

Range of *Ixodes laguri*, a nidicolous tick that parasitizes critically endangered rodents, with details on its western distribution limit in Austria

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Abstract

The nidicolous tick *Ixodes laguri* is a nest-dwelling parasite of small mammals that mainly infest rodents of the families Cricetidae, Gliridae, Muridae and Sciuridae. There is no proven vectorial role for *I. laguri*, although it is suggested that it is a vector of *Francisella tularensis*. In this study, a first map depicting the entire geographical distribution of *I. laguri* based on georeferenced locations is presented. For this purpose, a digital data set of 141 georeferenced locations from 16 countries was compiled. Particular attention is paid to the description of the westernmost record of *I. laguri* in the city of Vienna, Austria. There, *I. laguri* is specifically associated with its main hosts, the critically endangered European hamster (*Cricetus cricetus*) and the European ground squirrel (*Spermophilus citellus*). These two host species have also been mapped in the present paper to estimate the potential distribution of *I. laguri* in the Vienna metropolitan region. The range of *I. laguri* extends between 16–108° E and 38–54° N, i.e. from Vienna in the east of Austria to Ulaanbaatar, the capital of Mongolia. In contrast to tick species that are expanding their range and are also becoming more abundant as a result of global warming, *I. laguri* has become increasingly rare throughout its range. However, *I. laguri* is not threatened by climate change, but by anthropogenic influences on its hosts and their habitats, which are typically open grasslands and steppes. Rural habitats are threatened by the intensification of agriculture and semi-urban habitats are increasingly being destroyed by urban development.

Keywords: Ixodid tick, Species distribution, Ground squirrel, Hamster

1 Introduction

2 The geographical distribution of the nidicolous tick *Ixodes laguri* Olenev,
3 1929 is only partially known. So far, two maps have been published showing
4 georeferenced locations of *I. laguri*. The first map by Feider (1965) shows
5 13 locations between Hungary in the west and Kazakhstan, the region north
6 of the Aral Sea, in the east. The second, more up-to-date map by Mihalca
7 and D'Amico (2017) shows three times as many locations, but goes only
8 as far as to Ukraine and Turkey in the east. A further map, published
9 online by Kolonin (2009), did not contain any georeferenced tick locations
10 but estimated the range of *I. laguri* as described by Siuda and Sebesta (1997).
11 Unfortunately, this map is no longer online and was not available for this work
12 either. Reference is therefore made to the earlier map by Kolonin (1981). In
13 summary, there is no map that covers the entire known distribution area of *I.*
14 *laguri* based on georeferenced findings. However, there is a current list on the
15 geographic distribution of *I. laguri* by countries and territories (Guglielmone
16 et al., 2023).

17 *Ixodes laguri* is a nest-dwelling parasite of small mammals that mainly
18 infests rodents of the families Cricetidae, Gliridae, Muridae and Sciuridae.
19 The most comprehensive list of all host animals on which *I. laguri* has been
20 found was compiled by Anastos (1957). Cases of people being attacked by
21 immature stages have been reported by Filippova (1977), and female adult
22 *I. laguri* found on humans have been reported from Turkey (Bursali et al.,
23 2011; Keskin et al., 2015). It is assumed that there is no difference in the host
24 preferences of immatures and adults, with the exception that adult males are
25 not parasitic (Siuda and Sebesta, 1997). As a very host-specific tick, *I. laguri*
26 is only found in the habitats of its hosts as mentioned above. In Central Eu-
27 rope, the main hosts are European hamster (*Cricetus cricetus*) and European
28 ground squirrel (*Spermophilus citellus*), which inhabit cultivated lands such
29 as fallows, grasslands, vineyards, but also golf courses and airfields (Rubel,
30 2024). Further east, *I. laguri* also inhabits steppe, less often semisteppe and
31 semidesert habitats. In Trans-Caucasia, i.e. Armenia, Georgia, and Azer-
32 baijan, the tick inhabits mountain steppes up to altitudes of 1500 m, where
33 Kirschenblatt (1936) found it on gerbils (*Meriones tristrami*), steppe lem-
34 mings (*Lagurus lagurus*), hamsters (*C. cricetus*, *Mesocricetus brandti*) and
35 ground squirrels (*Spermophilus pygmaeus*).

36 The three-host tick *I. laguri* is nidicolous (Gray et al., 2014), although it
37 has occasionally been found questing in very close proximity to the burrows

38 of its hosts (Mihalca and D'Amico, 2017). Usually only a few tick specimens
39 were found in individual nests. A maximum of 28 larvae and 100 nymphs was
40 collected from one nest of the European ground squirrel by Černý (1990).
41 In the 1970s, Honzáková et al. (1980) investigated the development of *I.*
42 *laguri* in the nests of the European ground squirrel. For this purpose, ticks
43 were taken from the nests of wild ground squirrels in Slovakia and kept
44 in a field experiment as well as under controlled laboratory conditions. The
45 measurements of the microclimate in ground squirrel nests previously carried
46 out in the field showed an average temperature of 15–17° C. In a burrow
47 depth of 2 m, these temperatures occur in June–October. Additionally, a
48 high relative humidity of 90% was measured. The application of these rather
49 constant conditions in the laboratory experiments, together with the field
50 experiments, led to the determination of the natural life cycle of *I. laguri*
51 of 2–3 years. Life cycles significantly less than one year, as determined by
52 Russian authors (Anastos, 1957), are not possible in Central Europe and
53 the Balkans. Honzáková et al. (1980) describes the following life cycle in
54 Slovakia: Females moult in mid-summer, feed in April of the following year
55 and oviposit in May. Larvae hatch and feed in August. Nymphs moult in
56 November, hibernate in a hungry state and feed in April. Adults moult in
57 July. This is in accordance with observations in Romania, where the highest
58 female activity has been reported in spring and larvae were found in summer.
59 Peaks in nymphal *I. laguri* activity have been reported in spring and autumn
60 (Feider, 1965).

61 Adequate illustrations and morphological characteristics of *I. laguri* can
62 be found in Feider (1965) and Mihalca and D'Amico (2017), although the
63 four subspecies introduced in the historical literature (Anastos, 1957) are not
64 discussed. Biometric measures of morphological features compared to *Ixodes*
65 *ricinus*, *Ixodes persulcatus* and *Ixodes acuminatus* (syn. *I. redikorzevi*) have
66 been investigated by Voltzit and Pavlinov (1996). Haller's organ of *I. laguri*
67 was also examined using scanning electron microscopy (Honzáková et al.,
68 1975; Suppan, 2013). The 16S rDNA (Orkun, 2018), COX1 (Radulović et al.,
69 2017; Numan et al., 2023), and ITS2 (Radulović et al., 2017) phylogenetics
70 indicate that *I. laguri* is a member of the *I. ricinus* complex.

71 The only evidence of pathogens occurring in *I. laguri* dates back to work
72 in the former Soviet Union in the 1950s. Accordingly, the causative agent
73 of tularaemia, *Francisella tularensis*, was detected in *I. laguri* in Volgograd
74 Oblast and infection with rickettsia was also reported (Zhmaeva and Kor-
75 shunova, 1953; Philip and Burgdorfer, 1961; Pollitzer, 1963). Based on this

76 and the fact that *I. laguri* has often been found in tularaemia endemic areas
77 (Bozhenko and Shevchenko, 1956), the tick has repeatedly been referred to
78 as a vector of *F. tularensis* (Kiefer et al., 2010; Musaev et al., 2019; Zabashta
79 et al., 2022). However, without proven capability of transmission, the vector
80 function of a given tick species for a given pathogen is not substantiated
81 (Kahl et al., 2002). Since there are no transmission experiments known with
82 *I. laguri* for any pathogen, no vector function has been proven.

83 2. Materials and Methods

84 To determine the range of *I. laguri* in Eurasia, the literature list of re-
85 views on the geographical distribution of *I. laguri* (Siuda and Sebesta, 1997;
86 Guglielmone et al., 2023) was used and supplemented by further literature
87 covering the western distribution area. Since the publications on documented
88 localities of *I. laguri* in its eastern distribution area are not listed in PubMed
89 or Scopus, an extensive Google and Cyber Leninka search was carried out
90 in Russian and Ukrainian language. In addition, the translated summary
91 of the United States Department of Agriculture (USDA) was used, in which
92 historical *I. laguri* locations from Azerbaijan, Bulgaria, Georgia and Russia
93 were documented (Doss et al., 1978). According to Table 1 the following
94 numbers of *I. laguri* locations were incorporated: 4 in Armenia, 1 in Austria,
95 4 in Azerbaijan, 5 in Bulgaria, 4 in Georgia, 3 in Hungary, 15 in Kazakhstan,
96 2 in Moldova, 2 in Mongolia, 7 in Romania, 36 in Russia, 11 in Serbia, 18 in
97 Slovakia, 14 in Turkey, 1 in Turkmenistan, and 14 in Ukraine.

98 Almost all tick findings were digitized based on text information on the
99 locations or printed maps. These digitized locations, of course, are generally
100 of lower accuracy than locations described by geographical coordinates de-
101 termined by GPS in the field. To provide evidence of this, accuracy measures
102 were given for all data referenced in Table 1 in accordance with a scheme es-
103 tablished in previous studies (Rubel and Brugger, 2022). It is distinguished
104 between high (h $\approx \pm 0.1$ km), medium (m $\approx \pm 1$ km), low (l $\approx \pm 10$ km)
105 and very low (v) accuracies. The latter has been applied here for the first
106 time, and identifies all reports that relate only to political districts, moun-
107 tain ranges or river sections. Such information is obligatory in Russian and
108 Ukrainian literature and was used in the absence of more precise location
109 information.

110 Despite including all available information, the number of georeferenced
111 locations of *I. laguri* is one order of magnitude lower than that of comparable

112 tick species such as *Ixodes trianguliceps* (Rubel and Kahl, 2023). This is also
113 because *I. laguri* is associated to specific hosts, some of which are now threat-
114 ened with extinction. The distribution of the hosts is therefore of particular
115 importance, as it can indirectly be used to determine the distribution of *I.*
116 *laguri*. The main host species were determined using an abundance count.
117 For the metropolitan area of Vienna, the distribution map of main hosts, i.e.
118 European hamsters and European ground squirrels, from Rubel (2024) was
119 adapted to depict the exact locality of *I. laguri*. For this purpose and to
120 visualize the global distribution of *I. laguri*, the georeferenced locations were
121 plotted on terrain maps (OpenStreetMap contributors, 2017).

122 3. Results and Discussion

123 The main result of the present study is a map of the entire distribution
124 areas of the tick *I. laguri* with the total number of 141 georeferenced lo-
125 cations for the period 1957–2022 (Fig. 1). The westernmost location was
126 documented in the city of Vienna, Austria, at about 16° E (Fig. 2), and
127 is confirmed by a location in Dvorniky, Slovakia, 100 km further to the east
128 (Černý, 1990). The eastern distribution limit, however, is considered less cer-
129 tain. It may be at 82° E, where several authors have documented locations
130 on both sides of the Russia-Kazakhstan border (Amirova et al., 1989; Obert
131 et al., 2015; Grigor’evich, 2016). However, two locations were also reported
132 near the Mongolian capital Ulaanbaatar, which is 1900 km further east. The
133 first record of *I. laguri* in Mongolia dates back to 1974 (Dash, 1986), after
134 which the tick was found on the Mongolian gerbil (*Meriones unguiculatus*)
135 10 km southeast of Ulaanbaatar. In 2006, the same German-Mongolian con-
136 sortium documented the tick northwest of Ulaanbaatar, also on Mongolian
137 gerbils (Kiefer et al., 2010). These findings are considered realistic because
138 the type of habitat and the host species are similar to those in the western
139 distribution area, and Josef Nosek, a recognized expert in the morphology
140 of ticks from the Slovak Academy of Science (Nosek and Sixl, 1972), was
141 involved in the first description of this tick species in Mongolia. However,
142 to date, confirmation of the occurrence of *I. laguri* in Mongolia by other
143 independent scientists is still pending. The eastern distribution limit was
144 therefore provisionally set at 108° E. The north-south extension is largest in
145 the Asian part of the range and extends from the steppe of Turkmenistan at
146 about 38° N (Berdyev and Annayev, 1997) to Western Siberia, Russia, at
147 about 54° N (Grigor’evich, 2016). Note that only a single record of *I. laguri*

148 has been found in Turkmenistan, so this southernmost record also awaits
149 confirmation. It is also worth mentioning that in Central Europe *I. laguri*
150 generally only occurs south of 49° N. The distribution area therefore extends
151 between 16–108° E and 38–54° N, i.e. from Vienna in the east of Austria to
152 Ulaanbaatar, the capital of Mongolia.

153 A frequency distribution of *I. laguri* hosts is shown in Fig. 3. If one takes
154 into account only those studies from which georeferenced locations could
155 be generated (Table 1), then most of the studies report the tick *I. laguri*
156 on hamsters (*C. cricetus*, *Nothocricetulus migratorius*, *Mesocricetus auratus*,
157 *Mesocricetus newtoni*, *Mesocricetus raddei*, *M. brandti*) and ground squir-
158 rels (*S. citellus*, *S. pygmaeus*). Other hosts, summarized in the frequency
159 distribution in Fig. 3, are voles (*Arvicola terrestris*, *Myodes rutilus*, *Myo-*
160 *des glareolus*, *Microtus subterraneus*), mice (*Mus musculus*, *Apodemus agrar-*
161 *ius*, *Apodemus sylvaticus*), gerbils (*M. unguiculatus*, *M. tristrami*), hedgehogs
162 (*Erinaceus concolor*), rats (*Rattus norvegicus*, *Hemiechinus auritus*), moles
163 (*Talpa altaica*), blind mole-rats (*Spallax* sp.), shrews (*Crocidura* sp.), mar-
164 mots (*Marmota sibirica*), and lemmings (*L. lagurus*). In addition, the tick
165 was found in Ukraine on predators such as the steppe polecat (*Mustela ev-*
166 *ersmanii*) and the red fox (*Vulpes vulpes*) (Sklyar, 2002).

167 Although the occurrence of *I. laguri* in Austria was already mentioned
168 by Radda et al. (1986), there is currently no description of a location in
169 the international literature, which is now being done here. Fig. 2 depicts a
170 recent location of *I. laguri* in the city of Vienna, Austria. These specimens of
171 *I. laguri* were collected from European hamsters, which were caught with live
172 traps on the grounds of the clinic Favoriten at the geographical coordinate
173 16.3442° E/48.1739° N (Siutz and Millesi, 2012). In this study from 2005,
174 reproductive timing in female hamsters, which affects offspring development
175 and survival, was investigated. Therefore, the study by Siutz and Millesi
176 (2012) does not contain any information about collected ticks, although these
177 were mentioned in the master thesis of Suppan (2013). The latter examined
178 the structure of dermal glands associated with spiracles using a scanning
179 electron microscope, primarily of *I. ricinus* but also of *I. laguri*. Since there
180 are no further data on the occurrence of *I. laguri* in Vienna, this location was
181 overlaid on a map of the most important hosts, the European hamster (*C.*
182 *cricetus*) and the European ground squirrel (*S. citellus*), which was adapted
183 from Rubel (2024). From this map, at least the possible range of *I. laguri*
184 in Vienna can be estimated, because ticks specifically associated with their
185 hosts are co-distributed with them (Mihalca et al., 2012). For example, the

186 distribution area of *I. laguri* from eastern Austria and Slovakia across the
187 Balkans to the Black Sea (Fig. 1) corresponds almost exactly to the global
188 distribution of *S. citellus* (Ramos-Lara et al., 2014).

189 In the metropolitan area of Vienna, which includes the outskirts of the
190 city (Fig. 2), the population of hamsters can be estimated at 4,000 and that of
191 ground squirrels at 16,000 individuals (Rubel, 2024). Thus, the total number
192 of these main hosts of *I. laguri* in the metropolitan area of Vienna is about
193 20,000 individuals. The systematic examination of European ground squirrels
194 for parasitic ticks in Serbia, 500 km away, indicates that *I. laguri* may not be
195 a rare tick species in Vienna. Radulović et al. (2017) found more than 1,000
196 ticks on 151 infested ground squirrels in this study, with 79% identified as *I.*
197 *laguri* and 21% as *Haemaphysalis concinna*. Ixodid ticks of the genera *Ixodes*
198 and *Haemaphysalis* were also found on European hamsters in Turkey (Uslu
199 et al., 2008), where *I. laguri* in rare cases also infests humans (Keskin et al.,
200 2007, 2015). In the Caucasus, Filippova and Stekolnikov (2007) found larvae
201 of *I. laguri* together with larvae of *I. ricinus* and *D. reticulatus*. *Ixodes laguri*
202 (Suppan, 2013) as well as *I. ricinus* and *D. reticulatus* (Vogelgesang et al.,
203 2020; Rubel and Brugger, 2022) also occur sympatrically in Vienna. That
204 there is only one documented location of *I. laguri* in Vienna up to now is
205 probably due to the fact that no studies concerning ticks on small mammals
206 were carried out for a long time. Since 2019, *C. cricetus* and *S. citellus* are
207 listed on *The IUCN Red List of Threatened Species* as critically endangered
208 (Banaszek et al., 2020; Hegyeli, 2020). Investigations of *I. laguri* in the nests
209 of *S. citellus*, like those from the field expeditions 1959–1976 (Černý, 1990),
210 are therefore hardly possible anymore in the European Union.

211 Further, a sharp decline in the main host populations of *I. laguri* has
212 been observed over the last few decades. For example, the global *C. cricetus*
213 population has declined by 75% (Surov et al., 2016). Something similar
214 has been reported for the Ciscaucasian or Georgian hamster (*M. raddei*),
215 whose population has also declined massively. Responsible for this were
216 the widespread ploughing of virgin and fallow lands, which began in the
217 middle of the last century, and the reduction of natural pasture areas. As
218 a consequence, this also led to a decrease of *I. laguri*, the suspected main
219 vector of the causative agent of tularaemia in that region (Zabashita et al.,
220 2022). There is strong evidence that *I. laguri* is one of those tick species that
221 are becoming rarer along with their hosts.

222 In summary, the 141 georeferenced *I. laguri* locations come from the fol-
223 lowing 16 countries: Armenia, Austria, Azerbaijan, Bulgaria, Georgia, Hun-

224 gary, Kazakhstan, Moldova, Mongolia, Romania, Russia, Serbia, Slovakia,
225 Turkey, Turkmenistan, and Ukraine. For comparison, Guglielmone et al.
226 (2023) listed 15 countries. Their list also includes the Czech Republic, for
227 which no data is available since all of locations described in former Czechoslo-
228 vakia (Černý, 1990) are in today's Slovakia. Conversely, the locations in Ser-
229 bia (Radulović et al., 2017) and the location in Austria described here are
230 missing from the list of countries by Guglielmone et al. (2023). The latter
231 was missing because there was no reference in the international literature to
232 date. In the book chapter on the distribution of *I. laguri* by Mihalca and
233 D'Amico (2017), the occurrence in Serbia (Radulović et al., 2017) could not
234 be taken into account because it was published at the same time. In addi-
235 tion, the occurrence of *I. laguri* in Belarus and the Baltic countries Estonia,
236 Latvia and Lithuania mentioned in the text might be an error because these
237 countries are too far north and no locations are depicted even in the map of
238 Mihalca and D'Amico (2017). This mismatch has already been considered
239 by Guglielmone et al. (2023). The Republic of Dagestan should also not be
240 listed as a separate country because it has been part of Russia since 1991. No
241 data could be found for Uzbekistan either, which is why the work of Mihalca
242 and D'Amico (2017) should be revised before it is used as a reference for the
243 distribution of *I. laguri*. In contrast, the distribution of *I. laguri* described
244 in the review by Siuda and Sebesta (1997) largely agrees with the collection
245 of georeferenced locations presented here. Accordingly, the distribution area
246 west of the Caspian Sea is divided into a wider northern and a narrower
247 southern part. The northern part extends from the southern Lower Volga
248 areas via Kazakhstan into Mongolia, while the southern part extends through
249 the Caucasus and Trans-Caucasia to western Turkmenistan.

250 4. Conclusions

251 Based on georeferenced locations, the first map of *I. laguri* covering the
252 entire distribution area was compiled. For this purpose, the westernmost lo-
253 cation of *I. laguri* in the city of Vienna was mapped along with its main hosts,
254 hamsters and ground squirrels. The findings at the eastern distribution limit
255 in Ulaanbaatar, Mongolia, were also critically discussed. In addition, a list of
256 16 countries where the tick has been reported was compiled. However, it must
257 be noted that knowledge about the range, biology and vector competence of
258 *I. laguri* is limited, especially in comparison to other much more prominent
259 tick species of the *I. ricinus* complex (Kahl and Gray, 2023). Since *I. laguri*

260 can only be found on its often highly endangered hosts and in their nests,
261 it can be assumed that this will remain the case in the future. In contrast
262 to tick species that are expanding their range and are also becoming more
263 abundant as a result of global warming, such as *I. ricinus* (Jaenson et al.,
264 2012; Nuttall, 2021) and *D. reticulatus* (Mierzejewska et al., 2015; Brugger
265 and Rubel, 2023), *I. laguri* is becoming increasingly rare. *Ixodes laguri*, a ni-
266 dicolous tick of grasslands and steppes, is not threatened by climate change,
267 but by anthropogenic influences on its hosts and their habitat. Rural habitats
268 are threatened by the intensification of agriculture and semi-urban habitats
269 are increasingly being destroyed by urban development (Rubel, 2024).

270 References

- 271 Akimov, I.A., Nebogatkin, I.V., 2016. Ticks in urban landscapes of Kyiv
272 (in Russian). National Academy of Sciences of Ukraine, Schmalhausen
273 Institute of Zoology, 156pp.
- 274 Amirova, N.A., Pakizh, V.I., Chepeljuk, M.A., Suprun, V.G., Sergeeva, N.I.,
275 Tilik, A.N., 1989. Ixodid ticks from the Pavlodar district and their partic-
276 ipation in the tularemia infection circulation (in Russian). *Parazitologiya*
277 23, 267–274.
- 278 Anastos, G., 1957. The Ticks, or Ixodides, of the U.S.S.R.: A Review of the
279 Literature. U.S. Dept. of Health, Education, and Welfare.
- 280 Arnaudov, A., Georgiev, D., 2022. Ixodid ticks in Sarnena Sredna Gora–
281 published data and new records, in: Georgiev, D., Bechev, D., Yancheva,
282 V. (Eds.), *Fauna of Sarnena Sredna Gora Mts.*, part 3, suppl. 11. *Zoo*
283 *Notes*, pp. 46–52.
- 284 Arthur, D.R., 1957. Studies on exotic *Ixodes* ticks (Ixodoidea, Ixodidae)
285 from United States navy and army activities. *J. Parasitol* 43, 681–694.
286 <https://doi.org/10.2307/3286566>.
- 287 Banaszek, A., Bogomolov, P., Feoktistova, N., La Haye, M.,
288 Monecke, S., Reiners, T.E., Rusin, M., Surov, A., Wein-
289 hold, U., Ziomek, J., 2020. *Cricetus cricetus*. The IUCN
290 Red List of Threatened Species 2020: e.T5529A111875852.
291 <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5529A111875852.en>
292 (accessed, 2 Nov. 2023).

- 293 Berdyyev, A., Annayev, Y., 1997. A fauna of ixodid ticks from the Kopetdagh
294 in relation to the compilation of their check-list (in Russian). *Parazi-*
295 *tologiya* 31, 104–115.
- 296 Bozhenko, V.P., Shevchenko, S.F., 1956. To the ecology of the tick *Ixodes*
297 *laguri laguri* Ol. in connection with its significance in the maintenance of
298 some natural foci of tularemia (in Russian). *Zool. Zhurnal.* 35, 837–842.
- 299 Brugger, K., Rubel, F., 2023. Tick maps on the virtual globe: First results
300 using the example of *Dermacentor reticulatus*. *Ticks Tick Borne Dis.* 14,
301 102102. <https://doi.org/10.1016/j.ttbdis.2022.102102>.
- 302 Bursali, A., Keskin, A., Simsek, E., Keskin, A., Tekin, S.,
303 2015. A survey of ticks (Acari: Ixodida) infesting some wild
304 animals from Sivas, Turkey. *Exp. Appl. Acarol.* 66, 293–299.
305 <https://doi.org/10.1007/s10493-015-9898-z>.
- 306 Bursali, A., Tekin, S., Keskin, A., Ekici, M., Dundar, E., 2011. Species
307 diversity of ixodid ticks feeding on humans in Amasya, Turkey: Seasonal
308 abundance and presence of Crimean-Congo hemorrhagic fever virus. *J.*
309 *Med. Entomol.* 48, 85–93. <https://doi.org/10.1603/me100342>.
- 310 Černý, V., 1990. Occurrence of the tick *Ixodes laguri* Ol. on the territory of
311 Czechoslovakia. *Folia Parasitol.* 37, 92–92.
- 312 Dash, M., 1986. Ixodid ticks and their control in the Mongolian People's
313 Republic (in Russian). Doctoral thesis, Humbolt Univ. Berlin, 239pp.
- 314 Dilbaryan, K.P., Hovhannisyan, V.S., 2016. Arthropods (Arthro-
315 poda) of Armenia of medical importance, their biological and eco-
316 logical peculiarities (in Russian). *Med. Sci. Armenia* 56, 81–89.
317 <https://doi.org/10.54503/0514-7484>.
- 318 Doss, M.A., Farr, M.M., Roach, K.F., Anastos, G., 1978. Index-Catalogue
319 of Medical and Veterinary Zoology. Ticks and Tickborne Diseases IV. Ge-
320 ographical distribution of ticks. US Department of Agriculture (USDA),
321 available as Google Book.
- 322 Evstafiev, I.L., 2017. Results of a 30-years-long investigation of small mam-
323 mals in Crimea. Part 3. Parasites and epizootiology (in Russian). *Proc.*
324 *Theriological School* 15, 111–135.

- 325 Feider, Z., 1965. Fauna Republicii Populare Romne Arachnida Acaromor-
326 pha Suprafamilia Ixodoidea (Cüpuşe) (in Romanian). Editura Academiei
327 Republicii Populare Romne, Bucarest, 5(2), 401pp.
- 328 Filippova, N.A., 1977. Ixodid ticks (Ixodinae) (in Russian). In: Fauna USSR
329 New Series, 4(4), Nauka, Moscow, Leningrad, 396pp.
- 330 Filippova, N.A., 2008. Type specimens of argasid and ixodid ticks (Ixodoidea:
331 Argasidae, Ixodidae) in the collection of the Zoological Institute, Rus-
332 sian Academy of Sciences (St. Petersburg). Entomol. Rev. 88, 1002–1011.
333 <https://doi.org/10.1134/S0013873808080149>.
- 334 Filippova, N.A., Stekolnikov, A.A., 2007. Materials on the preimaginal stages
335 of the ticks collected from small mammals in western and northern Cau-
336 casus (Acari: Ixodidae). Parazitologiya 41, 3–22.
- 337 Gray, J.S., Estrada-Peña, A., Vial, L., 2014. Ecology of nidicolous ticks,
338 in: Sonenshine, D.E., Roe, R.M. (Eds.), Biology of Ticks. Vol. 2/2. Univ.
339 Press, Oxford, UK, pp. 39–60.
- 340 Grigor'evich, F.V., 2016. Some information about mites of the Ixodoidea
341 superfamily sporadically met within the territory of western Siberia (in
342 Russian). Almanac Modern Science and Education 109, 114–117.
- 343 Guglielmone, A.A., Nava, S., Robbins, R.G., 2023. Geographic
344 distribution of the hard ticks (Acari: Ixodida: Ixodidae) of
345 the world by countries and territories. Zootaxa 5251(1), 1–274.
346 <https://doi.org/10.11646/zootaxa.5251.1.1>.
- 347 Guven, E., Akyuz, M., Kirman, R., Balkaya, I., Avcioglu, H.,
348 2022. Zoonotic *Babesia microti* infection in wild rodents in Erzu-
349 rum province, northeastern Turkey. Zoon. Publ. Health 9, 875–883.
350 <https://doi.org/10.1111/zph.12983>.
- 351 Hegyeli, Z., 2020. *Spermophilus citellus*. The IUCN Red
352 List of Threatened Species 2020, e.T20472A91282380.
353 <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T20472A91282380.en>
354 (accessed, 2 Nov. 2023).

- 355 Honzáková, E., Cerný, V., Daniel, M., Dusbábek, F., 1980. Development
356 of the tick *Ixodes laguri* Ol. in the nests of the European suslik *Citellus*
357 *citellus* (L.). Folia Parasitol. 27, 71–75.
- 358 Honzáková, E., Sixl, W., Waltinger, H., 1975. Scanning electron microscopy
359 of the ticks *Ixodes laguri* and *Ixodes arboricola*: surface structures of
360 Haller's organ. Folia Parasitol. 22, 241–243.
- 361 Hubálek, Z., 2009. Biogeography of tick-borne Bhanja virus (Bunyaviridae)
362 in Europe. Int. Persp. Inf. Dis. 2009, 372691. [https://doi.org/DOI:](https://doi.org/DOI:10.1155/2009/372691)
363 [10.1155/2009/372691](https://doi.org/10.1155/2009/372691).
- 364 Jaenson, T.G.T., Jaenson, D.G.E., Eisen, L., Petersson, E., Lindgren, E.,
365 2012. Changes in the geographical distribution and abundance of the tick
366 *Ixodes ricinus* during the past 30 years in Sweden. Parasit. Vectors 5, 8.
367 <https://doi.org/10.1186/1756-3305-5-8>.
- 368 Janisch, M., 1959. A hazai kullancs fauna feltérképezése (in Hungarian).
369 Állattani Közlemények 47, 103–110.
- 370 Kahl, O., Gern, L., Eisen, L., Lane, R., 2002. Ecological research on *Borrelia*
371 *burgdorferi* sensu lato: terminology and some methodological pitfalls, in:
372 Gray, J., Kahl, O., Lane, R., Stanek, G. (Eds.), Lyme Borreliosis: Biology,
373 Epidemiology and Control. CABI Publishing, New York, NY, pp. 29–46.
- 374 Kahl, O., Gray, J.S., 2023. The biology of *Ixodes ricinus* with
375 emphasis on its ecology. Ticks Tick Borne Dis. 14, 102114.
376 <https://doi.org/10.1016/j.ttbdis.2022.102114>.
- 377 Katuova, J.U., Sayakova, Z.Z., Jaimakhova, A.J., Koylybaev, T.T.,
378 Utemisova, R.A., 2021. Information about the fauna of ixodid ticks (Acari,
379 Ixodidae) in the north of the Aktobe region. Biol. Sci. Kazakhstan 2021/1,
380 85–98.
- 381 Kdysikh, B.G., Kdysikhova, G.G., Surov, V.V., Gaisiev, A.B.,
382 2021. Gray rat (*Rattus norvegicus* Berk., 1769) in the West Kaza-
383 khstan region and possible reasons for its disappearance in the
384 Trans-Ural steppe centre of plague (in Russian). Proc. IX Int.
385 Symp. Steppes of Northern Eurasia, Uralsk, Kazakhstan, 380–384.
386 <https://doi.org/10.24412/c1-36359-2021-380-384>.

- 387 Keskin, A., Bulut, Y.E., Keskin, A., Bursali, A., 2007. Tick attachment sites
388 in humans living in the Tokat province of Turkey. *Turk. Hij. Den Biyol.*
389 *Derg.* 74, 121–128. <https://doi.org/10.5505/TurkHijyen.2017.24993>.
- 390 Keskin, A., Keskin, A., Bursali, A., Tekin, S., 2015. Ticks (Acari: Ixodida)
391 parasitizing humans in Corum and Yozgat provinces, Turkey. *Exp. Appl.*
392 *Acarol.* 67, 607–616. <https://doi.org/10.1007/s10493-015-9966-4>.
- 393 Keskin, A., Selcuk, A.Y., Kefelioglu, H., 2019. Ticks (Acari: Ixodidae) infest-
394 ing some wild animals and humans in Turkey: Notes on a small collection.
395 *Acarol. Stud.* 1, 11–15.
- 396 Kiefer, D., Pfister, K., Tserennorov, D., Bolormaa, G., Otgonbaatar, D.,
397 Samjaa, R., Burmeister, E.G., Kiefer, M.S., 2010. Current state of Ixo-
398 didae research in Mongolia. *Exploration into the Biological Resources of*
399 *Mongolia*, 11, 405–418.
- 400 Kirillova, N.Y., Kirillov, A.A., 2018. Overview of ectoparasites of vertebrates
401 in the Samara region (in Russian). *News of the Samara Scientific Center*
402 *of the Russian Academy of Sciences* 20, 180–195.
- 403 Kirschenblatt, Y.D., 1936. Beiträge zur paläarktischen Zeckenfauna (in Ger-
404 man). *Zool. Anz. Leipzig* 114, 93–97.
- 405 Kolonin, G.V., 1981. World distribution of ixodid ticks (genus *Ixodes*) (in
406 Russian). Nauka, Moscow.
- 407 Kolonin, G.V., 2009. Fauna of ixodid ticks of the world (Acari, Ixodidae).
408 Webpublication available at <http://www.kolonin.org> (last accessed 10 Jun.
409 2014).
- 410 Kormilenko, I.V., Moskvitina, E.A., 2009. Tick-borne natural focal infections
411 in the territory of the Rostov region. Part 1. The fauna of Ixodidae ticks
412 (in Russian). *Probl. Part. Dang. Inf.* 99, 23–27.
- 413 Kuznetsov, V.L., Bondarev, V.Y., 2007. Distribution of ixodid ticks (Ixo-
414 didae) in the Lugansk region (in Russian). *Proc. 4th Int. Sci. Conf. on*
415 *Biodiversity and the Role of Animals in Ecosystems, Dnipropetrovsk*, p.
416 343.

- 417 Lesheva, G.A., Galceva, G.V., Gorodin, V.N., Badmaraeva, E.K., 2013. The
418 Crimean hemorrhagic fever is an actual problem of Kalmyc Republic (in
419 Russian). *Public Health and Environment - ZNISO* 2013/1, 26–28.
- 420 Mierzejewska, E.J., Estrada-Peña, A., Alsarraf, M., Kowalec, M.,
421 Bajer, A., 2015. Mapping of *Dermacentor reticulatus* expansion
422 in Poland in 2012–2014. *Ticks Tick Borne Dis.* 7, 94–106.
423 <http://dx.doi.org/10.1016/j.ttbdis.2015.09.003>.
- 424 Mihalca, A.D., D’Amico, G., 2017. *Ixodes laguri* Olenov, 1929, in: Estrada-
425 Peña, A., Mihalca, A.D., Petney, T.N. (Eds.), *Ticks of Europe and North*
426 *Africa. A Guide to Species Identification*. Springer, Cham, pp. 219–223.
427 https://doi.org/10.1007/978-3-319-63760-0_43.
- 428 Mihalca, A.D., Dumitrache, M.O., Magdas, C., Gherman, C.M., Domsa,
429 C., Mircean, V., Ghira, I.V., Pocora, V., Ionescu, D.T., Barabási,
430 S.S., Cozma, V., Sándor, A.D., 2012. Synopsis of the hard
431 ticks (Acari: Ixodidae) of Romania with update on host associa-
432 tions and geographical distribution. *Exp. Appl. Acarol.* 58, 183–206.
433 <https://doi.org/10.1007/s10493-012-9566-5>.
- 434 Musaev, Z.G., Abdulmagomedov, S.S., Begieva, S.A., Bittirov,
435 A.M., 2019. Epidemiological significance of ixodid ticks in
436 the flat, foothill and mountain zones of Dagestan (in Rus-
437 sian). *Proc Int. Sci. Conf. on Theory and Practice of Com-*
438 *bating Parasitic Diseases*, 15–17 May 2019, Moscow, 384–387.
439 <https://doi.org/10.31016/978-5-9902340-8-6.2019.20.384-387>.
- 440 Nosek, J., Sixl, W., 1972. Central-European Ticks (Ixodoidea) – Key for
441 determination. *Mitt. Abt. Zool. Landesmus. Joanneum*, 1, 61–92. available
442 at <https://www.zobodat.at/> (accessed, 11 Feb. 2024).
- 443 Numan, M., Alouffi, A., Almutairi, M.M., Tanaka, T., Ahmed, H., Akbar,
444 H., Rashid, M.I., Tsai, K.H., Ali, A., 2023. First detection of *Theileria*
445 *sinensis*-like and *Anaplasma capra* in *Ixodes kashmiricus*: With notes on
446 cox1-based phylogenetic position and new locality records. *Animals* 13,
447 3232. <https://doi.org/10.3390/ani13203232>.
- 448 Nuttall, P.A., 2021. Climate change impacts on ticks
449 and tick-borne infections. *Biologia* 77, 1503–1512.
450 <https://doi.org/10.1007/s11756-021-00927-2>.

- 451 Obert, A.S., Kurepina, N.Y., Bezrukov, G.V., Merkushev, O.A.,
452 Cherkashina, E.N., Kalinina, U.V., 2015. Ixodic ticks as carriers of hu-
453 man transmissible infectious diseases in Altai Krai (in Russian). Bulletin
454 Altai Branch Russian Geogr. Soc. 37, 82–89.
- 455 OpenStreetMap contributors, 2017. Planet dump retrieved from
456 <https://planet.osm.org>. <https://www.openstreetmap.org>.
- 457 Orkun, O., 2018. Molecular characterization based on 16S rDNA phylogeny
458 of some ixodid ticks in Turkey (in Turkish). *Turkiye Parazitol. Derg.* 42,
459 121–129. <https://doi.org/10.5152/tpd.2018.5882>.
- 460 Philip, C.B., Burgdorfer, W., 1961. Arthropod vectors as reser-
461 voirs of microbial disease agents. *Ann. Rev. Entomol.* 6, 391–412.
462 <https://doi.org/10.1146/annurev.en.06.010161.002135>.
- 463 Pollitzer, R., 1963. A review of selected problems of tularemia in the Soviet
464 Union. Part 1: History and recent incidence of the disease. *Inst. Contemp.*
465 *Russ. Stud.*, Fordham Univ., New York.
- 466 Porshakov, A.M., Korneev, M.G., Matrosov, A.N., 2020. Historical aspects
467 of studies of the Ixodida order ticks found in the Saratov region (in Rus-
468 sian). *Meditsinskaia Parazitologiya i Parazitarnye Bolezni* 2020/1, 42–52.
469 <https://doi.org/10.33092/0025-8326mp2020.1.42-52>.
- 470 Radda, A., Burger, I., Stanek, G., Wewalka, G., 1986. Austrian hard ticks
471 as vectors of *Borrelia burgdorferi*, overview. *Zbl. Bak. Hyg. A* 263, 79–82.
- 472 Radulović, Z., Mihaljica, D., Ćosić, N., Penezić, A., Ćakić, S., Sukara, R.,
473 Ćirović, D., Tomanović, S., 2017. Hard ticks parasitizing European ground
474 squirrel, *Spermophilus citellus* (L., 1766) (Rodentia: Sciuridae) in Serbia.
475 *Acta Zool. Bulg.* 49, 547–554.
- 476 Ramos-Lara, N., Koprowski, J.L., Kryštufek, B., Hoffmann, I.E., 2014. *Sper-*
477 *mophilus citellus* (Rodentia: Sciuridae). *Mammalian Species* 46, 71–87.
478 <https://doi.org/10.1644/913.1>.
- 479 Rubel, F., 2024. Hamster (*Cricetus cricetus*) and ground squir-
480 rel (*Spermophilus citellus*) in the metropolitan area of Vienna, Aus-
481 tria: Urban development vs. species protection. bioRxiv preprint
482 doi:10.1101/2024.02.08.579520.

- 483 Rubel, F., Brugger, K., 2022. Maps of ticks (Acari: Argasidae, Ixodidae)
484 for Austria and South Tyrol, Italy. *Exp. Appl. Acarol.* 86, 211–233.
485 <https://doi.org/10.1007/s10493-022-00688-w>.
- 486 Rubel, F., Kahl, O., 2023. The Eurasian shrew and vole tick *Ixodes tri-*
487 *anguliceps*: geographical distribution, climate preference, and pathogens
488 detected. *Exp. Appl. Acarol.* 90, 47–65. doi:10.1007/s10493-023-00797-0.
- 489 Shaposhnikova, L.I., Sakhno, N.V., 2012. To the study of the fauna of ixodid
490 ticks in the Republic of Abkhazia (in Russian). *Infect. Immun.* 2, 213–213.
- 491 Siuda, K., Sebesta, R., 1997. Central European ticks – a zoogeographical
492 review (Acari: Ixodida). *Genus* 8, 115–133.
- 493 Siutz, C., Millesi, E., 2012. Effects of birth date and natal dispersal on faecal
494 glucocorticoid concentrations in juvenile common hamsters. *Gen. Comp.*
495 *Endocrinol.* 178, 323–329.
- 496 Sklyar, V.E., 2002. Ectoparasites of some predatory mammals (Carnivora)
497 in the steppe and forest-steppe zones of Ukraine (in Russian). *Proc. 12th*
498 *Conf. Ukrainian Soc. Parasitol.*, 10-12 Sept. 2002, Sevastopol, 104-104.
- 499 Sljar, V.E., 1970. On the fauna of ixodid ticks from southern Donetsk district
500 (in Russian). *Parazitologiya* 4, 524–527.
- 501 Stupnitskaya, V.M., Marinov, M.P., Litvinenko, Y.F., Slesarenko, V.V., Sle-
502 sarenko, A.S., Khizh'nskaya, O.P., Stepanova, I.A., Buyalo, S.G., 1964.
503 Natural tularemia foci on the territory of the Ukrainian SSR (in Rus-
504 sian). *Zhurnal Mikrobiologii, Epidemiologii i Immunobiologii* 10, 94–98.
505 Translated in 1965 by R. M. Koplen, U.S. Army Biol. Lab. Fort Detrick,
506 Frederick, Maryland.
- 507 Suppan, J., 2013. Structure and possible functions of the spiracle
508 glands in *Ixodes ricinus* L. Master thesis, Univ. of Vienna, 47pp.
509 <https://doi.org/10.25365/thesis.30523>.
- 510 Surov, A., Banaszek, A., Bogomolov, P., Feoktistova, N., Monecke, S., 2016.
511 Dramatic global decrease in the range and reproduction rate of the Eu-
512 ropean hamster *Cricetus cricetus*. *Endang. Species Res.* 31, 119–145.
513 <https://doi.org/10.3354/esr00749>.

- 514 Uslu, U., Dik, B., Gökçen, A., 2008. Ectoparasites of the ground squirrel
515 (*Citellus citellus* (L.)) in Turkey. *Türkiye Parazitoloji Dergisi* 32, 142–
516 145.
- 517 Vladimirovna, K.O., 2014. Species diversity of ixodid ticks (Acarina: Ixo-
518 didae) in some recreational zones of the Republic of Moldova (in Roma-
519 nian). *Symp. on Sustainable Use and Protection of Animal World Diver-*
520 *sity, Chişinău, Moldova, 30–31 Oct. 2014, 139–140.*
- 521 Vogelgesang, J.R., Walter, M., Kahl, O., Rubel, F., Brugger, K., 2020. Long-
522 term monitoring of the seasonal density of questing ixodid ticks in Vi-
523 enna (Austria): setup and first results. *Exp. Appl. Acarol.* 81, 409–420.
524 doi:10.1007/s10493-020-00511-4.
- 525 Voltzit, O.V., Pavlinov, I.Y., 1996. Application of the methods of a geomet-
526 rical morphometrics to the ixodid ticks (Ixodidae) taxonomy (in Russian).
527 *Parazitologiya* 30, 292–301.
- 528 Voronova, N.V., Gorban, V.V., Luginin, N.S., 2012. Ecological specifics of
529 ticks (Ixodidae) in Zaporizhzhya area (in Ukrainian). *Monograph of the*
530 *Zaporizhzhya National University, 243pp.*
- 531 Zabashta, M.V., Pichurina, N.L., Khametova, A.P., Zabashta, A.V.,
532 Orekhov, I.V., Dobrovolsky, O.P., Stakheev, V.V., Fomina, E.S., Kovalev,
533 E.V., Fedchenko, A.V., Noskov, A.K., 2022. Epizooty of tularemia, de-
534 tected in the population of the common vole in the natural focus of steppe
535 type in the south-east of the Rostov region in 2020 (in Russian). *Problems*
536 *of Particularly Dangerous Infections* 2022/3, 75–81. doi:10.21055/0370-
537 1069-2022-3-75-81.
- 538 Zhmaeva, Z.M., Korshunova, O.S., 1953. On the natural infection of the tick
539 *Ixodes laguri laguri* Ol. with rickettsia (in Russian). *Parazitol. i Med. Zool.*
540 *Moskva* 8, 19–22.

Table 1: Number, accuracy (high, medium, low and very low), country, and reference of georeferenced *Ixodes laguri* sampling sites compiled in this study.

No.	Acc.	Country	References
1	v	Armenia	Anastos (1957)
1	l	Armenia	Filippova (2008)
2	l	Armenia	Dilbaryan and Hovhannisyanyan (2016)
1	h	Austria	Suppan (2013)
1	v	Azerbaijan	Anastos (1957)
3	v	Azerbaijan	Doss et al. (1978)
2	v	Bulgaria	Doss et al. (1978)
1	l	Bulgaria	Hubálek (2009)
2	l	Bulgaria	Arnaudov and Georgiev (2022)
2	v	Georgia	Doss et al. (1978)
2	l	Georgia	Shaposhnikova and Sakhno (2012)
3	l	Hungary	Janisch (1959)
5	v	Kazakhstan	Anastos (1957)
1	v	Kazakhstan	Feider (1965)
4	v	Kazakhstan	Doss et al. (1978)
3	l	Kazakhstan	Amirova et al. (1989)
1	l	Kazakhstan	Katuova et al. (2021)
1	v	Kazakhstan	Kdyrsikh et al. (2021)
1	v	Moldova	Feider (1965)
1	m	Moldova	Vladimirovna (2014)
2	l	Mongolia	Kiefer et al. (2010)
2	v	Romania	Feider (1965)
5	l	Romania	Mihalca et al. (2012)
7	v	Russia	Anastos (1957)
3	v	Russia	Doss et al. (1978)
13	l	Russia	Filippova and Stekolnikov (2007)
1	l	Russia	Filippova (2008)
1	v	Russia	Kormilenko and Moskvitina (2009)
1	v	Russia	Lesheva et al. (2013)
1	v	Russia	Obert et al. (2015)
3	l	Russia	Grigor'evich (2016)
2	l	Russia	Kirillova and Kirillov (2018)
1	v	Russia	Musaev et al. (2019)
3	l	Russia	Porshakov et al. (2020)
11	l	Serbia	Radulović et al. (2017)

Table 1: (continued)

No.	Acc.	Country	References
18	l	Slovakia	Černý (1990)
3	l	Turkey	Arthur (1957)
3	l	Turkey	Keskin et al. (2007, 2015, 2019)
6	v	Turkey	Bursali et al. (2011, 2015)
2	l	Turkey	Güven et al. (2022)
1	l	Turkmenistan	Berdyayev and Annayev (1997)
1	v	Ukraine	Anastos (1957)
1	m	Ukraine	Stupnitskaya et al. (1964)
1	v	Ukraine	Feider (1965)
2	v	Ukraine	Sljar (1970)
2	v	Ukraine	Sklyar (2002)
1	v	Ukraine	Kuznetsov and Bondarev (2007)
4	l	Ukraine	Voronova et al. (2012)
1	l	Ukraine	Akimov and Nebogatkin (2016)
1	l	Ukraine	Evstafiev (2017)
141		Total	

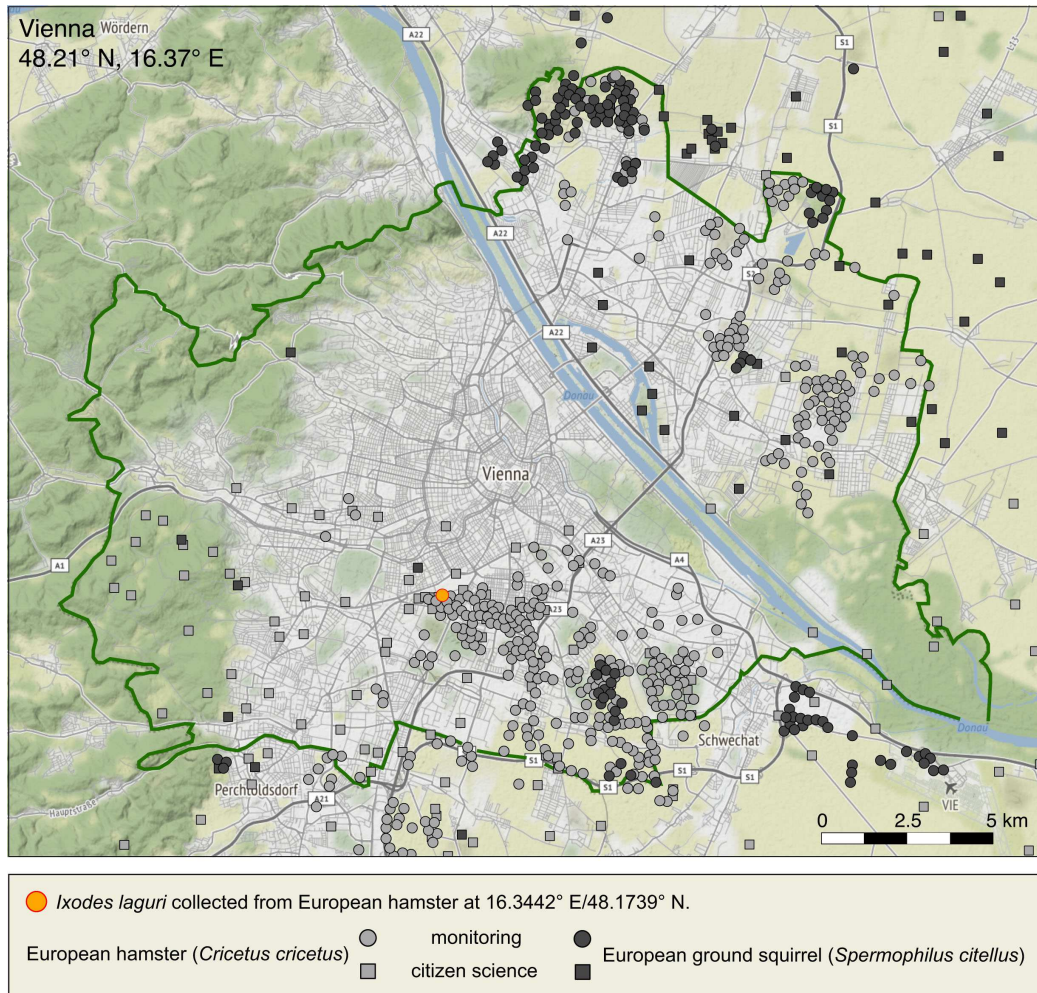


Figure 2: City map of Vienna showing the exact location of *Ixodes laguri* together with the distribution of its main hosts, the European hamster (*Cricetus cricetus*) and the European ground squirrel (*Spermophilus citellus*). Host data representative for the period 2000–2023 according to Rubel (2024).

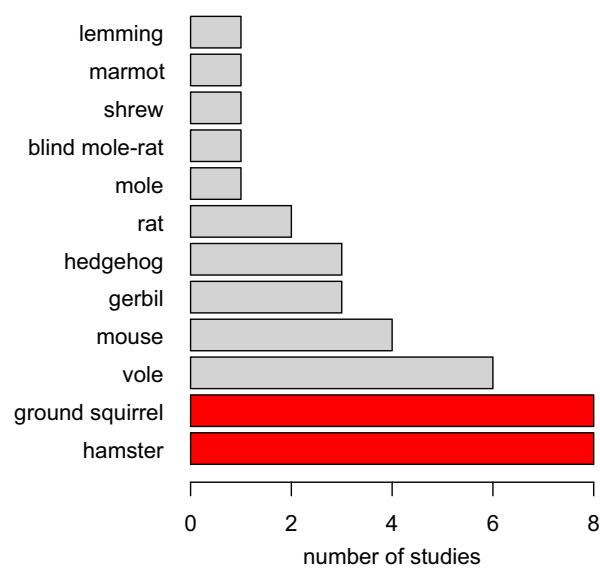


Figure 3: Number of studies reporting locations of small mammals invested with *Ixodes laguri*. Most studies (red bars) report finding the tick on hamsters (mainly *Cricetus cricetus*) and ground squirrels (mainly *Spermophilus citellus*).