



Pathogens in the garden dormouse *Eliomys quercinus*

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Abstract

Wild rodents are important reservoirs and vectors of various pathogens, and play a crucial role in the spread of zoonotic pathogens. The garden dormouse (*Eliomys quercinus*), an arboreal nocturnal rodent species native to Europe, has declined throughout much of its natural range in recent decades. The reason for this ongoing decline is not yet fully understood, but infectious diseases may play a role. This study aimed to review the diversity of pathogens associated with the garden dormouse. For this purpose, a comprehensive review of the existing literature on garden dormouse-associated viruses, bacteria and protozoa was conducted. In parallel, we analysed samples from 294 garden dormice, that were found dead in Germany, for rodent-associated and zoonotic pathogens. The scientific literature currently, comprising 53 references, covers 73 years and primarily addresses *Borrelia* spp. and *Eimeria myoxi*. In the literature, a total of eight pathogens have been detected in garden dormice. In our own investigations, we were able to detect four different pathogens as well as antibodies against hepatitis E virus. The most prevalent pathogen found in our study was *Staphylococcus aureus* (29%, $n=58$). *Borrelia spielmanii* and *B. afzelii* were found in 5.6% of garden dormice ($n=143$) and 22% of the ticks attached to garden dormice ($n=32$). This study reports the first documentation of *Leptospira* spp. in garden dormice, with *L. borgpetersenii*, serogroup Sejroe, sequence type 197 detected in 2 of 176 animals. Beside these zoonotic pathogens metagenomic sequencing of selected samples revealed representatives of multiple DNA-virus families, including *Parvoviridae* and *Polyomaviridae*, most likely without zoonotic potential. There is currently no evidence, either from the literature or from our own investigations, that pathogens play a significant role in the decline of the garden dormouse in Germany.

Keywords Viruses · Bacteria · Protozoa · Zoonosis · *Borrelia* spp. · Metagenomic sequencing

Introduction

The garden dormouse (*Eliomys quercinus*), an arboreal rodent species native to Europe, occurring in the western Iberian Peninsula, Italy, France and on some Mediterranean islands, extending further to central and eastern Europe and the Urals (Storch 1978; Bertolino et al. 2008), has disappeared from a large part of its geographic range in recent decades (Bertolino 2017). Consequently, it is listed as

vulnerable by the International Union for Conservation of Nature (IUCN) (Bertolino et al. 2024). Garden dormice commonly inhabit broad-leaved, mixed, or coniferous forests, but can also be found in high-altitude shrubs and rocky slopes (Büchner et al. 2024). They make use of rocky environments with tree or shrub cover (Bertolino et al. 2005) and can be found in these habitats from sea level to the upper limit of the arboreal vegetation (2,000–2,200 m) (Bertolino et al. 2008). Garden dormice are also synanthropic, in some

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regions occupying gardens, orchards, vineyards and even houses within human settlements (Gil-Delgado et al. 2010; Büchner et al. 2018).

The decline in garden dormouse populations appears to be the result of multiple, interacting factors. Habitat loss and fragmentation, reduced food availability, and exposure to environmental toxins such as rodenticides have been identified as primary drivers (Büchner et al. 2024; Famira-Parcetich et al. 2024). However, the role of infectious diseases is yet to be established.

Wild rodents are natural reservoirs for a diverse array of viruses, bacteria, fungi, and parasites. While many of these pathogens persist asymptotically in their reservoir hosts, they can cause severe or even fatal disease in other species, including humans (Meerburg et al. 2009; Nakamura et al. 2013; Yarto-Jaramillo 2015; Kirilov et al. 2022). Globally, approximately one-third of infectious agents detected in rodents – including viruses, bacteria, and protozoa – are capable of infecting humans (Han et al. 2015). Because garden dormice, similar to house mice (*Mus musculus*, *M. domesticus*) and rats (*Rattus* spp.), may occur in close proximity to human dwellings, the potential for zoonotic transmission – particularly via arthropod vectors – warrants detailed investigation.

Vector-borne zoonotic pathogens

Among rodent-associated vector-borne zoonotic bacteria, the *Borrelia burgdorferi* sensu lato complex is particularly noteworthy. These spirochetes, which cause Lyme disease – the most prevalent tick-borne disease in humans in the Northern Hemisphere (Matuschka and Spielmann 1986) – are transmitted by *Ixodes* ticks. The vectors acquire the infection during larval feeding on infected rodents and subsequently transmit the bacteria to new hosts during the blood meal as nymphal stage (Steere AC 1989; Donahue et al. 1987; Lane and Loya 1991). Distinct *Borrelia* genospecies differ in their host associations: *B. afzelii* is maintained mainly by mice (*Apodemus* spp.) and voles (*Clethrionomys* spp.) (Wolcott et al. 2021), whereas *B. spielmanii* has been closely linked to the garden dormouse (Richter et al. 2004, 2006).

Rodents also serve as reservoirs for other tick-borne pathogens, including tick-borne encephalitis virus (*Flaviviridae*), and intracellular bacteria of the order Rickettsiales, such as *Anaplasma* spp., *Ehrlichia* spp. and *Rickettsia* spp. Additionally, protozoan parasites such as *Babesia* spp. and *Theileria* spp., which are of veterinary relevance, have been documented in rodent hosts (Meerburg et al. 2009; Kirilov et al. 2022).

Non vector-borne zoonotic pathogens

Beyond vector transmission, rodents can carry numerous viruses and bacteria that are directly transmissible to humans. Hantaviruses (*Hantaviridae*) are a prominent example, with species from the families *Muridae* and *Cricetidae* serving as reservoirs. In Europe, Puumala virus (PUUV) is the most commonly detected zoonotic rodent-borne hantavirus, though symptoms in humans are typically mild to moderate. However, hantavirus species such as Seoul virus (SEOV) and Dobrava-Belgrade virus (DOBV), which may cause more severe symptoms, are also present (Klempa et al. 2006).

Rodents and shrews in Europe are also known to transmit encephalitis-causing viruses such as bornaviruses and lymphocytic choriomeningitis virus (LCMV).

The variegated squirrel bornavirus 1 (VSBV-1) is associated with exotic squirrel species, while Borna disease virus 1 (BoDV-1) is maintained in bicolored white-toothed shrews (*Crocidura leucodon*) (Dürrwald et al. 2014; Hoffmann et al. 2015; Schlottau et al. 2017). In humans and other mammals, BoDV-1 infections can cause fatal, immune-mediated non-suppurative encephalitis with neurological deficits (Richt et al. 2001; Rubbenstroth et al. 2019; Schulze et al. 2020). Similarly, arenaviruses (*Arenaviridae*) can cause encephalitis in humans and are transmitted primarily by rodents of the families *Muridae* and *Cricetidae*. The lymphocytic choriomeningitis virus, the only arenavirus with a global distribution, is hosted mainly by the house mouse but has also been detected in wood mice (*Apodemus sylvaticus*) from Germany (Mehl et al. 2024) and Spain (Ledesma et al. 2009) and pet Syrian golden hamsters (*Mesocricetus auratus*) (Ackermann et al. 1972). Human infections occur through direct contact with rodents or their excreta and may cause aseptic meningoencephalitis or congenital malformations of the central nervous system (CNS) and eyes of embryos (Ackermann et al. 1972, 1975; Jay et al. 2005).

Other zoonotic rodent-borne viruses from Germany include hepeviruses, such as rat hepatitis E virus (ratHEV) (Johne et al. 2010), which may cause acute or persistent hepatitis in humans (Andonov et al. 2019) and orthopoxviruses such as cowpox virus (CPXV) or monkeypox virus (MPV) (Ntumvi et al. 2018; Meseiko et al. 2023; Jo et al. 2024).

Among bacteria zoonoses, *Streptobacillus moniliformis*, the causative agent of rat bite fever, is noteworthy. This pathogen is transmitted directly via bites or indirectly through contaminated food or water, leading to fever, arthritis, and a maculopapular, petechial or pustular rash, and occasionally to life-threatening complications (Kondruweit et al. 2007; Eisenberg et al. 2017).

In Europe, the European brown hare (*Lepus europaeus*) is the main reservoir host for *Francisella tularensis*, the causative agent of tularemia, but *F. tularensis* has been detected also in voles of different species (Kaysser et al. 2008; Runge et al. 2011; Jeske et al. 2019).

Rodents also serve as important reservoirs for pathogenic *Leptospira* spp., spirochete bacteria that cause leptospirosis – one of the most widespread zoonotic diseases worldwide. Symptoms range from mild (headaches, chills) to severe forms such as Weil's disease or pulmonary involvement (Karesh et al. 2012; Hamond et al. 2023).

Rodent specific and wildlife-relevant pathogens

Not all rodent-associated pathogens are zoonotic. Some are host-specific commensals or affect other wildlife species, potentially influencing population dynamics. A good example is the decline of the European red squirrel (*Sciurus vulgaris*) in Great Britain, which was driven largely by the introduction of invasive Eastern grey squirrels (*Sciurus carolinensis*) carrying squirrelpox virus (SPPV). While grey squirrels remain unaffected, the virus is lethal to red squirrels (Rushton et al. 2006; Lurz et al. 2025). The effects of this introduced pathogen is exacerbated by anthropogenic influences, such as deforestation, habitat degradation, and resource competition. In addition, British red squirrels are threatened by *Staphylococcus aureus*, which can cause fatal exsudative dermatitis (Simpson et al. 2013). In these cases, rats (*Rattus norvegicus*, *Rattus rattus*) and moles (*Talpa europaea*) are considered reservoir hosts. Rodents may also carry host-specific viruses – such as herpesviruses and polyomaviruses – that do not infect other mammalian species but may still impact rodent health (Ehlers et al. 2007, 2019). Likewise, certain animal pathogens, such as rustrela virus (Bennett et al. 2020), can be transmitted from rodents to larger mammals, where they may cause disease in susceptible hosts.

This study aims to (i) provide a comprehensive literature review of known bacterial, viral, and protozoan pathogens in *E. quercinus*, and (ii) present original pathogen screening results from incidental collected samples from dead garden dormice found in Germany, to assess whether pathogens may be contributing to the species' decline, and additionally whether *E. quercinus* poses a zoonotic risk, given that they often inhabit areas in close proximity to humans. This pathogen screening was based on pathogen-specific and non-targeted metagenomic analyses, and existing sequence read archive (SRA) evaluation.

Materials and methods

Literature review

Relevant papers were searched and selected in January 2025 using the international online databases: PubMed and Web of Science. The searches covered the scientific literature published up to, and including, December 2024 with no time or language limits. To find studies on garden dormice, the following search strings were used: (Viruses OR Bacteria OR Protozoa OR Disease OR Pathogen) AND (Garden dormouse OR *Eliomys quercinus* OR *Eliomys* OR Gliridae). The workflow followed the PRISMA guidelines (Page et al. 2021).

Sample collection and pathogen screening

Carcasses of 294 garden dormice found dead in Germany between 2015 and 2021 (Fig. 1), were subjected to post-mortem examination (Famira-Parcsetich et al. 2024), during which, samples were taken for further analysis. The number of samples submitted for testing for various pathogens, including various bacteria and viruses, varied due to a number of factors, including the sometimes poor quality of the sample material, resulting from decomposition. For example, samples were not used if the organs had become desiccated or severely autolytic due to prolonged exposure to the elements, whereas samples were used even after a prolonged period of freezing (Nippert et al. 2023). Other factors included differing funding sources and the time at which the samples were analysed during the course of the project. We engaged in numerous collaborative endeavours with diverse research laboratories, coordinated by the network “Rodent-borne pathogens” (Ulrich et al. 2009, 2025 in press).

Depending on the tissue tropism of each pathogen, relevant tissues were homogenized and nucleic acids were extracted. Detection of pathogens or their nucleic acids, or reactive antibodies was performed according to previously established protocols. Detailed information including examined pathogens, methods and references can be found in Table 1.

Metagenomic sequencing

A subset of obtained kidney samples ($n=73$) was subjected to metagenomic next-generation sequencing (NGS). For this purpose, DNA was extracted from kidney tissue and amplified

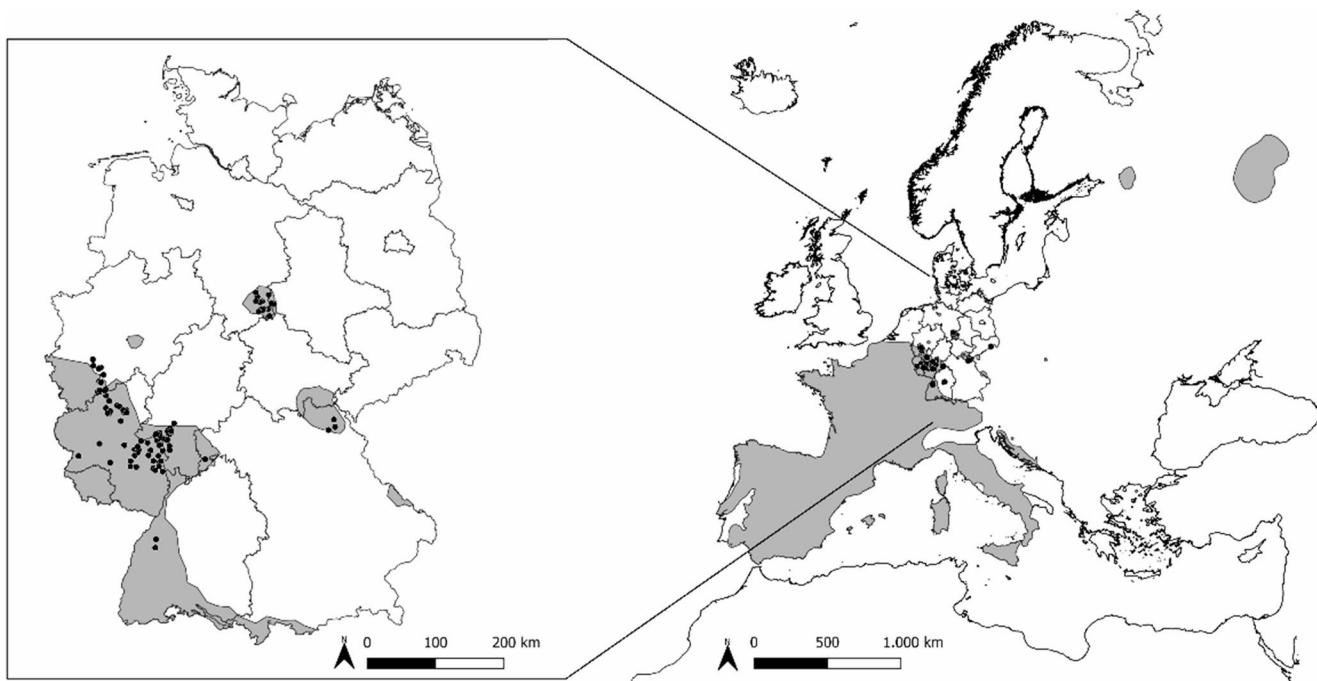


Fig. 1 Distribution range of garden dormice in Europe, and Germany in particular (grey, IUCN 2023). Origin of the specimens examined in this study (black dots). ©EEA 2022 and ©GeoBasis-DE/BKG 2021

via strand displacement amplification (SDA) with EquiPhi29 DNA polymerase as described previously (Vasiliūnaitė et al. 2024). Seven such DNA samples were used directly for sequencing library preparation. Another 66 samples were randomly combined into three pools for sequencing (details available at Online Resource 1). Sequencing libraries were prepared with Nextera XT library preparation kit (Illumina Inc., San Diego, CA, USA) and sequenced using a NovaSeq Xplus 10B machine with 2×150 bp (bp) paired-end reads at the Sequencing Facility of Center for Cancer Research, National Cancer Institute, (Frederick, MD, USA). Additionally, 161 garden dormouse associated Sequence Read Archive (SRA) datasets available online before 2025-02-01 were downloaded and analyzed in parallel (list of SRA datasets available at Online Resource 2). Obtained sequencing reads from both our study and the publicly available SRAs were trimmed with fastp tool (v0.24.0) (Chen 2023). Sequences were assembled de novo with megahit (v1.2.9.) (Liu et al. 2023), and viral sequences longer than 300 nucleotides (nt) were annotated with Cenotaker3 (v3.3.2) (Tisza et al. 2021). Additionally, MetaPhlAn 4.0.3 (database vJun23) (Blanco-Míguez et al. 2023) analysis was performed with standard parameters to determine the presence of bacterial pathogens.

The computational resources of the National Institutes of Health high-performance computing cluster Biowulf were utilized. Sequencing reads were uploaded at the National Center for Biotechnology Information (NCBI) under Bio-Project accession number PRJNA1241767.

Furthermore, samples were analysed for the presence of polyomaviruses. The results of these analyses have been previously published and appear in the literature review (Vasiliūnaitė et al. 2024).

Results

Literature review

The literature search yielded a total of 53 publications, covering a 73-year period (1951–2024), and describes the detection of eight different pathogens in garden dormice (Table 2). Prior to 2010, fewer than one manuscript was published per year, but since 2011 an increase was observed. In the current decade, an average of 3.25 manuscripts were published per year (Fig. 2). However, 40 of the 53 publications were excluded from the analysis because, on closer inspection, they did not meet the search criteria (Fig. 3). Two of the literature sources do not address pathogens or the garden dormouse. Four of the sources address the garden dormouse, but do not discuss pathogens. Pathogens in other species, such as the edible dormouse (*Glis glis*), are discussed in 23 publications. Eleven of the papers focus on endoparasites such as nematodes or cestodes that do not align with the aims of this study (Fig. 3).

Of the remaining 13 publications (Table 2), three manuscripts were published in the 1950s and 1970s and focus on

Table 1 Analysis of garden dormouse samples for 16 pathogens, including sample material, sample size, detection method and respective references and results of the examinations with information on the number of positive samples (and precise pathogen differentiation) and the resulting prevalences. Responsible laboratories are indicated as footnotes

Pathogen	Sample Material	Sample Size	Method Type	Reference	Positive Samples	Prevalence (%)	95% Confidence Interval
RNA – Viruses							
pan-hantavirus ¹	Lung	19	RT – PCR, L segment	Klempa et al. (2006)	0	0	
Puumala virus and related ¹	Lung	19	RT-PCR, S segment	Schmidt et al. (2016)	0	0	
Borna disease-virus-1 ¹	Brain	60	RT - qPCR	Schulze et al. (2020)	0	0	
Arenaviruses ¹	Kidney	176	RT - PCR	Vieth et al. (2007)	0	0	
Hepatitis E-Virus ¹	Liver	19	RT - PCR	Ryll et al. (2017)	0	0	
SARS-CoV-2 ²	Throat Swab	23	RT - PCR	Corman et al. (2020)	0	0	
DNA – Viruses							
Herpesviruses ¹	Spleen	64	PCR	Chmielewicz et al. (2001)	0	0	
Orthopoxviruses ¹	Nasal septum	70	qPCR	Scaramozzino et al. (2007)	0	0	
Bacteria							
<i>Streptobacillus moniliformis</i> ³	Throat swab	28	qPCR	Fawzy et al. (2022)	0	0	
<i>Leptospira</i> spp. ⁴	Kidney	176	qPCR MLST	Stoddard et al. (2009) Victoria et al. (2008) Boonslip et al. (2013)	2 (<i>Leptospira borgpetersenii</i> , serogroup Sejroe, sequence type 197)	1.1	0–3%
<i>Borrelia</i> spp. ⁵	Skin	143	Nested-PCR	Richter and Matuschka (2006)	8 (<i>Borrelia spielmanni</i> (7/8), <i>Borrelia afzelii</i> (1/8))	5.6	9–18%
<i>Borrelia</i> spp. ⁵	Ticks	32	Nested-PCR	Richter and Matuschka (2006)	7 (<i>Borrelia spielmanni</i>)	22	7–36%
<i>Anaplasma/Ehrlichia</i> spp. ¹	Spleen	18	PCR	Parola et al. (2000)	0	0	
<i>Rickettsia</i> spp. ¹	Spleen	18	PCR	Regnery et al. (1991)	0	0	
<i>Staphylococcus aureus</i> ⁶	Nose	58	Selective media, agglutination test, PCR	Mrochen et al. (2018)	17	29	17–41%
Protozoa							
<i>Babesia</i> spp. ¹	Spleen	18	PCR	Hilpertshauser et al. (2006)	0	0	
Serology							
Anti-HEV antibodies ⁷	Chest cavity fluid	68	Indirect-IgG-ELISA	Simanavicius et al. (2018)	1 (IgG to rat HEV CP(112–608) and IgG to HEV GT3 CP (1–660))	1	0–4%

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CP capsid protein, GT3 genotype 3, HEV hepatitis E virus, IgG immunoglobulin G, ratHEV rat hepatitis E virus, SARS-CoV-2 severe acute respiratory syndrome coronavirus 2, MLST Multi locus sequence typing

viruses, bacteria and protozoa in garden dormice, including tick-borne pathogens, such as *Rickettsia prowazekii* (Perez Gallardo et al. 1951) and *Coxiella burnetii* (Perez Gallardo et al. 1952). A further increase in the number of publications on tick-borne bacteria in garden dormice was observed

between 1999 and 2011, particularly with regard to *Borrelia* spp. in France and Germany (Matuschka et al. 1999; Richter et al. 2004, 2011). From 2005 onwards, several publications on protozoa emerged (Bertolino and Canestri-Trottini 2005; Kvičerová et al. 2011; Azami-Conesa et al. 2023;

Table 2 Results of the literature search for bacteria, viruses and protozoa in garden dormice. Pathogens analysed in publications and determined prevalences

Pathogen	Reference	Country	Prevalence (cohort size)	95% Confidence Interval
RNA-Viruses				
Borna disease virus	Fischer et al. (2018a)	Germany	0% (n=156)	
DNA-Viruses				
Polyomavirus	Vasiliūnaitė et al. (2024)	Germany	3% (n=74)	0–6%
Anti-polyomavirus antibodies	Vasiliūnaitė et al. (2024)	Germany	17% (n=69)	8–26%
Bacteria				
<i>Enterococcus faecium</i>	Silva et al. (2012)	Portugal	97% (n=33)	91–100%
<i>Enterococcus faecalis</i>	Silva et al. (2012)	Portugal	3% (n=33)	0–8%
Spirochetal infection	Matuschka et al. (1999)	France	91% (n=60)	85–99%
<i>Borrelia afzelii</i>	Richter et al. (2004)	France	31% (n=35)	16–47%
<i>Borrelia spielmanii</i>	Richter et al. (2004)	France	80% (n=35)	67–93%
<i>Rickettsia</i> spp.	Richter et al. (2011)	Germany	1	
<i>Staphylococcus aureus</i>	Gómez et al. (2014)	Spain	0% (n=1)	
<i>Coxiella burnetii</i>	Perez Gal-lardo et al. (1952)	Spain	1	
<i>Rickettsia</i> spp.	Perez Gal-lardo et al. (1951)	Spain	1	
Protozoa				
<i>Eimeria</i> sp.	Fischer et al. (2018a)	Germany	2% (n=57)	0–5%
<i>Eimeria myoxi</i>	Cuoso-Pérez et al. (2023)	Spain	57% (n=28)	39–75%
	Kvičerová et al. (2011)	Czech Republic	85% (n=54)	76–95%
	Bertolino et al. (2005)	Italy	64.7% (n=17 in 2000) and 54.6% (n=11 in 2002)	42–87% and 25–84%
<i>Eimeria melanuri</i>	Bertolino et al. (2005)	Italy	82.4% (n=17 in 2000) and 36.4% (n=11 in 2002)	64–100% and 8–65%
<i>Leishmania infantum</i>	Azami-Conesa et al. (2023)	Spain	0% (n=1)	

¹These publications are based on experimental infection trials, no prevalences are given.

Couso-Pérez et al. 2023), and from the 2010s on, single publications on pathogens such as *Enterococcus* sp. (Silva et al. 2012), *Staphylococcus aureus* (Gómez et al. 2014) and polyomaviruses (Vasiliūnaitė et al. 2024) were published (Table 2).

Specific pathogen screening

In our own investigations, we were able to detect four different pathogens as well as antibodies against hepatitis E virus (HEV). *Leptospira* spp. DNA was found in two of 176 (1.1%, 95% CI 0–3%) kidney tissue samples. These were further identified by multi locus sequence typing (MLST) as *Leptospira borgpetersenii*, serogroup Sejroe, sequence type (ST) 197 (Table 1). The positive samples came from one animal in Rhineland-Palatinate (death 2019) and one animal in North Rhine-Westphalia (death 2021). In addition, DNA of *Borrelia burgdorferi* s.l. was detected in eight of 143 (5.6%, 95% CI 9–18%) skin samples. We detected *Borrelia spielmanii* in seven of the eight positive samples, and *Borrelia afzelii* in one sample. In seven of 149 ticks, from 32 different animals, we detected *B. spielmanii* DNA. Of the seven animals in which *B. spielmanii* was detected, three were found to be carrying ticks that also tested positive for this bacterial DNA. In one out of 68 (1%, 95% CI 0–4%) chest cavity fluid samples, antibodies against HEV (IgG to rat HEV CP (112–608) and IgG to HEV GT3 CP (1–660)) were detected. The highest prevalence was found for *Staphylococcus aureus* at 29% (95% CI 17–41%), with 17 out of 58 nose samples testing positive (Table 1). Of these 7/17 (41%) belonged to the lineage clonal complex (CC) 121/CC1956. Moreover, we isolated several CC188 (n=3), CC49 (n=2), CC15 (n=2) strains, as well as single isolates belonging to CC5, CC7, CC121, CC130 and CC133. All isolates were methicillin susceptible *S. aureus* (MSSA), with singular isolates showing resistances to penicillin, ciprofloxacin, erythromycin and others (Table 3).

Metagenomic sequencing

MetaPhlAn analysis of metagenomic sequencing data from garden dormouse kidney-derived DNA extracts (n=73) and publicly available SRA datasets obtained from different garden dormouse tissues (feces, gut, liver, muscle, hypothalamus, other unidentified tissue, n=161) revealed a diverse range of bacterial pathogens (Fig. 4, Online Resource 3 and 4). The highest diversity of the species identified was observed in fecal samples (30 species). Detection of *Enterococcus faecium* and *E. faecalis* in fecal samples was consistent with previously reported findings, however other *Enterococcus* and other species not previously reported in garden dormouse were also identified (Table 2;

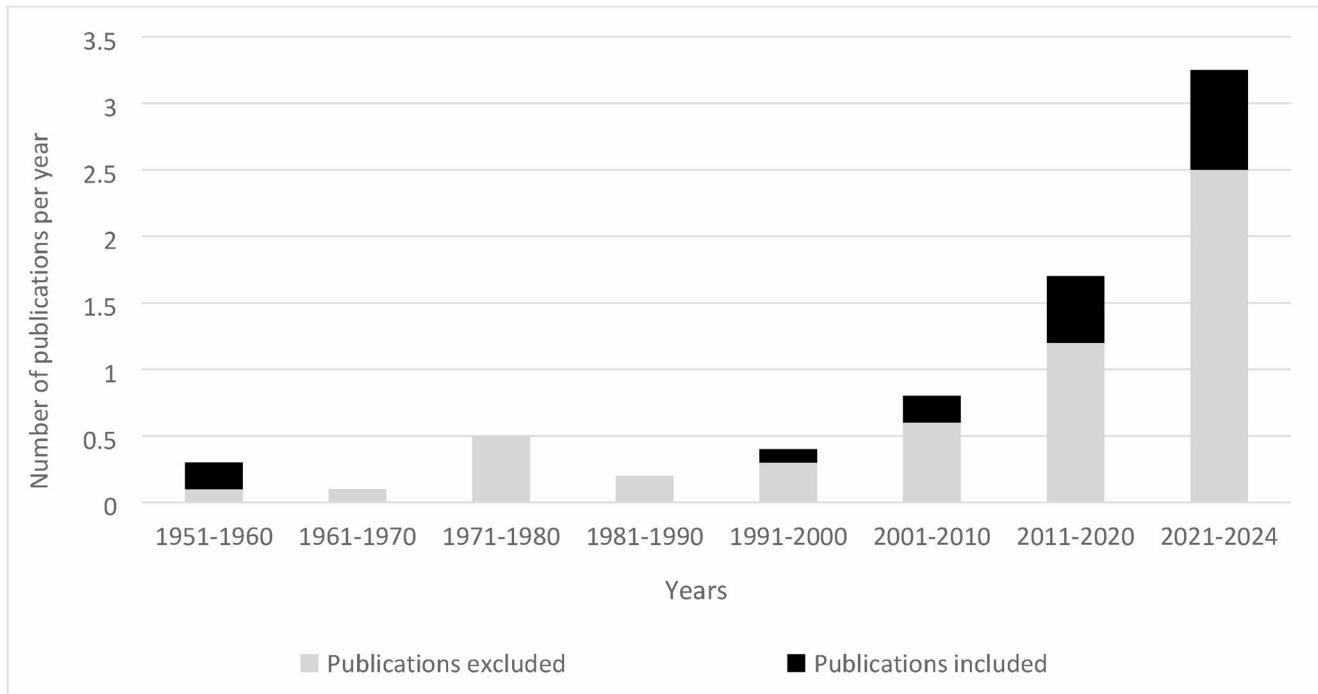


Fig. 2 Results of the literature search are presented as the number of publications per year, within a defined time period. The results are presented in their entirety, with those dealing with the topics of interest

est (viruses, bacteria, protozoa in garden dormice) in black, and those which were excluded in light grey

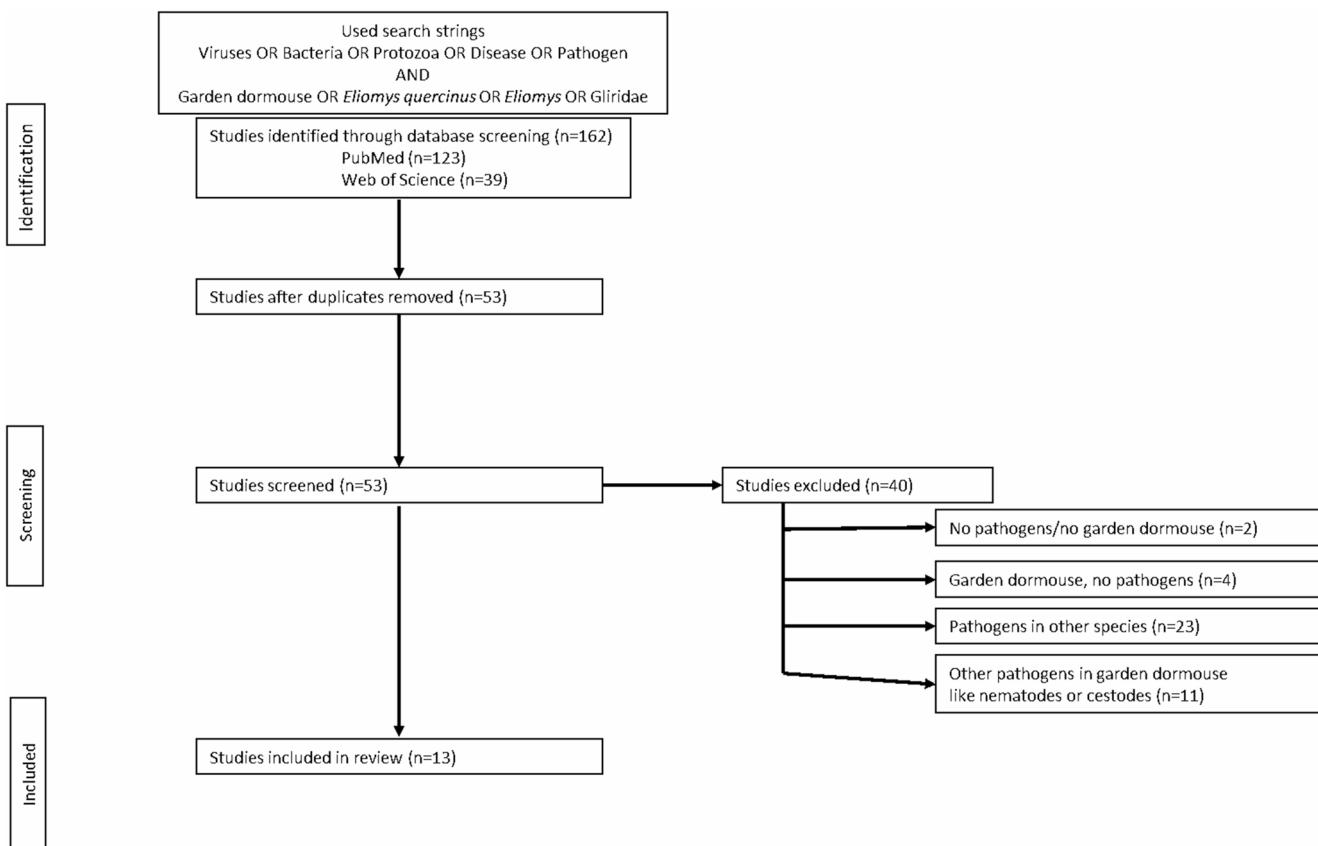


Fig. 3 Overview of the search strategy for viruses, bacteria, and protozoa in garden dormice and the results of the literature research, PRISMA flowchart adapted from Page et al. (2021)

Table 3 Virulence gene and resistance patterns of *Staphylococcus aureus* isolates from garden dormice

Sample ID	spa type	spa repeats	MLST	deduced	CC	gyr	mecA	mecC	mecU	luk-PV	sak	chp	scn	sa3int	Cefoxitin-Screen	Benzylpenicillin	Oxacillin	Oxacillin + Cefazolin	Genta-mycin
KS19/0211	t105	26-23- 17-34- 17-20- 17-17- 16	-	CC5	+	-	-	-	-	-	+	+	+	-	-	S	S	S	S
KS19/0196	t091	07-23- 21-17- 34-12- 23-02- 12-23	-	CC7	+	-	-	-	-	-	+	+	+	-	-	S	S	S	S
KS19/1334	t084	07-23- 12-34- 34-12- 12-23- 02-12- 23	-	CC15	+	-	-	-	-	-	-	-	-	-	-	S	S	S	S
KS19/1351	t084	07-23- 12-34- 34-12- 12-23- 02-12- 23	-	CC15	+	-	-	-	-	-	+	+	+	-	-	S	S	S	S
KS19/1310	t208	04-20- 17-17- 31-31- 24-17- 17-17- 17-25	-	CC49	+	-	-	-	-	-	-	-	-	+	-	S	S	S	S
KS19/0204	t13540	14-44- 34-17	ST19472	CC121/1956	+	-	-	-	-	-	-	-	-	-	-	S	S	S	S
KS19/0213	t3750	04-20- 25-23- 24-17	ST2328	CC121/1956	+	-	-	-	-	-	-	-	-	+	-	S	S	S	S
KS19/1302	t3750	04-20- 25-23- 24-17	-	CC121/1956	+	-	-	-	-	-	-	-	-	+	-	S	S	S	S
KS19/1303	t3750	04-20- 25-23- 24-17	-	CC121/1956	+	-	-	-	-	-	-	-	-	-	-	R	S	S	S
KS19/1305	t11686	14-44- 34-50- 17	ST1956	CC121/1956	+	-	-	-	-	-	-	-	-	+	-	S	S	S	S
KS19/1308	t524	04-17	ST2328	CC121/1956	+	-	-	-	-	-	-	-	-	-	-	S	S	S	S

Table 3 (continued)

Sample ID	spa type	spa repeats	MLST	deduced CC	gyr	mecA	mecC	mecU	luk-PV	sak	clp	scrn	sa3int	Cefoxitin-Screen	Benzylpenicillin	Oxacillin	Oxacillin+Cefazolin	Gentamycin		
KS19/1318	t3750	03-16-21-7-	-	CC12/1956	+	-	-	-	-	+	-	+	+	-	-	S	S	S		
		21-7-																		
		23-13-																		
KS19/0195	t3568	04-39-17	ST130	CC130	+	-	-	-	-	-	-	+	-	-	S	S	S	S		
		21-17-																		
		23-13-																		
		17-17																		
KS19/1312	t189	07-23-12-21-	-	CC188	+	-	-	-	-	+	-	+	+	-	R	S	S	S		
		17-34																		
KS19/1317	t189	07-23-12-21-	-	CC188	+	-	-	-	-	+	-	+	+	-	S	S	S	S		
		17-34																		
KS19/1320	t189	07-23-12-21-	-	CC188	+	-	-	-	-	+	-	+	+	-	S	S	S	S		
		17-34																		
Sample ID	Gentamicin+Ciprofloxacin		Levofloxacin		Levofloxacin+Moxi-floxacin		inducible clindamycin resistance		Erythro-mycin		Clindamycin		Line-zolid		Daptomyein		Teicoplanin		Vancomycin	
KS19/0211	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/0196	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1334	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1351	1	1	S	+	R	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1310	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/0204	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/0213	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1302	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1303	R	1	ND	-	S	S	S	S	S	S	R	S	S	R	S	S	S	S		
KS19/1305	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1308	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1318	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/0195	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1321	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1312	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1317	R	1	ND	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		
KS19/1320	1	1	S	-	S	S	S	S	S	S	S	S	S	S	S	S	S	S		

MLST Multi locus sequence typing, CC clonal complex, gyr gyrase, mec methicillin, luk leukocidin, sak staphylococcal complement inhibitor, sa3int S. aureus integrase 3, scrn sensitive, R resistant, *R AEC modified resistant, ND not determined.

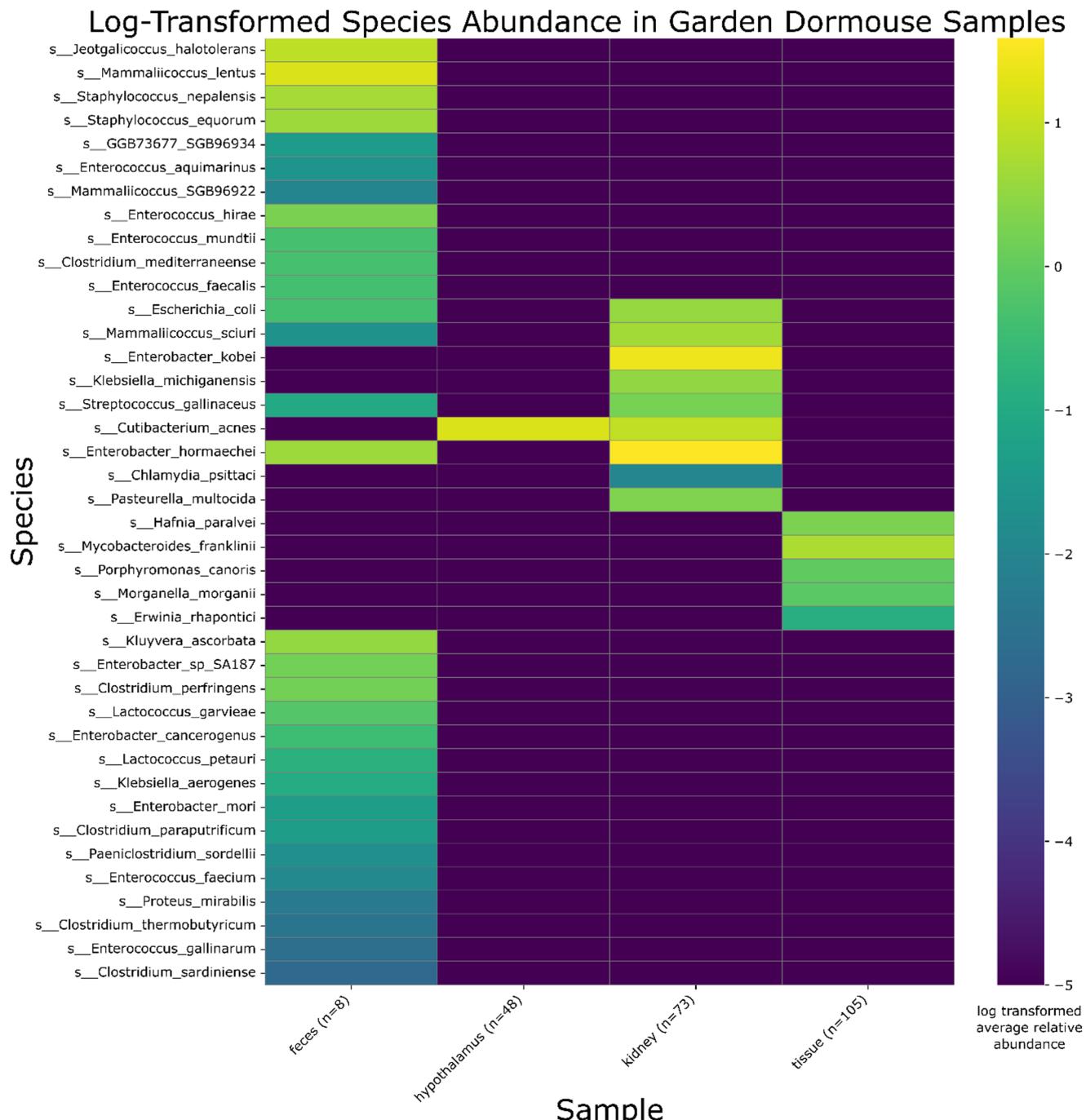


Fig. 4 Log-transformed heatmap of microbial species abundance across garden dormouse samples. The species were profiled using MetaPhlAn4 (Blanco-Míguez et al. 2023). The analysis included garden dormouse kidney samples sequenced in this study and the garden dormouse sequence read archive (SRA) datasets, and abundance values are expressed as log-transformed relative abundances. Warmer

colors (e.g. yellow) indicate higher log-abundance values, while colder colors (e.g. blue) indicate lower or absent microbial presence in that tissue. MetaPhlAn4 screen results were combined by sequenced tissue type (feces; hypothalamus; kidney; gut, liver, muscle, and other unidentified tissue), and average relative abundance was determined for each tissue type for each microbial species detected

Fig. 4). *Cutibacterium acnes* was the only bacterial pathogen detected in the hypothalamus samples; however, this species has been previously reported as a contaminant in certain laboratory reagents and kits (Liu et al. 2022). In

addition *Chlamydia psittaci*, *Pasteurella multocida*, *Enterobacter hormaechei* and *E. kobei*, which are known opportunistic agents in animals (Seriki et al. 2025; Smallman et al. 2024; Wang et al. 2024), were detected in kidney derived

samples. In other tissue samples, opportunistic and environmental bacteria such as *Hafnia paralvei*, *Mycobacteroides franklinii*, *Porphyromonas canoris*, *Morganella morganii*, and *Erwinia rhamontici* were detected at low abundance. Investigation for viral sequences, with Cenote-Taker3, identified 129 viral contigs of at least 300 nt in length in 54 of the sequenced samples (, revealing the presence of viruses of multiple DNA-virus families, including *Parvoviridae*, *Adenoviridae*, *Circoviridae*, *Polyomaviridae*, *Anelloviridae* and *Genomoviridae* (Online Resource 5). Parvovirus-related sequences belonging to diverse representatives of the family *Parvoviridae* were present in five out of ten kidney sequencing libraries prepared, and in at least four analyses of SRA datasets. Complete genome sequences of 13 circular viruses were assembled (12 without previously identified polyomavirus, Table 4, Online Resource 6). Assembled viral sequences had very low to no similarity to each other on the nucleotide sequence level, however, some resembled previously identified sequences. For example, a circular gemykrogvirus genome (*Genomoviridae*) extracted from a pooled kidney sample of garden dormice, showed almost 99% identity to the sequence LK931484.1, previously identified in a sample of healthy bovine blood. The near-identical dormouse-derived gemykrogvirus sequence to one reported

from bovine blood likely reflects the common environmental source of genomviruses, which are commonly detected in diverse vertebrate and non-vertebrate samples (Kazlauskas et al. 2019). In contrast, multiple genomovirus-related sequences were recovered from pooled kidney samples, highlighting diverse circular single stranded (ss) DNA viruses in the dormouse-associated virome.

Discussion

As part of this study, we conducted an extensive literature review, which shows that prior to 2010, the number of publications concerning pathogens of garden dormice was minimal, with even fewer addressing the bacteria, viruses and protozoa that are present in these animals. This low level of research interest in pathogens in garden dormice is in line with the overall decline in research and publications on garden dormice in general between 2000 and 2017 compared to the period 1950 to 1999, with an apparent increase only in 2017 (Lang et al. 2022). With regard to publications on pathogens in garden dormice, the annual publications increased since 2011. This may be because emerging zoonotic diseases have become a focal point in research, with

Table 4 Complete viral genomes recovered from garden dormouse kidney samples or sample pools. Summary of complete viral genomes identified using Cenote-Taker3 and screened with NCBI BLAST. Sequences were classified into viral families using top NCBI BLAST results, with percent identity and accession numbers shown. Genomes were considered complete based on full-length alignment to reference genomes and the presence of terminal repeats (DTRs)

GenBank accession	Length, nucleotides	Virus family	NCBI blast	Description	Query Cover	%Identity	Acc. Length	Accession
PV685787	1901	<i>Circoviridae</i>	blastn	MAG: ssDNA virus sp. isolate 164Circo-2, complete genome	64%	96.76%	1898	OM892393.1
PV685788	2146	<i>Genomoviridae</i>	blastn	MAG: <i>Genomoviridae</i> sp. isolate ctdb80, complete genome	52%	92.07%	2153	NC_076323.1
PV685792	2202	<i>Genomoviridae</i>	blastn	Chicken genomovirus mg4_1196, complete genome	100%	79.91%	2191	MN379606.1
PV685789	2158	<i>Genomoviridae</i>	blastn	MAG: <i>Genomoviridae</i> sp. isolate <i>Genomoviridae</i> Dogfe418C1 genomic sequence	97%	91.56%	2156	OQ198078.1
PV685791	2125	<i>Genomoviridae</i>	blastn	Sorex coronatus feces associated gemy-circularvirus 11, complete genome	98%	91.01%	2126	PQ576940.1
PV685794	2204	<i>Genomoviridae</i>	blastn	Red panda feces-associated gemycircularvirus isolate AliP03geno09-2015 genomic sequence	57%	91.18%	2205	MZ556140.1
PV685796	2034	N/A ¹	blastn	Dulem virus 22 isolate Duke43_SS_313, complete genome	91%	93.40%	2046	PP498712.1
PV685795	2254	<i>Genomoviridae</i>	blastn	MAG: <i>Genomoviridae</i> sp. isolate 6537_278, complete genome	47%	73.75%	2191	MT309841.1
PV685790	2881	<i>Circoviridae</i>	blastx	MAG: hypothetical protein [<i>Cirlovirales</i> sp.]	35%	57.18%	342	XOF03152.1
PV685797	2191	<i>Genomoviridae</i>	blastn	MAG: <i>Genomoviridae</i> sp. isolate 210Gen-2, complete genome	17%	77.25%	2196	OM892312.1
PV685793	2121	<i>Genomoviridae</i>	blastn	HCB19.212 virus complete sequence	99%	98.72%	2121	LK931484.1
PV685798	2748	N/A ¹	blastx	-	23%	56.94%	234	XOE94280.1

¹N/A not available, MAG Metagenome-Assembled Genome

rodents being identified as reservoirs of many zoonotic pathogens (Karesh et al. 2012; Wu et al. 2018). Additional drivers, such as climate change and its associated alteration of the distribution of arthropods and arthropod-borne pathogens may influence the presence of pathogens in rodents (Caminade et al. 2019). Another aspect that may explain the increase in research on pathogens in garden dormice is the development and improvement of diagnostic methods (Liu et al. 2023). A novel polyomavirus detected in garden dormice by Vasiliūnaitė et al. (2024) serves as a notable illustration. Another factor might be the establishment and involvement of the network “Rodent-borne pathogens” (Ulrich et al. 2025 in press).

The samples analysed in this study were collected as part of an extensive research project carried out in Germany over a period of six years (Büchner et al. 2024). A major focus of this project was to investigate the causes of the decline of the garden dormouse in Germany. It is likely that this extensive project has helped to bring the garden dormouse back into the focus of research, resulting in a significant increase in annual publications since 2021. Because some of these publications also come from other European countries, such as Spain (Azami-Conesa et al. 2023; Couso-Pérez et al. 2023), it may be assumed that such extensive research initiatives in one country have also led to an increase in research on the garden dormouse in other countries. Furthermore, species are brought to public interest and the attention of financial supporters only in cases where they are listed as endangered or where negative population trends are observed. This in turn leads to increased research and, consequently, more publications (Jarić et al. 2017; Davies et al. 2018).

While numerous studies on endoparasites were identified in the literature (Makarikov 2017; Mas-Coma et al. 1977a, (1977b), (1982); Miquel et al. 1996), they were excluded from this review due to our selection criteria. Since these, like ectoparasites, were neglected in our own investigations as well, this represents a major limitation in our study. Notably, cestodes of the family *Hymenolepididae* have been reported in garden dormice but appear to have no impact on garden dormouse health (Makarikov and Georgiev 2020).

Vector-borne pathogens

In the past, a number of studies have focused on vector-borne pathogens such as *Rickettsia prowazeki* (Perez Gallardo et al. 1951), *Coxiella burnetii* (Perez Gallardo et al. 1952) and *Borrelia* spp. (Matuschka et al. 1999; Richter et al. 2004, 2011) in garden dormice. Even in our own investigations, representatives of *Borrelia* spp. were detected. Although *B. afzelii* has been detected in a related host, the edible dormouse (Fietz et al. 2014), we mainly detected *B. spielmanii* with only one instance of *B. afzelii* in our

samples. This confirms the role of the garden dormouse as the main reservoir host of *B. spielmanii*, as persistent infectivity of *B. spielmanii* in garden dormice for ticks has been experimentally demonstrated (Richter et al. 2011) and observed in the field (Richter et al. 2004 and manuscript in preparation).

Non-vector-borne pathogens

Of particular zoonotic relevance, here, is the first detection of *L. borgpetersenii* (serogroup Sejroe, ST 197) in the garden dormouse. This species has previously been found in the yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Myodes glareolus*) (Fischer et al. 2018b). Both species are widespread in Europe and Germany and, like the garden dormouse, inhabit broadleaf and mixed forests, as well as structurally rich gardens and hedges. It is therefore possible that the *Leptospira* were acquired from an environment contaminated by these two rodent species. The transmission of pathogens from other rodents to garden dormice must always be considered. This is illustrated by outbreaks of *Yersinia pseudotuberculosis* infections, and associated deaths, in two enclosure populations of garden dormice in 1991 (Meinig unpublished data) and in 2023 (Pöhle and Ulber unpublished data). In both cases, it was subsequently shown that the bacterium had been introduced by house mice, leading to fatal diseases in the affected animals.

The absence of hantavirus detection in garden dormice, in contrast to findings in edible dormice (Stanojevic et al. 2015), may reflect several contributing factors. Firstly, hantaviruses show a high level of host specificity and spill-over infections are detected only very rarely (Schlegel et al. 2014), suggesting that the garden dormouse may not serve as a natural reservoir in the way the edible dormouse does (Plyusnin et al. 2014). Additionally, the transmission and maintenance of a hantavirus within rodent host populations require a minimum host density, which may not be present for the garden dormouse, and certain demographic structures; below these thresholds, viral persistence may fail (Tian et al. 2019).

Like the edible dormouse (Ehlers et al. 2019), the garden dormouse has been shown to harbour an associated polyomavirus (Vasiliūnaitė et al. 2024), however respective viruses belong to different genera of the family *Polyomaviridae*. Both garden dormice in which the polyomavirus was detected showed signs of hepatic changes and a whitish substance was identified in the abdominal cavity of one of the two animals. In this animal, an infectious disease had been suspected as the cause of death (Vasiliūnaitė et al. 2024). However, none of the other tested pathogens were detected in these animals. Antibodies against the new polyomavirus were not detected in either of the two animals,

whereas antibodies were found in samples of 12 other garden dormice (Vasiliūnaitė et al. 2024). Although viral DNA and antibodies were detected in different individuals, phylogenetic analysis supports garden dormice as the natural host rather than incidental environmental exposure. The absence of antibodies in DNA-positive animals may reflect an acute infection prior to seroconversion or possible persistence in renal tissue, although the kidney has not yet been confirmed as a reservoir for this virus (Vasiliūnaitė et al. 2024).

Rodent-specific and wildlife-relevant pathogens

Staphylococcus aureus was detected at a high prevalence (29%) in the garden dormouse samples. *Staphylococcus aureus* is an opportunistic pathogen in many small mammals, including mice, shrews, voles, rats and squirrels (Mrochen et al. 2018; Raafat et al. 2020; Yebra et al. 2024). The predominant *S. aureus* lineages that we detected in the garden dormice are also common in other wild small mammals. For instance, CC121/CC1956 is common in mice, shrews and voles (Mrochen et al. 2018), and CC49 is the dominant lineage in wild small rodents (voles and mice), but rare in humans. CC188 is common in laboratory rats and other rodents, but rare in humans. This suggests that certain rodent-adapted *S. aureus* lineages are circulating among different small mammal species, with some overlap between the species. The absence of typical human or livestock CCs, such as CC398-MRSA, in this wild rodent *S. aureus* population, as well as the lack of antibiotic resistances, suggest limited interaction of the garden dormouse population with the human or livestock *S. aureus* population. The lack of typical signs of *S. aureus* infections (i.e. purulent skin infections, abscesses) in the analysed garden dormice, and the high genetic diversity of the *S. aureus* isolates, suggest a commensal relationship rather than active infection, unlike in British red squirrels (Simpson et al. 2013).

Metagenomic sequencing

MetPhlAn analysis revealed a variety of bacterial pathogens. Some of the pathogens were reported in previous studies, such as *Enterococcus faecium* and *E. faecalis*, in garden dormouse feces (Silva et al. 2012), however, to our knowledge, the majority were identified here for the first time. Several of these species, like *Chlamydia psittaci*, *Pasteurella multocida* and *E. hormaechei*, are recognized zoonotic pathogens, and their detection in dormouse kidneys, a normally sterile site, could be relevant. The presence of *P. multocida* may also be attributable to contact with domestic cats, as some of the garden dormice were bitten or even predated on by domestic cats (Famira-Parcsetich et al. 2024). Furthermore, *E. hormaechei* was detected in

garden dormouse feces datasets and in 5 out of 10 kidney sequencing libraries with relatively high abundance. Others (e.g., *C. acnes*, *Mammaliicoccus sciuri*) may represent low-virulence commensals or environmental contaminants. It should be noted that the publicly available SRA datasets and our kidney-derived libraries were generated using different protocols, enrichment strategies, and sequencing approaches (metagenomic, genomic, and transcriptomic), reflecting differing study aims. Therefore, these results are exploratory and require confirmation in dedicated follow-up studies.

Metagenomic sequencing revealed viruses from multiple DNA-virus families, including *Parvoviridae*, *Adenoviridae*, *Circoviridae*, *Polyomaviridae*, *Anelloviridae*, and *Genomoviridae*. With the exception of *Polyomaviridae*, previously reported in garden dormice (Vasiliūnaitė et al. 2024), representatives of all other virus families are reported here in garden dormice for the first time. The majority of viral sequences from this study, particularly those from small circular DNA viruses, were highly divergent from previously published sequences and likely represent novel rodent-associated lineages. Notably, all 12 complete circular genomes assembled here were derived from our kidney libraries that were enriched for circular molecules (both pooled and individual samples); none of the publicly available SRA datasets used such enrichment, which likely explains why substantially more circular DNA viruses were recovered in our dataset. Parvovirus sequences were found in five of ten kidney libraries and several SRA datasets; the longest fragment (3056 nt) closely matched a rat-associated parvovirus (98.57% identity), while others were more divergent, suggesting multiple parvovirus lineages. Because many viral detections originate from pooled samples and sequencing strategies varied widely between datasets, abundance signals are exploratory and cannot confirm systemic infection or individual prevalence. Nonetheless, the consistent detection of diverse circular DNA viruses sequences in kidney tissue raises the possibility of active or persistent infections in dormice, warranting targeted follow-up studies to clarify host range and pathogenic potential.

Zoonotic risk and decline of the garden dormouse

The garden dormouse often inhabits areas in close proximity to human settlements, which could facilitate contact between wildlife, humans, and ectoparasites. According to our findings, to date, the results indicate that – apart from *B. spielmanii* and *B. afzelii* – zoonotic pathogens can only be detected in garden dormice in rare cases. Nevertheless, their frequent association with tick populations, capable of feeding on both garden dormice and humans, underscores a potential indirect public health risk, as infected ticks may be

transmitted between wildlife reservoirs and people. Monitoring tick-borne pathogens in these habitats remains important to assess and manage local zoonotic risk. Furthermore, the samples examined exhibited a limited presence of pathogens. This finding suggests that infectious diseases may not be the primary factor contributing to the observed decline in the population of garden dormice under the prevailing conditions. In case that a single pathogen is responsible for the observed decline, a higher detection rate than observed in this study should be assumed.

Limitations

Due to the suboptimal quality of the samples, as the animals examined were already undergoing auto- and heterolysis and had been deep-frozen prior to the examination, which made it difficult to detect minor pathological abnormalities or to carry out histopathological examinations, it was not possible to carry out targeted tests for specific pathogens. Given that all garden dormice were found to be deceased, and the majority of these died as a result of predation, it is likely that deaths due to pathogens are underrepresented, and there is also a bias in the detected prevalences. The presence of negative results and low prevalences necessitates careful interpretation, as the sample sizes were too small in some cases to draw reliable conclusions. Furthermore, due to constrained financial resources and laboratory capacity, pathogens such as fungi or helminths, which could also contribute to the decline of the garden dormouse, were not investigated.

Conclusion

Our investigations suggest that, with exception of *B. spielmanni*, *B. afzelii* and *L. borgpetersenii*, no other pathogens with zoonotic potential were present to any significant extent in the garden dormice investigated from Germany. A more thorough analysis, incorporating NGS of RNA viruses, should be done since there might be even more unknown pathogens infecting garden dormice that were missed so far. The novel polyomavirus, that was detected in a previous study, is a good example. Moreover, further investigation into the viruses detected is recommended, as they may potentially be a contributing factor to the observed decline. The literature review revealed that the garden dormouse, and the pathogens affecting this species, have been understudied in the past. Although this study provides valuable data on infectious agents, pathogens alone are unlikely to explain the decline of *E. quercinus*. However, the increasing number of studies on this topic in

recent years has created a growing body of research that may help identify the causes of the garden dormouse's decline or, as in the case of pathogens, rule them out as possible factors. Future research should therefore integrate ecological, environmental, and anthropogenic factors to better understand its population dynamics and conservation needs.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10344-025-02008-0>.

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Author contributions S.P.S wrote the main manuscript and did the literature review. E.M.K. dissected a major part of the animals, sent the organs for examination and collated the results. C.J. dissected some of the animals and organised the first examinations. C.M., R.R., E.H., D.R., D.H., E.V., C.B.B., I.K.-K., A.G., P.K., V.C.H., V.S., S.H., C.K., T.E., M-C.A., S.D., K.J., C.R., H.M., A.O., M.P., D.R., D.P., C.U., C.S. worked in the different laboratories and analysed the samples for the various pathogens. S.B., R.G.U., M.L. and J.L. supervised the study.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval All samples were sourced from deceased animals that were collected as part of the project "In search of the Garden Dormouse". It was not an animal experiment.

Competing interests J.L. and S.B. are editors of the special collection to which this manuscript is submitted. The other authors have no competing interests to declare that are relevant to the content of this article.

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