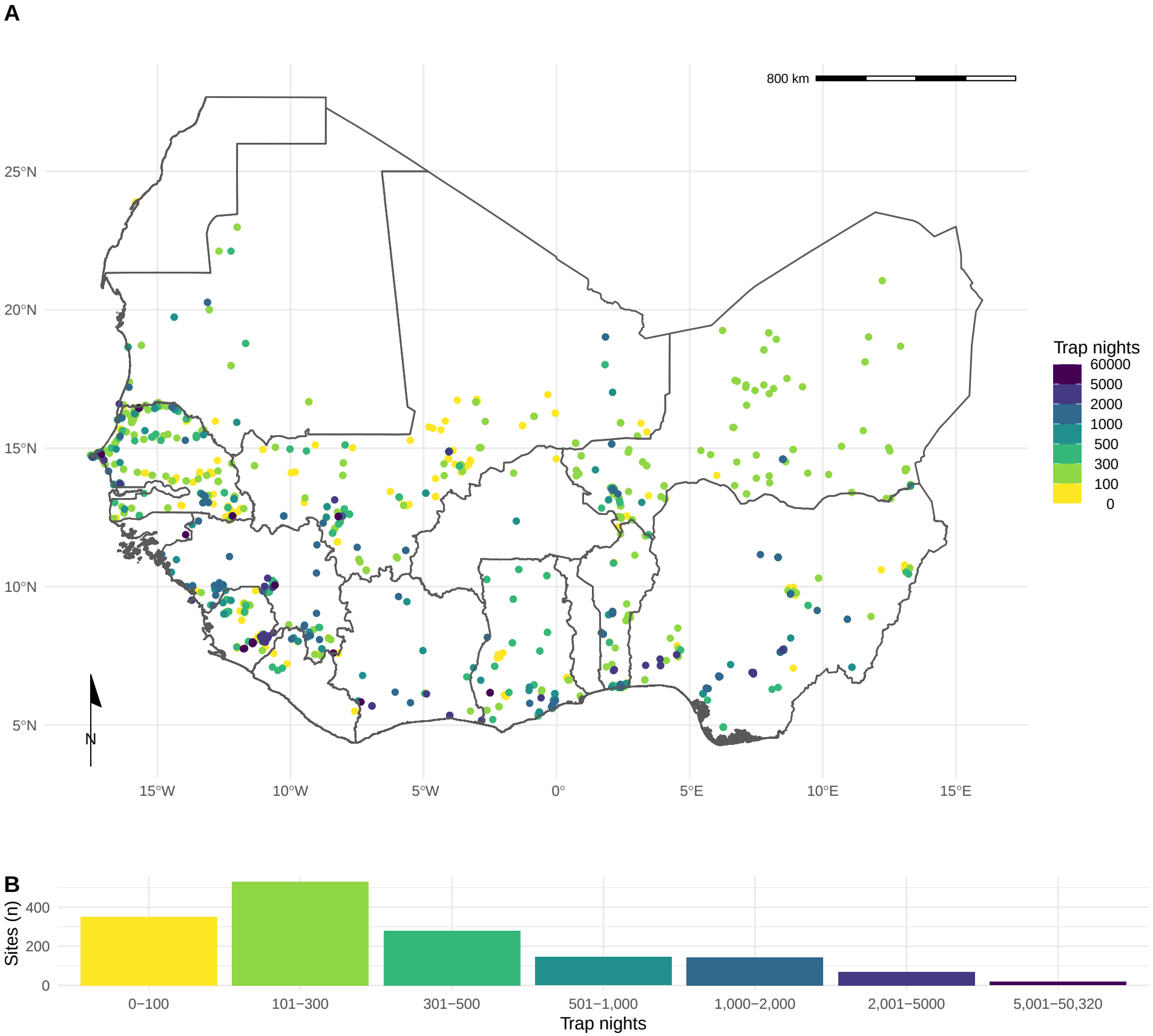
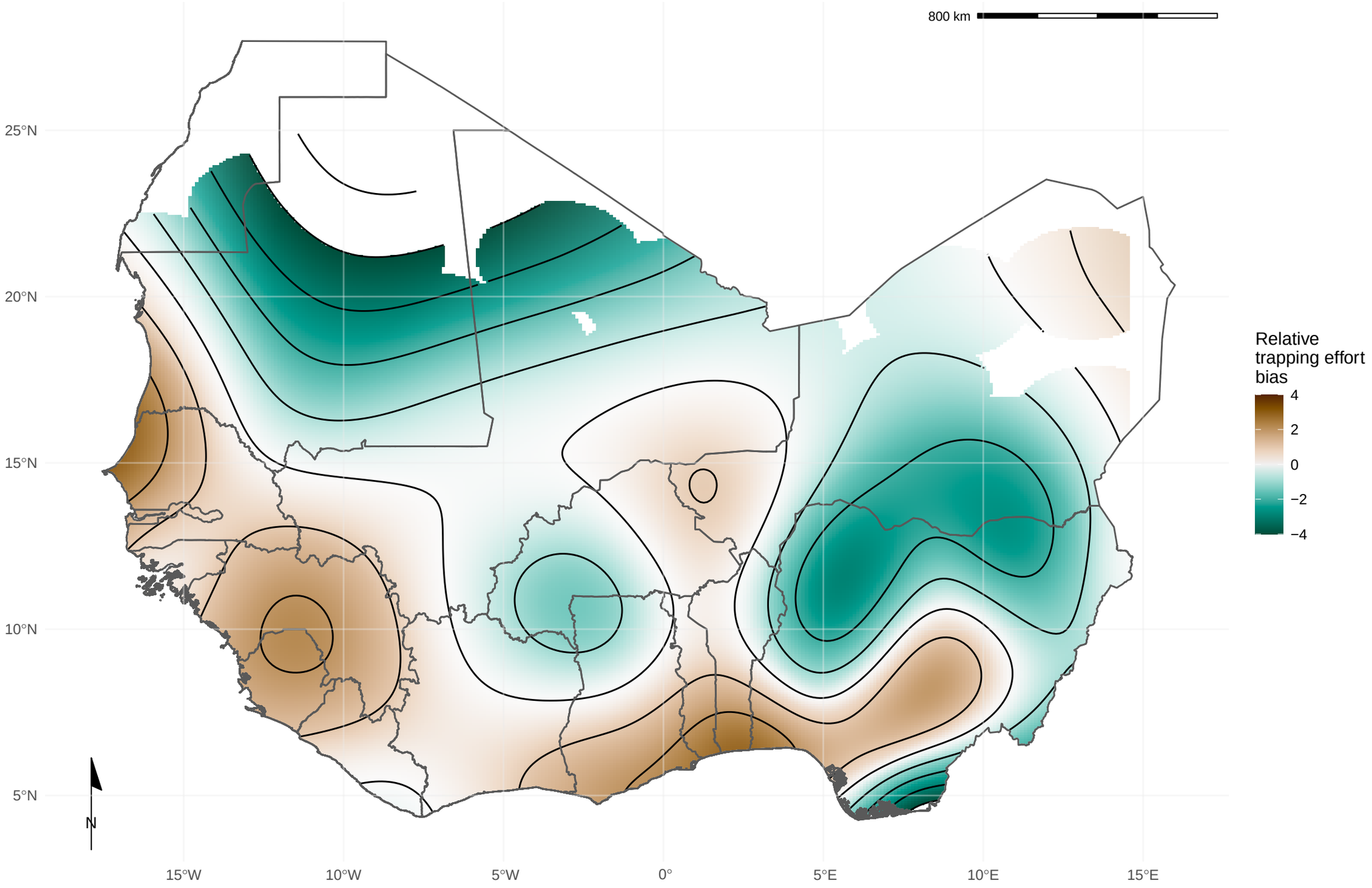

A
800 km
25°N
20°N
15°N
10°N
5°N
N
15°W
10°W
5°W
0°
5°E
10°E
15°E
Trap nights
60000
5000
2000
1000
500
300
100
0
B
Sites (n)
400
200
0
0–100
101–300
301–500
501–1,000
1,000–2,000
2,001–5000
5,001–50,320
Trap nights


800 km
25°N
20°N
15°N
10°N
5°N
15°W
10°W
5°W
0°
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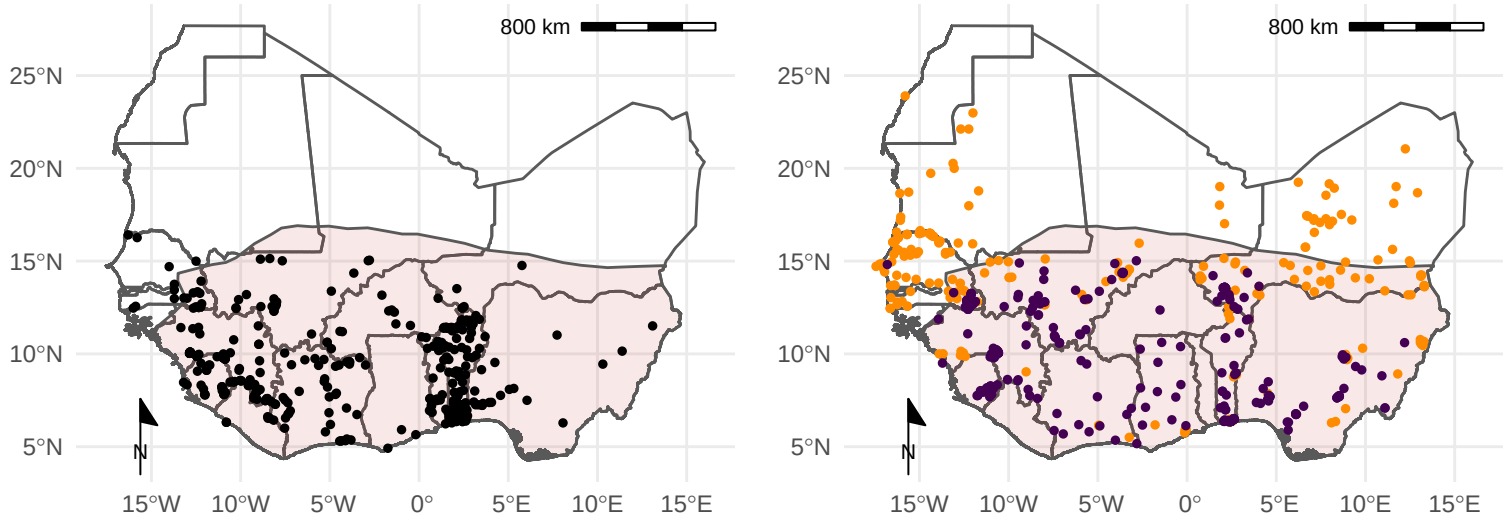
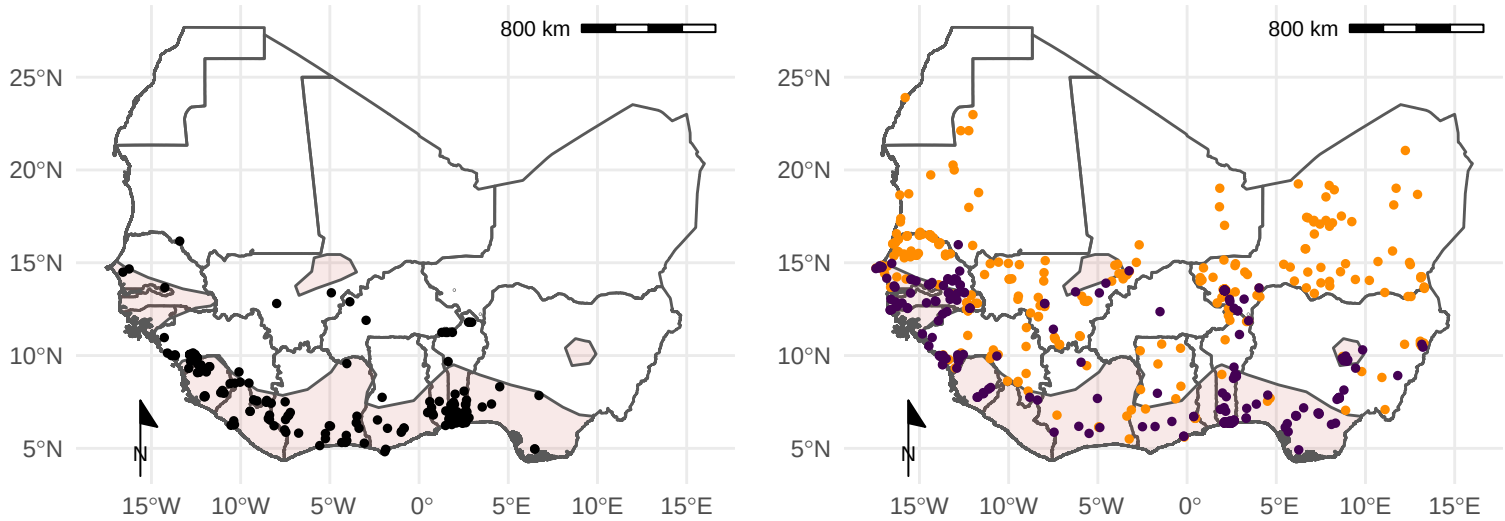
10°E
15°E
N
Relative trapping effort bias
4
2
0
−2
−4

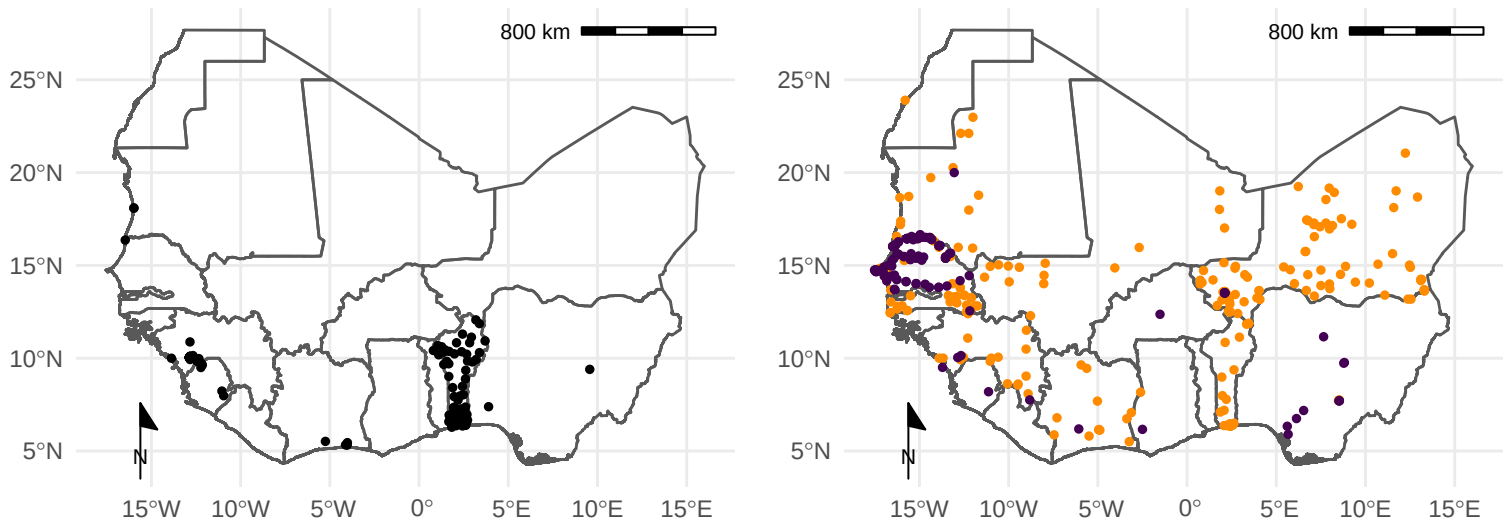
Mastomys natalensis



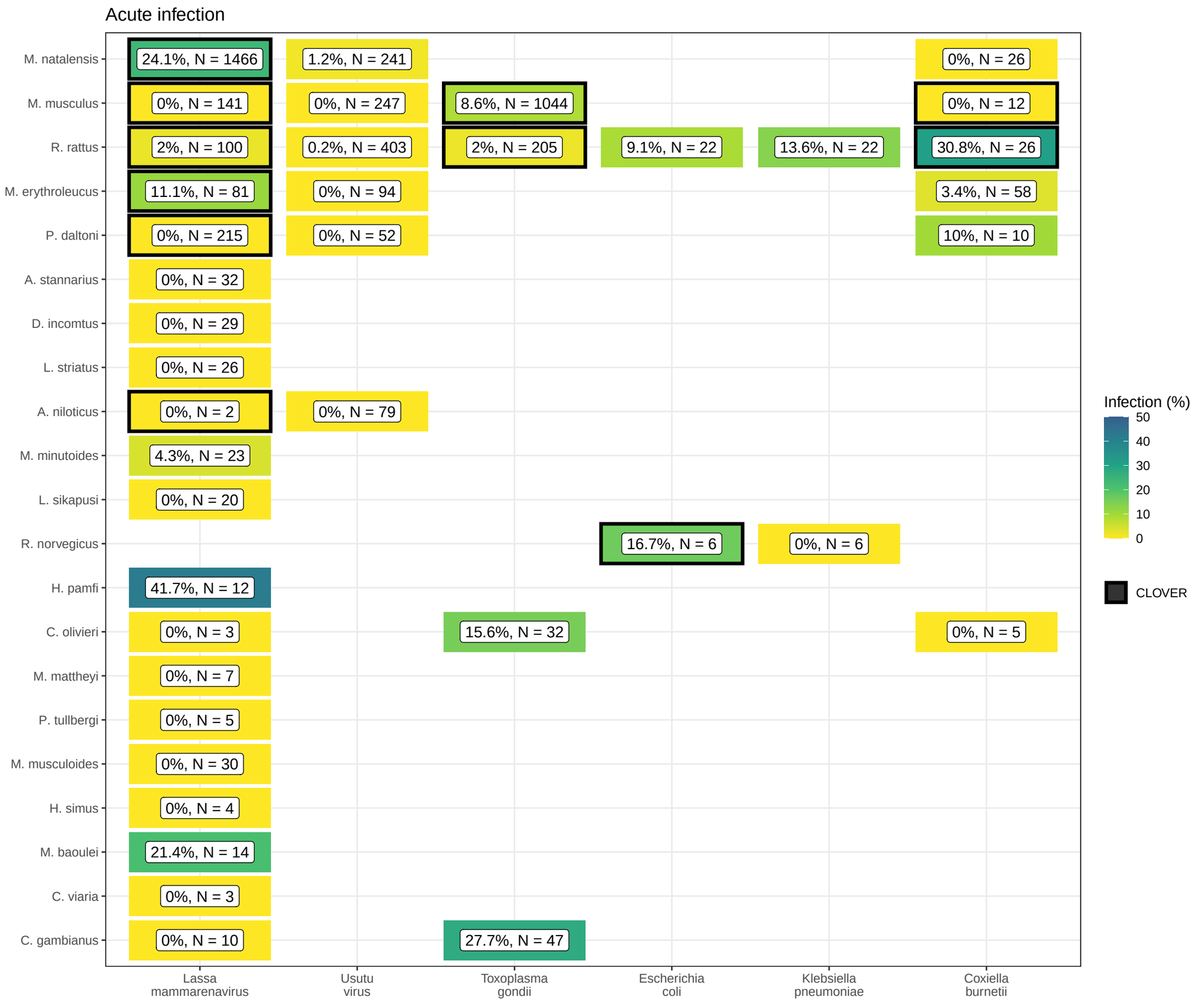
Rattus rattus

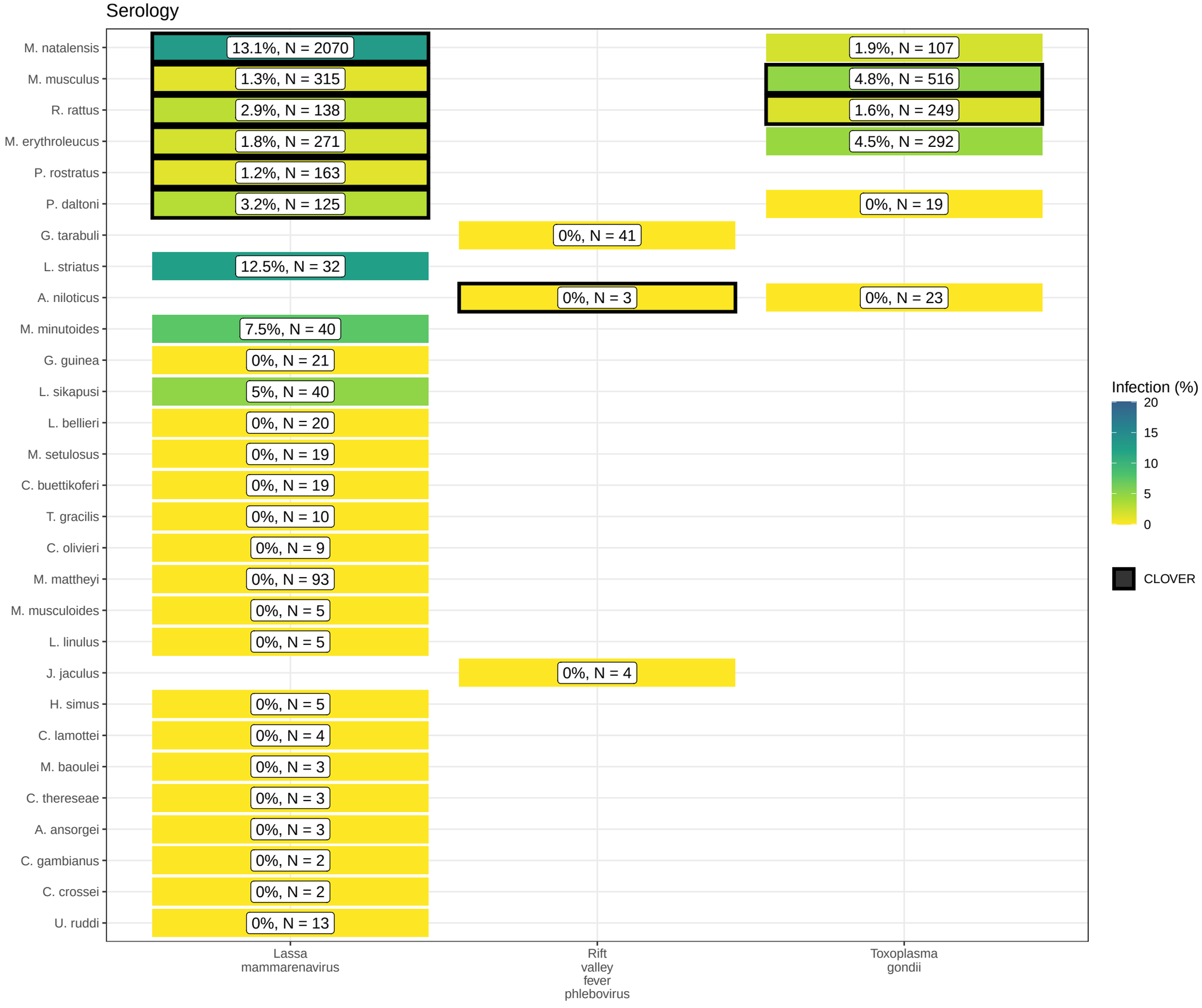


Mus musculus



Detection/Non−detection ● Detection ● Non−detection


Acute infection
M. natalensis
M. musculus
R. rattus
M. erythroleucus
P. daltoni
A. stannarius
D. incomtus
L. striatus
A. niloticus
M. minutoides
L. sikapusi
R. norvegicus
H. pamfi
C. olivieri
M. mattheyi
P. tullbergi
M. musculoides
H. simus
M. baoulei
C. viaria
C. gambianus
24.1%, N = 1466
1.2%, N = 241
0%, N = 26
0%, N = 141
0%, N = 247
8.6%, N = 1044
0%, N = 12
2%, N = 100
0.2%, N = 403
2%, N = 205
9.1%, N = 22
13.6%, N = 22
30.8%, N = 26
11.1%, N = 81
0%, N = 94
3.4%, N = 58
0%, N = 215
0%, N = 52
10%, N = 10
0%, N = 32
0%, N = 29
0%, N = 26
0%, N = 2
0%, N = 79
4.3%, N = 23
0%, N = 20
16.7%, N = 6
0%, N = 6
41.7%, N = 12
0%, N = 3
15.6%, N = 32
0%, N = 5
0%, N = 7
0%, N = 5
0%, N = 30
0%, N = 4
21.4%, N = 14
0%, N = 3
0%, N = 10
27.7%, N = 47
Lassa mammarenavirus
Usutu virus
Toxoplasma gondii
Escherichia coli
Klebsiella pneumoniae
Coxiella burnetii
Infection (%)
50
40
30
20
10
0
CLOVER


Serology
M. natalensis
M. musculus
R. rattus
M. erythroleucus
P. rostratus
P. daltoni
G. tarabuli
L. striatus
A. niloticus
M. minutoides
G. guinea
L. sikapusi
L. bellieri
M. setulosus
C. buettikoferi
T. gracilis
C. olivieri
M. mattheyi
M. musculoides
L. linulus
J. jaculus
H. simus
C. lamottei
M. baoulei
C. thereseae
A. ansorgei
C. gambianus
C. crossei
U. ruddi
13.1%, N = 2070
1.3%, N = 315
2.9%, N = 138
1.8%, N = 271
1.2%, N = 163
3.2%, N = 125
12.5%, N = 32
7.5%, N = 40
0%, N = 21
5%, N = 40
0%, N = 20
0%, N = 19
0%, N = 19
0%, N = 10
0%, N = 9
0%, N = 93
0%, N = 5
0%, N = 5
0%, N = 5
0%, N = 4
0%, N = 3
0%, N = 3
0%, N = 3
0%, N = 2
0%, N = 2
0%, N = 13
0%, N = 41
0%, N = 3
0%, N = 4
1.9%, N = 107
4.8%, N = 516
1.6%, N = 249
4.5%, N = 292
0%, N = 19
0%, N = 23
Lassa mammarenavirus
Rift valley fever phlebovirus
Toxoplasma gondii
Infection (%)
20
15
10
5
0
CLOVER