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Original article

# From import to establishment? Experimental evidence for seasonal outdoor survival of two *Rhipicephalus* species in Germany

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ABSTRACT

The brown dog tick (*Rhipicephalus sanguineus* s.l.), though not endemic in Germany, is regularly introduced via travelers with dogs and imported rescue dogs. Due to its relevance in veterinary and human medicine, its potential to establish in Germany's climate is of interest. Although previous studies confirm indoor survival and reproduction of *R. sanguineus* s.s. in Germany, climate change and milder winters may also allow outdoor survival. This study assessed the survival of *R. sanguineus* s.s. and *R. innaei* from February 2023 to May 2024 using laboratory-bred ticks placed at indoor and outdoor sites. Tick survival (adults, nymphs, larvae) was monitored weekly, along with temperature and humidity. Reproductive success was evaluated via oviposition and larval hatching.

*R. sanguineus* s.s. adults survived up to 44 weeks, nymphs up to 20 weeks, and larvae up to 5 weeks. *R. innaei* showed shorter survival (37, 10, and 4 weeks, respectively). Successful oviposition and larval hatching occurred outdoors between May23 and September23 for both species. However, winter survival was not observed; all ticks died following sub-zero temperatures in December23.

Despite the inability to overwinter outdoors, both species can survive for extended periods in spring and summer and may enter homes via dogs, where conditions favor year-round survival. Their ability to transition indoors via dogs, where conditions favor year-round survival, suggests a potential for establishment in Germany through combined indoor and seasonal outdoor persistence.

## 1. Introduction

The brown dog tick (*Rhipicephalus sanguineus* s.l.) consists of numerous cosmopolitan ectoparasites of dogs, that can carry the ticks into non-endemic areas through travel or importation (Dantas-Torres, 2010; Rubel et al., 2023; Fachet-Lehmann et al., 2025). *R. sanguineus* s.l. is a part of the *Rhipicephalus sanguineus* complex which include, among others, *R. sanguineus* s.s., *R. linnaei* and *R. rutilus* (Zemtsova et al., 2016; Dantas-Torres et al., 2024; Hekimoğlu, 2024; Kelava et al., 2025). *R. sanguineus* s.s. and *R. rutilus* are endemic species in southern Europe and Mediterranean countries and *R. linnaei* is an endemic species of Africa (Estrada-Peña et al., 2018; Chitimia-Dobler et al., 2024; Hekimoğlu, 2024). *R. sanguineus* s.l. as a competent vector for several pathogens including *Rickettsia* spp., *Babesia vogeli, Ehrlichia canis* and *Hepatozoon canis* is therefore of great importance to veterinary and human medicine (Baneth et al., 2007; Dantas-Torres, 2010; Eremeeva et al., 2011; Gray et al., 2013; Ghodrati et al., 2024). In endemic areas, *R. sanguineus* s.l. lives in close and semi-permanent association with dogs. Consequently, a urban distribution of ticks close to buildings is common (Dantas-Torres, 2008, 2010). The fast reproduction and a high number of laid eggs make *R. sanguineus* s.l. a serious threat for dog owners and dogs themselves. Under suitable conditions *R. sanguineus* s.l. can develop up to four generations per year, and females lay an average of 4,000 eggs (Louly et al., 2007; Dantas-Torres, 2010) both resulting in a prolonged high tick burden in infested areas. Furthermore, *R. sanguineus* s.l. can survive and reproduce indoors or in weather-protected places such as kennels. As a three-host tick, bloodmeals are taken once per developmental stage and molting or oviposition happens in cracks and crevices (Gray et al., 2013). Although the dog is the preferred host of *R. sanguineus* s.l., observations of juvenile stages on other mammals such as rodents, foxes and cats have been published (Millán et al., 2007; Mihalca et al., 2012; Hornok et al., 2018).

The distribution of *R. sanguineus* s.l. was predicted to shift northwards and has already been observed in Central and Eastern European countries (Beugnet et al., 2011; Dantas-Torres et al., 2011; Duscher and Leschnik, 2011; Mihalca et al., 2012). A population of *R. sanguineus* s.s.

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that is considered established in the Alsace region in France has probably led to its introduction into Germany by travelers with their dogs (ECDC, 2023; Fachet-Lehmann et al., 2025). The proximity to the German border and comparable climatic conditions in Germany and France suggest that *R. sanguineus* s.s. may build stable populations and become established in Germany. There, *R. sanguineus* s.l. was identified in houses early as the 1960s and 1970s, with no distinction made between single species. In some cases, it was assumed that *R. sanguineus* s.l. was indeed a native species, but most cases indicated an import background, such as introduction by military dogs from the USA or imported goods from Morocco (Zumpt, 1946; Gothe and Hamel, 1973a, 1973b; Hoffmann, 1981, 1986; Dongus et al., 1996). Since 2019, introductions of *Rhipicephalus* species have led to high infestation rates in several households with hundreds of tick individuals and successful reproduction of offspring (Rubel et al., 2022; Rubel et al., 2023; Fachet-Lehmann et al., 2025). The most introduced species, with more than 60 %, was identified as *R. sanguineus* s.s. originating from European countries like France, Spain, Romania, Greece, Italy and Croatia. Also, ticks of the species *R. linnaei* were introduced from Croatia by vacationers with dogs, despite this species being non-endemic to the region (Fachet-Lehmann et al., 2025).

Nevertheless, the survival of *R. sanguineus* s.l. in outdoor areas within Germany has been ruled out thus far, as *R. sanguineus* s.l. is adapted to warm and arid conditions, whereas the climate in Germany is considered cold and humid (Zumpt, 1940; Gothe and Hamel, 1973a; Hoffmann, 1979; Prosl and Kutzer, 1986; Chitimia-Dobler and Dobler, 2019). However, in recent years climate change has led to milder winters in Germany, and prolonged warm and dry summers provide better conditions for *R. sanguineus* s.l. to survive. Additionally, several apparently established tick infestations raised the question of whether *Rhipicephalus* species can survive in outdoor areas, at least temporarily. To become established outdoors, not only must all developmental stages of the ticks survive and molt, but oviposition and hatching of the larvae are also prerequisites for the establishment of populations (Clout et al., 2000; Mata et al., 2013). For this reason, two *Rhipicephalus* species, *R. sanguineus* s.s. and *R. linnaei*, were studied under field conditions to determine whether they can meet the requirements for survival outdoors. Both *Rhipicephalus* species have already been introduced to Germany several times (Fachet-Lehmann et al., 2025).

## 2. Material and methods

The survival data of *Rhipicephalus sanguineus* s.s. and *Rhipicephalus linnaei* were collected from two outdoor and two indoor areas at the University of Hohenheim in Germany between February 2023 and May 2024. Additionally, oviposition and hatchability of larvae of both species were also monitored.

### 2.1. Experimental sites

Two different outdoor sites were selected to study the influence of vegetation as well as to abiotic factors such as temperature and humidity (Fig. 1). In both outdoor sites tick individuals were exposed to sunlight, drought, and heat in summer and waterlogging, frost and snow in autumn and winter without any retreat options provided. Since outdoor areas can differ significantly in their habitat characteristics, two areas were chosen to represent distinct vegetation types and varying exposure to weather conditions. The site selected for Out 1 was a meadow surrounded by vegetation such as trees and bushes, which provided temporary protection from sunlight, offering a mix of sun and shade and mitigated strong winds and rainfall. Out 2 was characterized by a complete absence of vegetation and the rocky habitat offered no protection from sunlight, heat, rain or wind (Fig. 1).

As *R. sanguineus* s.l. is known to be adapted to urban areas and can survive and reproduce indoors (Gray et al., 2013), experimental sites Co 1 and Co 2 were chosen to represent protected indoor areas (Fig. 1). As indoor areas can differ significantly, for example due to temperature, two distinct scenarios were selected. Co 1 was designed to simulate a potential retreat site in Germany after an importation, in which ticks fell off the dog in a kennel or a doghouse and found protective structures for oviposition or moulting. For this purpose, the experimental setup was placed in a garden shed, where the indoor climate followed outdoor temperature and humidity with a short delay. Additionally, an insulated indoor room was selected for experimental site Co 2, corresponding to a residential room protected from all weather conditions and equipped with temperature regulation. Since the room was part of a temperature-controlled building, it was indirectly heated by the heating system of adjacent rooms but was not actively affected by room heating, etc. (Fig. 1). At each experimental site, temperature and relative humidity were recorded hourly using climate loggers (EasyLog, EL-USB-2, Lascar Electronics Limited, UK). Each experimental site was equipped with one experimental setup.

The University of Hohenheim's internal meteorological data indicated a consistent increase in the location of experiments, with the mean annual temperature had risen from 8 °C (1878) to 10.2 °C (2010) and 11.6 °C (2024). Seasonal fluctuations in temperature and precipitation are commonplace, with the winter months (Dezember–March) being the coldest. Despite a decline in the number of frost days (Tmax <0 °C), from an average of 110 days (1878) to approximately 75 (2010) and 70 days (2024), accompanied by temperatures reaching below -10 °C, the overall trend was evident. Snowfall is typically expected in winter, but numbers of snowfall days decreased significantly to 6 days in 2024. The spring season, which typically extends from March to May, is characterized by average temperatures that generally remain above the freezing point, with an average temperature of approximately 10 °C recorded. However, the occurrence of frost and icy days is to be

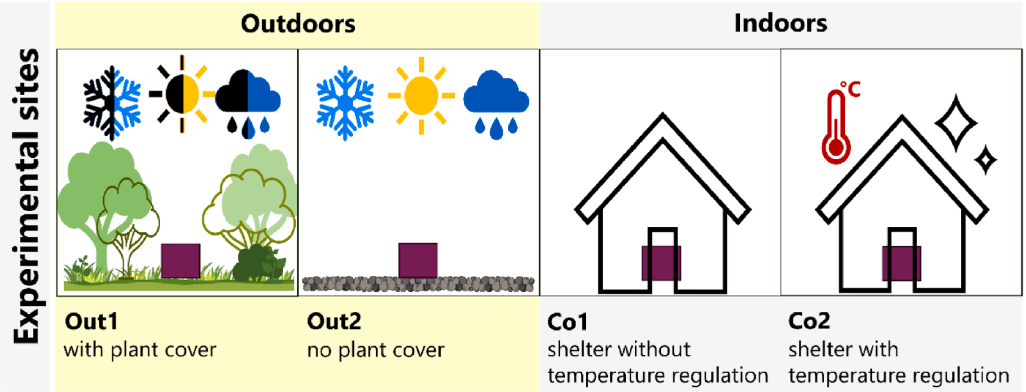

**Fig. 1.** Model of experimental sites, represented by two outdoor and two indoor sites. Violet square: experimental setup.

expected, as are occasional snowfalls and sunny days. The summer months, which extend from June to August, are characterized by elevated temperatures and abundant sunlight. However, these conditions are often accompanied by periods of drought. In Hohenheim, the number of days with temperatures above 25 °C (i.e. summer days, Tmax >25 °C) had increased from an average of 30 days (1878) to 42 (2010) and 45 days (2024), with temperatures exceeding 30 °C. The autumnal period, which extends from September to November, is distinguished by precipitation and a decline in temperature. Temperatures ranging from 0 °C to 30 °C are possible, with the potential for frost and sub-zero temperatures. Rainfall is observed throughout the year, with fewer rainy days in the summer months and more frequent rainfall in autumn. Precipitation had fallen on average from 800 l/sqm to 700 l/sqm (2024) since 1998 (Bauer, 2024).

### 2.2. Experimental setup

Test cages, containing ticks or egg masses and dummy cages, were placed in a plate array at random (Fig. 2). The plate array was surrounded by a closed stainless-steel cage (plot) of 1 $m^2$ and a height of 80cm (Brista, Franz Brinkmann GmbH, Germany). The plot had a movable lid and a mesh size of 40 mm x 15 mm. The plot was welded to a perforated, 1mm thick stainless-steel plate with 3 mm diameter holes at the bottom, that was also covered with weed fleece to drain moisture and exclude plants and animals. To prevent waterlogging the plot was filled to a height of 10 cm with expanded clay (Westland Deutschland GmbH, Germany) and was lifted by an additional 20 cm to eliminate the influence of ground frost of the surrounding (Fig. 2).

Inside each plot, a plate array was provided with 81 holes (slots) into which test cages and dummy cages were inserted randomly (Fig. 2). Each slot in the plate array was filled with either a test or a dummy cage to exclude the influence of wind or shade. The plate array was set up at a 45-degree angle to prevent rainwater from accumulating inside the test cages. Test cages were made of prepared screw-top containers (200 ml neoLab®Migge GmbH, Germany) with drilled holes of 6 cm in diameter in the top and bottom of each test cage and covered with gauze (150 µ mesh size Franz Eckert GmbH, PA-150/38/FDA, Germany) to ensure climatic exchange with the environment. Dummy cages are identical screw-top containers.

### 2.3. Handling of ticks

Unfed larvae, nymphs and adults of *R. sanguineus* s.s. and *R. linnaei* were obtained from IS Insect Services (GmbH, Germany) in February, May, June and November 2023 (Table 1). Only freshly hatched or molted specimens were used to ensure maximum longevity. Only ticks, that were reactive to external stimuli after an acclimatization period of 24h at room temperature were included in the experiments. Ticks were then grouped by species and developmental stage and then assigned to one of the four experimental sites in individual test cages. Individual test cages contained, either 50 adult ticks, 30 nymphs, or 30 larvae respectively (Table 1). The survival rate of tick individuals at experimental sites was monitored at weekly intervals. Live ticks were counted, and dead ticks were removed with tweezers from the test cages and stored in dummy cages to prevent mold growth in test cages. Dead ticks were kept in the plate array until the end of the experiment (Fig. 2). Ticks were defined as dead if they either showed clear signs of fungal growth, desiccation or strong discoloration, or failed to respond to stimulation by blowing and vibration for five minutes.

Engorged females of both species were obtained from IS Insect Services GmbH in February, May, July, September and November 2023 (Table 1). After 24 hours of acclimatization, one engorged female of each species was placed in a test cage each and assigned to one of the four experimental setups (Fig. 2). Oviposition success was monitored at weekly intervals.

Additionally, one engorged female of each species was kept separately in a humidity chamber at 90 % relative humidity and room temperature until oviposition was completed. The laboratory produced egg patch of each female was then divided equally into four egg masses that were placed into test cages and then allocated to the four experimental setups. Hatching success as well as the hatching rate (signed in percent) and survival time of freshly hatched larvae was documented in weekly intervals.

Both species were confirmed by Insect Services as genetically identified. *R. sanguineus* s.s. was first obtained from Crete in 2000 and is now in its 25th generation of laboratory breeding. *R. linnaei* was introduced to Germany from an unknown origin and has been maintained in laboratory breeding since 2017, i.e. marking its sixth generation. For both species wild-caught specimens are crossed when available (personnel communications Insect Services).

In addition to survival time, the $LT_{50}$ (time at which 50 % of the population died) was calculated (Koch and Tuck, 1986). The beginning of individual placements as well as the number of ticks per test cage are shown in Table 1. Due to the species-specific developmental periods at Insect Services GmbH of both tick species, simultaneous placement of adults together with juvenile stages was not possible.

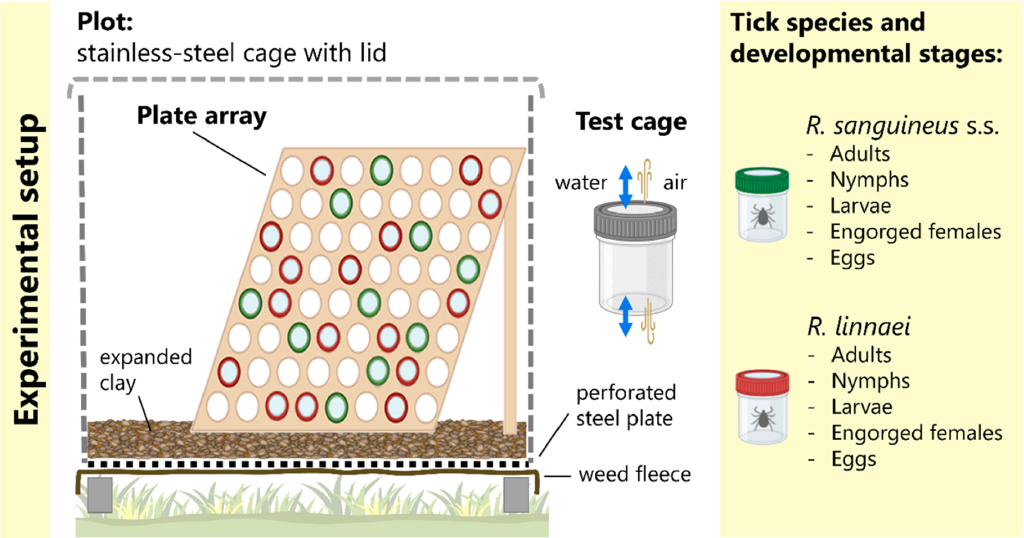

**Fig. 2.** Model of experimental setup, represented by a plate array with test cages (containing ticks or egg masses) inside a stainless-steel cage.

**Table 1**
Number of ticks and beginning of individual experiments at each experimental site. Included in the study were two species in separated cages (*R. sanguineus* s.s. RS/RL *R. linnaei*) at four experimental sites. The study trial took place between February 2023 and May 2024. No placements of ticks or egg masses are marked with np.

| Developmental stage | Month of placement | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Feb 2023 | Mar 2023 | Apr 2023 | May 2023 | June 2023 | July 2023 | Aug 2023 | Sep 2023 | Oct 2023 | Nov 2023 |
| | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL | RS/RL |
| Adults | 50/50 | np | np | np | 50/50 | np | np | np | np | 50/50 |
| Nymphs | np | np | np | 30/30 | 30/30 | np | np | np | np | 30/30 |
| Larvae | np | np | np | 30/30 | 30/30 | np | np | np | np | 30/30 |
| Engorged females | 0/1 | np | np | 1/1 | np | 1/1 | np | 1/1 | np | 0/1 |
| Egg masses | np | np | 1/1 | 1/1 | np | 1/1 | np | 1/1 | np | 1/1 |

### 2.4. Statistical analysis

Data analysis was conducted using DATAtab's online statistics calculator (DATAtab Team, 2025). Survival analysis was assessed with the Log-Rank Test. Man-Whitney-U tests were used to compare temperature and relative humidity data between experimental sites. Differences were considered statistically significant if the p-value was 0.05 or less ($p \leq 0.05$).

## 3. Results

### 3.1. Climate data

In outdoor sites, peak values of relative humidity remained high, whereas temperature spikes of up to 50 °C were still recorded during the trial period (Table 2), with temperatures falling below 0 °C in winter (February and December). Minimal temperatures of -7 °C in December as well as 17 %rH in March were measured.

For indoor sites Co 1 and Co 2 differed in temperature and humidity. While Co 1 showed only less fluctuations in both temperature and humidity (Fig. 3). Temperatures remained between approximately 5 °C and 20 °C throughout the trial period, while relative humidity consistently ranged between 37.5 % and 90.5 % (Table 2). For Co 2 the temperature remained consistent at around 20 °C during the trial period and relative humidity was maintained within a range of 23 % to 85 %.

Over the duration of the project between all experimental sites significant differences in temperature and humidity appeared, except for Co 1 and Out 1 in parameter temperature (Mann-Whitney-U, p= 0.629).

### 3.2. Survival analysis

#### 3.2.1. Adults

Survival data of adult *R. sanguineus* s.s. and *R. linnaei* at all experimental sites are summarized in Fig. 4.

While adult *R. sanguineus* s.s. survived 26 to 44 weeks outdoors in February and June (Out 1, Out 2), *R. linnaei* reached a maximum survival time of 20-37 weeks (Table 3). The survival time of *R. sanguineus* s. s. differed significantly from that of *R. linnaei* independent of the month of placement and experimental site (supplementary Table I). Generally, adult *R. sanguineus* s.s. survived significantly longer than adult *R. linnaei*, with exceptions occurring after placements outdoors in November (Out1, Out2 - Table 3, Fig. 4). These results are also supported by the evaluation of the descriptive statistics, resulting in higher values for survival time of *R. sanguineus* s.s. (M = 7.7 weeks, SD = 10.08) than for *R. linnaei* (M = 5.8 weeks, SD = 6.48). The longest survival time of *R. sanguineus* s.s. exceeds the longest measured survival time of *R. linnaei* by 7 weeks at outdoor sites (Out 1, Out 2) and by 13 weeks in Co 2. Only after placements in November none of both species survived the 4th week after placement at outdoor sites (Out1, Out2). Regardless of the time of placement (February, June and November), all adult individuals died in December 2023 at outdoor sites.

**Table 2**
Descriptive statistical evaluations are based on the daily averages of temperature (°C) and relative humidity (%rH) separated to each experimental site n = 423 datapoints each.

| | Experimental sites | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Out 1 | | Out 2 | | Co 1 | | Co 2 | |
| | °C | %rH | °C | %rH | °C | %rH | °C | %rH |
| Median | 12.5 | 78.5 | 10.6 | 93.1 | 11.9 | 68.4 | 20.3 | 47.3 |
| Average | 13.1 | 78.3 | 11.6 | 86.8 | 12.9 | 70 | 20.2 | 48.9 |
| Minimum | -7 | 17 | -6.5 | 19.5 | -8 | 37.5 | 16.5 | 23 |
| Maximum | 50 | 100 | 43.5 | 100 | 39 | 90.5 | 24.5 | 85 |

The maximum survival times of both species at indoor sites (Co 1, Co 2) differed significantly from each other (Table 3). While indoor site Co 1, that simulated a kennel, showed significant differences in maximum survival time of both species - experimental site Co 2, that simulated a living room, constant maximum survival times and similar decrease in number were documented after placements in February, June and November'23 (Fig. 4).

Comparing outdoor and indoor sites, the survival time of both species is significantly longer in outdoor sites than in indoor sites (Table 3, supplementary Table II, III). Especially after placements in February and June, the adaptation of *R. sanguineus* s.s. to temperate climates becomes visible in a significantly longer survival time outdoors than indoors (Table 3). In general, *R. sanguineus* s.s. survived significantly longer outdoors than indoors but there is no significant difference in survival time between the outdoor sites Out1 and Out2 as well as between the indoor sites Co1 and Co2 after placement in June (supplementary Table II). However, a significant prolonged survival time was also observed for *R. linnaei* at outdoor sites compared to indoor sites (Fig. 4, supplementary Table III).

Besides the different maximum survival time of both species, the decrease in number between outdoor and indoor sites must be addressed. Generally, a more rapid decrease in number at indoor sites was documented for both species, with exceptions after placements in November, compared to outdoor sites. Both species revealed a much more rapid decrease in numbers in Co 1 compared to outdoor sites (Fig. 4). This observation is reflected in the evaluations of the $LT_{50}$. The average $LT_{50}$ of both species at outdoor sites showed strong differences between the species. Half of the adult *R. linnaei* individuals were dead after 49 % on average (3-13 weeks) of its maximum survival time (4-21 weeks). In contrast to *R. sanguineus* s.s., where half of the individuals were dead after 84 % on average (4-41 weeks) of its maximum survival time (4-44 weeks) (Fig. 4). *R. sanguineus* s.s. thus showed a significantly longer stable and high number of surviving individuals compared to *R. linnaei*, where a rapid decline in numbers early after placement was documented. This observation is consistent across all experimental sites (Table 3). Although an indoor environment like experimental site Co 2 was predicted to be ideal for long survival times (Dantas-Torres, 2008), the number of individuals declined rapidly in both species quickly after placement. This is also reflected in the evaluation of the $LT_{50}$ at Co 2. The number of the monitored adults was halved after 45 % (*R. linnaei*)

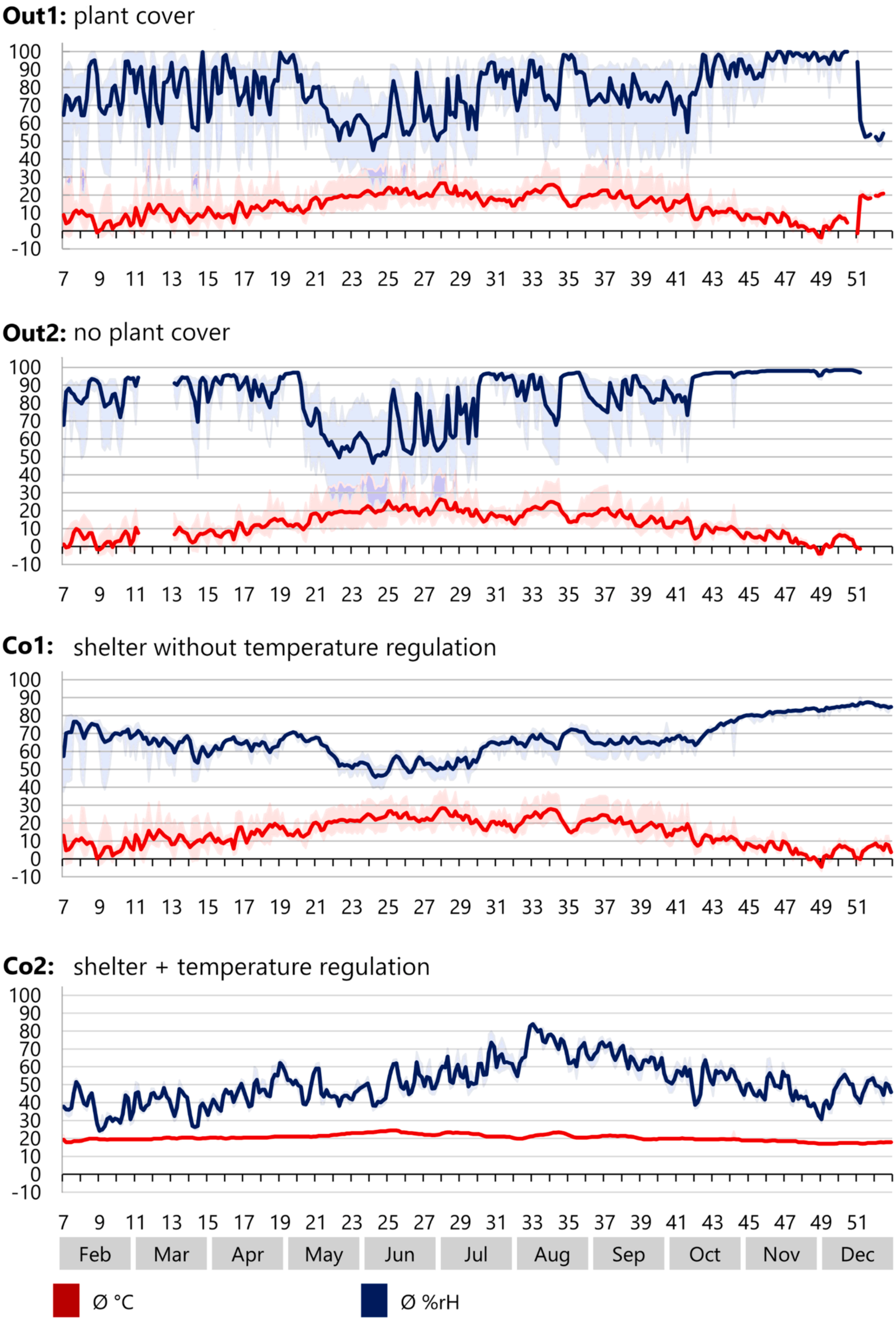

**Fig. 3.** Presentation of the climate data temperature (°C) and relative humidity (%rH) based on daily averages. Gaps in the graphs represent missing measurements due to technical difficulties.

and 58 % (*R. sanguineus* s.s.) on average of their maximum survival time (Fig. 4).

### *3.2.2. Nymphs*

Survival data of nymphal *R. sanguineus* s.s. and *R. linnaei* at all experimental sites are summarized in Fig. 5.

The maximum survival time of *R. sanguineus* s.s. nymphs was up to 20 weeks outdoors (Out1, Out2), and up to 6 weeks indoors (Co1, Co2), while *R. linnaei* nymphs survived only up to10 weeks outdoors and up to 6 weeks indoors as well. *R. sanguineus* s.s. consistently outlived *R. linnaei* at most sites maintaining higher survival times and later death of half of the individuals ($LT_{50}$), particularly outdoors. Exceptions occurred in November, where *R. linnaei* nymphs survived longer than *R. sanguineus* s. s. at both indoor and outdoor sites. $LT_{50}$ analyses further support a more

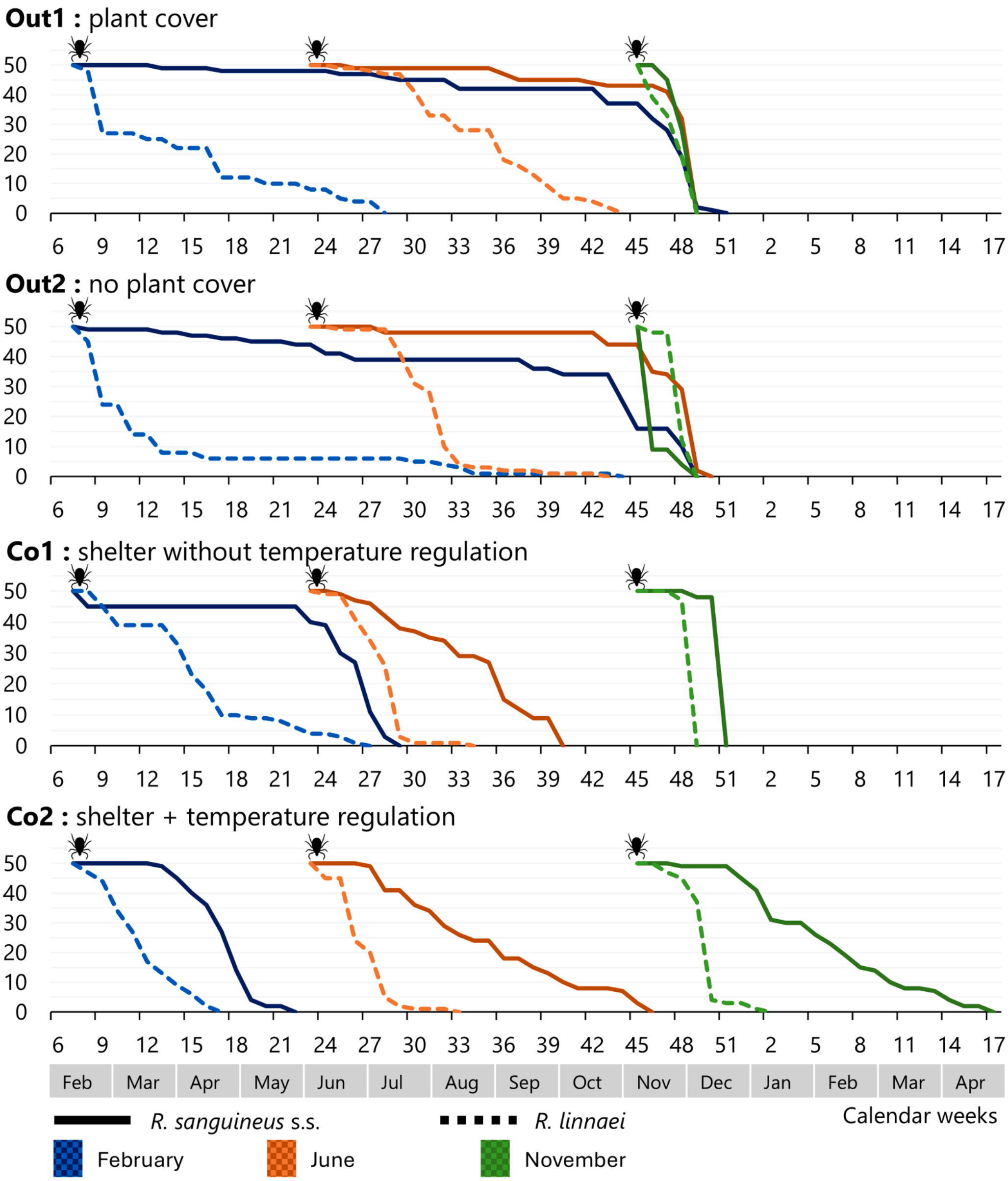

**Fig. 4.** Survival time of adult *R. sanguineus* s.s. and *R. linnaei* between February 2023 and May 2024 outdoors (Out 1, Out 2) and indoors (Co 1, Co 2). A placement of ticks into the experimental setup marked with a black tick. Numbers of surviving ticks placed in May are shown Blue, in July in Orange and in November in Green.

**Table 3**
Maximum survivability (max) and $LT_{50}$ (when half of population died) of adult *R. sanguineus* s.s. (RS) and *R. linnaei* (RL) at four experimental sites between February 2023 and May 2024 (adults n=50, each experimental site). Evaluation of survival time and $LT_{50}$ in weeks, decimals rounded.

| Species | Developmental stage of ticks | Experimental site | Survivability in weeks | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Feb | | June | | Nov | |
| | | | max | $LT_{50}$ | max | $LT_{50}$ | max | $LT_{50}$ |
| RS | Adults | Out 1 | 44 | 41 | 26 | 26 | 4 | 4 |
| | | Out 2 | 42 | 38 | 27 | 26 | 4 | 1 |
| | | Co 1 | 22 | 20 | 17 | 13 | 6 | 6 |
| | | Co 2 | 15 | 11 | 23 | 11 | 24 | 13 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 43 | 40 | 27 | 26 | 4 | 3 |
| | | Indoor (Co 1 + Co 2) | 19 | 16 | 20 | 12 | 15 | 10 |
| RL | Adults | Out 1 | 21 | 7 | 21 | 13 | 4 | 3 |
| | | Out 2 | 37 | 2 | 20 | 9 | 4 | 3 |
| | | Co 1 | 20 | 8 | 11 | 6 | 4 | 4 |
| | | Co 2 | 10 | 5 | 10 | 3 | 9 | 5 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 29 | 5 | 21 | 11 | 4 | 3 |
| | | Indoor (Co 1 + Co 2) | 15 | 7 | 11 | 5 | 7 | 5 |

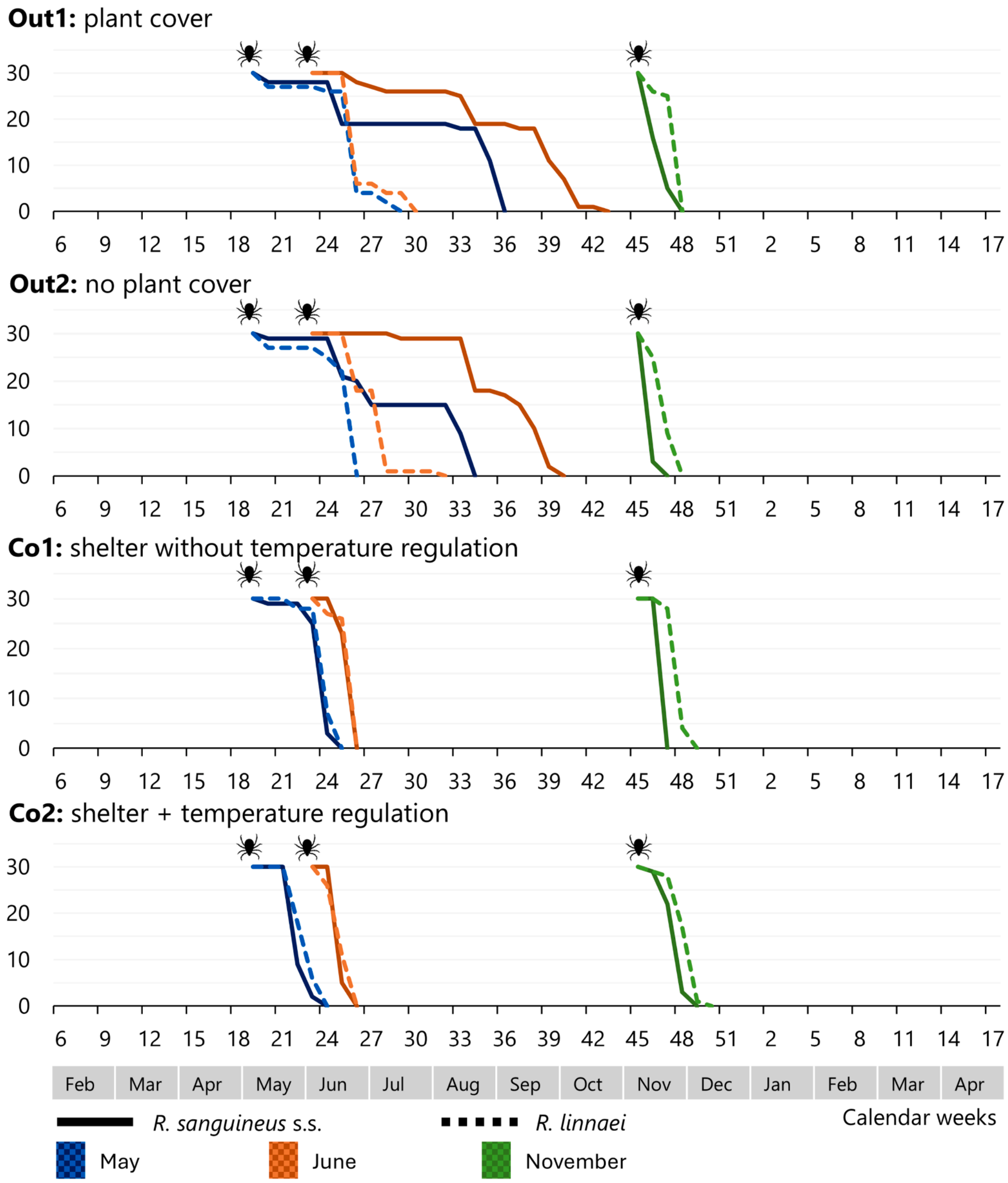

**Fig. 5.** Survival time of nymphal *R. sanguineus* s.s. and *R. linnaei* between February 2023 and May 2024 outdoors (Out 1, Out 2) and indoors (Co 1, Co 2). a placement of ticks into the experimental setup marked with a black tick. Numbers of surviving ticks placed in May are shown in a blue graph, in July (orange) and in November (green).

**Table 4**
Maximum survivability (max) and $LT_{50}$ (half of population died) of nymphal *R. sanguineus* s.s. (RS) and *R. linnaei* (RL) at four experimental sites between February 2023 and May 2024 (nymphs n=30 per experimental site). Evaluation of survival time and $LT_{50}$ in weeks, decimals rounded.

| Species | Developmental stage of ticks | Experimental site | Survivability in weeks | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | May | | June | | Nov | |
| | | | max | $LT_{50}$ | max | $LT_{50}$ | max | $LT_{50}$ |
| RS | Nymphs | Out 1 | 17 | 16 | 20 | 16 | 3 | 2 |
| | | Out 2 | 15 | 14 | 17 | 15 | 2 | 1 |
| | | Co 1 | 6 | 5 | 3 | 3 | 2 | 2 |
| | | Co 2 | 5 | 3 | 3 | 2 | 4 | 3 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 16 | 15 | 19 | 9 | 3 | 2 |
| | | Indoor (Co 1 + Co 2) | 6 | 4 | 3 | 3 | 3 | 3 |
| RL | Nymphs | Out 1 | 10 | 7 | 7 | 3 | 3 | 3 |
| | | Out 2 | 7 | 7 | 9 | 5 | 3 | 2 |
| | | Co 1 | 6 | 5 | 3 | 3 | 4 | 3 |
| | | Co 2 | 5 | 4 | 3 | 2 | 5 | 4 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 9 | 7 | 8 | 3 | 3 | 3 |
| | | Indoor (Co 1 + Co 2) | 6 | 5 | 3 | 3 | 5 | 4 |

stable population of *R. sanguineus* s.s., while *R. linnaei* exhibited earlier decrease in numbers, especially indoors (Fig. 5, Table 4).

Survival time of *R. sanguineus* s.s. nymphs was significantly longer at outdoor sites (Out 1, Out 2) compared to indoor sites (Co 1, Co 2), particularly after placements in May and June, with differences exceeding up to 13 weeks at the same experimental site (Table 4, supplementary Table I, IV). At Co 1, both species exhibited low maximum survival times and a rapid decline in numbers. In contrast, Co 2 showed moderately prolonged survival with a slower decline in numbers, that are still significantly shorter than at outdoor sites (Fig. 5).

### 3.2.3. *Larvae*

Survival data of larval *R. sanguineus* s.s. and *R. linnaei* at all experimental sites are summarized in Fig. 6.

Despite the generally expected short lifespan of *Rhipicephalus* larvae, the individuals of both laboratory-bred species died rapidly within six weeks after placement in every month and at every experimental site (Fig. 6, Table 5). *R. sanguineus* s.s. larvae survived the longest at both outdoor sites in May, while *R. linnaei* survived only 4 weeks and less. *R. sanguineus* s.s. larvae survived significantly longer at outdoor sites (Out 1, Out 2) compared to Co 1, and outlived *R. linnaei* significantly in May and June at Out 1, Out 2, and Co 2 (supplementary Tables I, V). Minimum survival times of 2 weeks were documented for *R. sanguineus* s.s. after placements in June and November at outdoor sites and only 1 week for *R. linnaei* at Out 2 and Co 2, respectively. The survival times of larvae of both species were comparable at Co 1 (May and June) and Co 2 (June, November).

### 3.2.4. *Oviposition and hatching of larvae*

Engorged females of both species were placed at all experimental sites simultaneously and several oviposition events were documented between February and November’23 (Fig. 7). Engorged females of both species laid eggs after placement in May, July and September (*R. sanguineus* s.s.) and February, May and July (*R. linnaei*). For both species oviposition was observed after placements in May and July at outdoor and indoor sites (Table 6). While *R. sanguineus* s.s. started

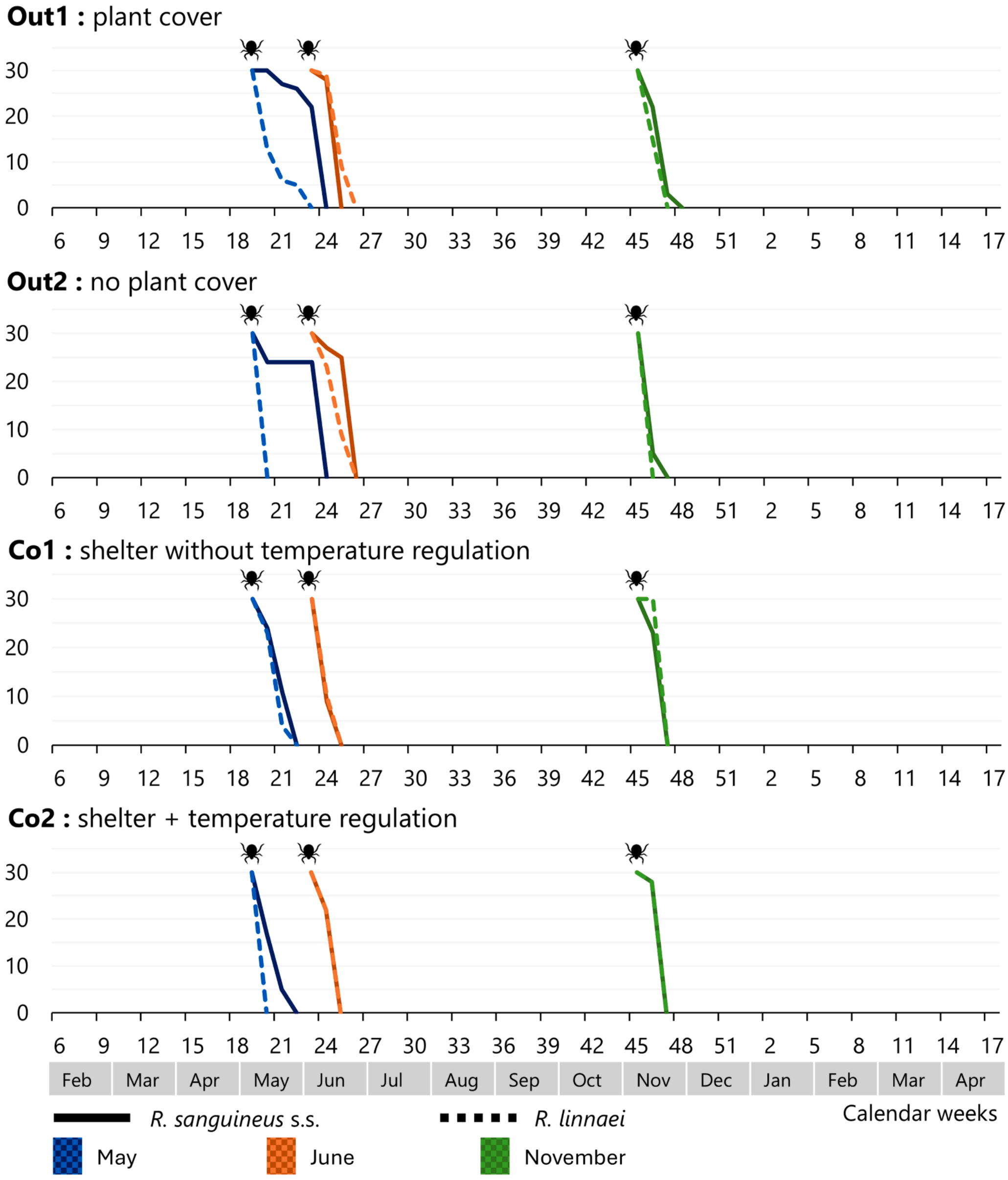

**Fig. 6.** Survival time of larval *R. sanguineus* s.s. and *R. linnaei* between February 2023 and May 2024 outdoors (Out 1, Out 2) and indoors (Co 1, Co 2). a placement of ticks into the experimental setup marked with a black tick. Numbers of surviving ticks placed in May are shown in a blue graph, in July in Orange and in November in Green.

**Table 5**

Maximum survivability (max) and $LT_{50}$ (half of population died) of larval *R. sanguineus* s.s. (RS) and *R. linnaei* (RL) at four experimental sites between February 2023 and May 2024 (larvae n = 30 per experimental site). Evaluation of survival time and $LT_{50}$ in weeks, decimals rounded.

| Species | Developmental stage of ticks | Experimental site | Survivability in weeks | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | May | | June | | Nov | |
| | | | max | $LT_{50}$ | max | $LT_{50}$ | max | $LT_{50}$ |
| RS | Larvae | Out 1 | 5 | 5 | 2 | 2 | 3 | 2 |
| | | Out 2 | 5 | 5 | 3 | 3 | 2 | 1 |
| | | Co 1 | 3 | 2 | 2 | 1 | 2 | 2 |
| | | Co 2 | 3 | 2 | 2 | 2 | 2 | 2 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 5 | 4 | 3 | 2 | 3 | 2 |
| | | Indoor (Co 1 + Co 2) | 3 | 2 | 2 | 2 | 2 | 2 |
| RL | Larvae | Out 1 | 4 | 1 | 3 | 2 | 2 | 2 |
| | | Out 2 | 1 | 1 | 3 | 2 | 1 | 1 |
| | | Co 1 | 3 | 2 | 2 | 1 | 2 | 2 |
| | | Co 2 | 1 | 1 | 2 | 2 | 2 | 2 |
| | Ø survivability | Outdoor (Out 1 + Out 2) | 3 | 1 | 3 | 2 | 2 | 2 |
| | | Indoor (Co 1 + Co 2) | 2 | 2 | 2 | 2 | 2 | 2 |

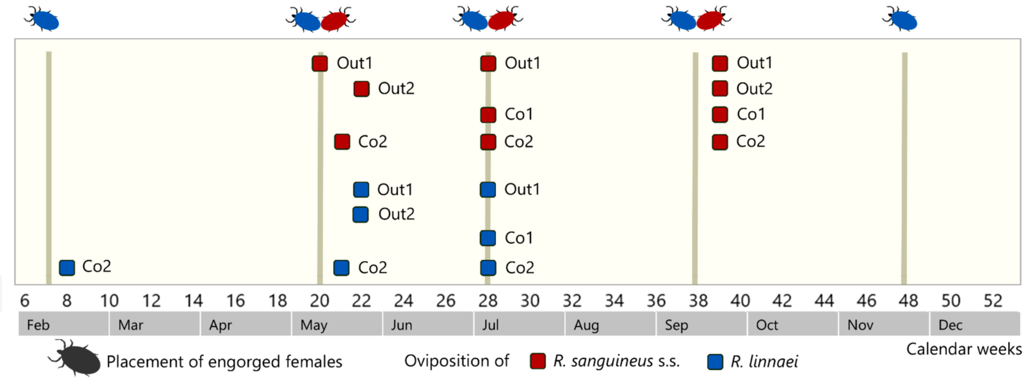

**Fig. 7.** Oviposition of *R. sanguineus* s.s. and *R. linnaei* females at experimental sites Out 1, Out 2, Co 1 and Co 2. Dots mark the start of oviposition after the placements in February, May, July, September and November 2023 (line).

**Table 6**

Evaluation of oviposition of engorged females for *R. sanguineus* s.s. and *R. linnaei* between February 2023 and May 2024 at outdoor (out1, out2) and indoor sites (Co1, Co2).

| Species | Developmental stage of ticks | Experimental site | Feb | May | July | Sep | Nov |
|---|---|---|---|---|---|---|---|
| *RS* | no. of released engorged females | Out 1 | | 1 | 1 | 1 | |
| | | Out 2 | | 1 | 1 | 1 | |
| | | Co 1 | | 1 | 1 | 1 | |
| | | Co 2 | | 1 | 1 | 1 | |
| | ovipositing females | Out 1 | | 1 | 1 | 1 | |
| | | Out 2 | | 1 | - | 1 | |
| | | Co 1 | | - | 1 | 1 | |
| | | Co 2 | | 1 | 1 | 1 | |
| | time until oviposition starts | Out 1 | | 0 weeks | 0 weeks | 1 week | |
| | | Out 2 | | 2 weeks | - | 1 week | |
| | | Co 1 | | - | 0 weeks | 1 week | |
| | | Co 2 | | 1 week | 0 weeks | 1 week | |
| *RL* | no. of released engorged females | Out 1 | 1 | 1 | 1 | 1 | 1 |
| | | Out 2 | 1 | 1 | 1 | 1 | 1 |
| | | Co 1 | 1 | 1 | 1 | 1 | 1 |
| | | Co 2 | 1 | 1 | 1 | 1 | 1 |
| | ovipositing females | Out 1 | - | 1 | 1 | - | - |
| | | Out 2 | - | 1 | - | - | - |
| | | Co 1 | - | - | 1 | - | - |
| | | Co 2 | 1 | 1 | 1 | - | - |
| | time until oviposition starts | Out 1 | - | 2 weeks | 0 weeks | - | - |
| | | Out 2 | - | 2 weeks | - | - | - |
| | | Co 1 | - | - | 0 weeks | - | - |
| | | Co 2 | 1 week | 1 week | 0 weeks | - | - |

oviposition immediately in Out 1 after placement in May, oviposition of *R. linnaei* was delayed for two weeks (Fig. 7). In July, immediate oviposition after placement was observed for both species in Out 1, Co 1 and Co 2. After placements in September only females of *R. sanguineus* s.s. started oviposition at each experimental site after one week.

Despite the absence of engorged Females in February and November, oviposition by *R. sanguineus* s.s. was documented ten times in total. In contrast, oviposition by *R. linnaei* females was documented seven times, despite two additional placements in December and February (Fig. 7). However, these placements occurred during the winter. No oviposition was documented for *R. sanguineus* s.s. at experimental sites Co 1 (May) and Out 2 (July). No oviposition was documented for *R. linnaei* after placements in September and November as well (Table 6). Oviposition stopped at latest with the death of the females (Table 6).

The egg masses produced in the laboratory and placed at experimental sites were monitored for larval hatching. Larvae hatched from egg masses of *R. sanguineus* s.s. at all experimental sites after placements in July after 3-4 weeks indoors and 4-5 weeks outdoors. *R. linnaei* larvae hatched after egg mass placement in July and in September at experimental sites Out1, Co1 and Co2 (Table 7). Larval hatching of *R. linnaei* started after 3-5 weeks indoors and 4 weeks outdoors after placement of egg masses. Maximum survival of freshly hatched larvae from egg masses placed in the experimental sites was also observed (Table 7). The time between the first documented hatched larvae and the death of the last was documented as the survival duration. The survival time of individual larvae was not documented. Freshly hatched larvae (Table 7) from egg masses placed in July and September showed a significantly longer survival time than laboratory-bred larvae (Table 5, chapter Larvae).

For *R. sanguineus* s.s., each of the egg masses could be considered as fully hatched (100 %) for placement in July. In addition to a 100 % hatching rate observed in Out 1 and Co 1, an estimated 60 % of *R. linnaei* eggs hatched after placements in July and 5 % in September at experimental site Co 2 (Fig. 8).

## 4. Discussion

The introduction of *Rhipicephalus* species to Germany has already occurred in recent years. This has resulted in severe infestations with hundreds of reproducing *R. sanguineus* s.s. ticks in private households. Some of these infestations occurred without prior travel activities. It is therefore possible that these cases could be considered as established populations (Fachet-Lehmann et al., 2025). Since populations of *R. sanguineus* s.s have also been detected in other non-endemic areas (such as Alsace or Hungary), i.e. in areas with similar climatic conditions to Germany, it cannot be ruled out that *Rhipicephalus* species can also become established outdoors in Germany or at least survive for a longer period of time (Beugnet et al., 2011; ECDC, 2023; van Wyk et al., 2024). Until now, it was assumed that *Rhipicephalus* species are not able to survive outdoors in Germany. Due to the changed climatic conditions this assumption needs to be reviewed. This study assessed whether *R. sanguineus* s.s. and *R. linnaei* can persist outdoors in Germany under extreme conditions. Our experimental setup at outdoor sites did not allow the ticks to retreat from weather conditions and therefore represents unfavorable conditions during the trial period. The unfavorable conditions include the fact that the ticks did not have any host interaction, and this resulted in a long period of starvation, which the ticks rarely have to withstand in nature. Conducted in southern Germany, our study offers initial insights into tick survival, oviposition, and egg hatching though it does not represent the full climatic spectrum of Germany. The ticks were kept in two different outdoor areas and were exposed to temperature profiles, ranging from -7 to 50 °C with daily and weekly temperature fluctuations, and very different levels of humidity throughout the trial period. Temperature and humidity were considered as primary influencing factors, while other environmental variables such as photoperiod, solar radiation, and wind were not included.

Our results show that both *Rhipicephalus* species can survive outside of buildings. So far, only a few studies have been carried out to study the survival abilities of *R. sanguineus* s.l. including *R. sanguineus* s.s. and *R. linnaei* as separated species or at least as temperate and tropical

**Table 7**

Evaluation of released egg masses and hatching of larvae of *R. sanguineus* s.s. and *R. linnaei* between February 2023 and May 2024 at outdoor (out1, out2) and indoor sites (Co1, Co2).

| Species | Developmental stage of ticks | Experimental site | Feb | Apr | May | July | Sep | Nov |
|---|---|---|---|---|---|---|---|---|
| *R. sanguineus* s.s. | No. of released egg masses | Out 1 | | 1 | 1 | 1 | 1 | 1 |
| | | Out 2 | | 1 | 1 | 1 | 1 | 1 |
| | | Co 1 | | 1 | 1 | 1 | 1 | 1 |
| | | Co 2 | | 1 | 1 | 1 | 1 | 1 |
| | egg masses that hatched | Out 1 | | | | 1 | | |
| | | Out 2 | | | | 1 | | |
| | | Co 1 | | | | 1 | | |
| | | Co 2 | | | | 1 | | |
| | time until hatching starts | Out 1 | | | | 4 weeks | | |
| | | Out 2 | | | | 5 weeks | | |
| | | Co 1 | | | | 3 weeks | | |
| | | Co 2 | | | | 4 weeks | | |
| | survival of freshly hatched larvae | Out 1 | | | | 10 weeks | | |
| | | Out 2 | | | | 12 weeks | | |
| | | Co 1 | | | | 8 weeks | | |
| | | Co 2 | | | | 10 weeks | | |
| *R. linnaei* | No. of released egg masses | Out 1 | | 1 | 1 | 1 | 1 | 1 |
| | | Out 2 | | 1 | 1 | 1 | 1 | 1 |
| | | Co 1 | | 1 | 1 | 1 | 1 | 1 |
| | | Co 2 | | 1 | 1 | 1 | 1 | 1 |
| | egg masses that hatched | Out 1 | | | | 1 | | |
| | | Out 2 | | | | - | | |
| | | Co 1 | | | | 1 | | |
| | | Co 2 | | | | 1 | 1 | |
| | time until hatching starts | Out 1 | | | | 4 weeks | | |
| | | Out 2 | | | | - | | |
| | | Co 1 | | | | 5 weeks | | |
| | | Co 2 | | | | 3 weeks | 5 weeks | |
| | survival of freshly hatched larvae | Out 1 | | | | 10 weeks | | |
| | | Out 2 | | | | - | | |
| | | Co 1 | | | | 10 weeks | | |
| | | Co 2 | | | | 4 weeks | 5 weeks | |

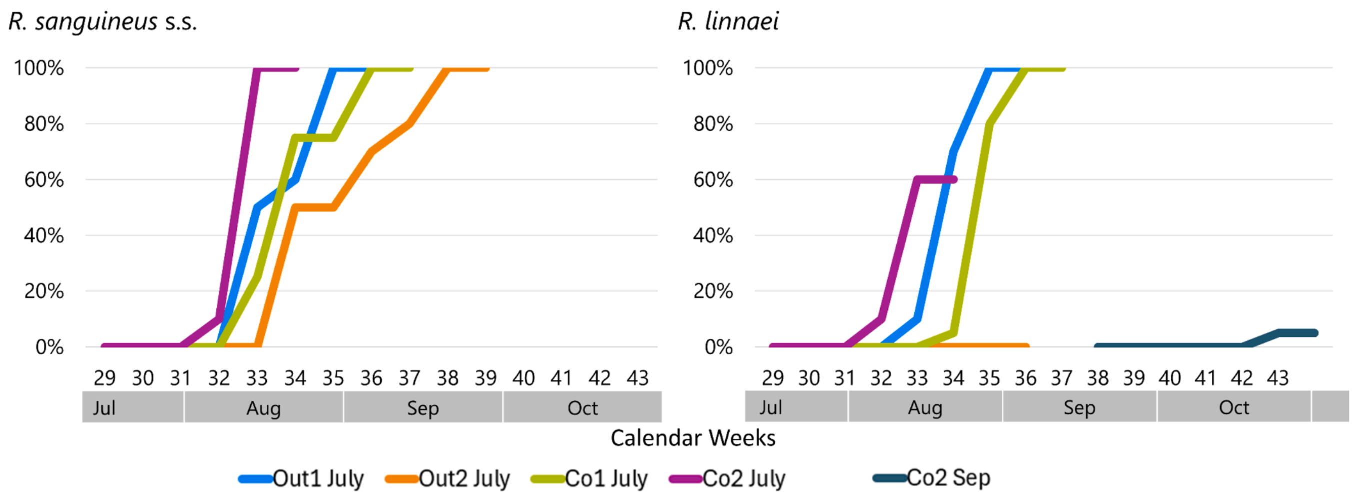

**Fig. 8.** Hatching rate of larvae from egg masses produced in the laboratory of *R. sanguineus* s.s. and *R. linnaei* after the placements in July and September 2023, given in percent. No hatchment of larvae in the months April, May and November were recorded.

lineage. Srivastava and Varma (1964) observed that "*R. sanguineus*" survived under constant laboratory conditions at 25 °C showing survival of adults up to 7 months. Biological parameters such as a short life cycle and four generations per year may suggest that the species collected in India (Madras) and designated as *R. sanguineus* could be *R. linnaei*. Dantas-Torres et al., (2012) compared the outdoor survival of *R. sanguineus* s.s. in Italy with survival under laboratory conditions. They demonstrated that adults survived significantly longer in the laboratory (26±1 °C, 70±10 % rH) than in nature with strong temperature and humidity fluctuations (-2 °C to 41 °C, 55-85 %rH). Labruna et al., (2017) investigated the survival time under laboratory conditions and different temperatures. The ticks that were kept at 16 °C survived significantly longer than ticks kept at 29 °C, indicating that temperature has a negative impact on survival.

**Table 8**
Comparison of maximum survival times of *R. sanguineus* s.s. and *R. innaei* in weeks for larvae (L), nymphs (N) and adults (A).

| Author | Species | survival in weeks | | | Method |
|---|---|---|---|---|---|
| | | L | N | A | |
| This study | *R. sanguineus* s.s. | 5 | 20 | 44 | Outdoors, changing climate |
| This study | *R. sanguineus* s.s. | 3 | 6 | 37 | Indoors, changing humidity |
| Dantas-Torres et al., 2012 | *R. sanguineus* s.s. | 5 | 6 | 55 | Outdoors, changing climate |
| Dantas-Torres et al., 2012 | *R. sanguineus* s.s. | 6 | 7 | 83 | Lab, constant conditions |
| Labruna et al., 2017 | *R. sanguineus* s.s. | 16 | 44 | 66 | Lab, constant conditions |
| Srivastava and Varma, 1964 | *R. sanguineus* s.l. | 16 | 8 | 28 | Lab, constant conditions |
| This study | *R. linnaei* | 4 | 10 | 37 | Outdoors, changing climate |
| This study | *R. linnaei* | 3 | 6 | 20 | Indoors, changing humidity |
| Labruna et al., 2017 | *R. linnaei* | 12 | 24 | 34 | Lab, constant conditions |

Although a comparison of laboratory-generated data with field data is limited, the data summarized in Table 8 show, especially for the field data, that *Rhipicephalus* species can also survive for a certain time in non-endemic areas such as Italy or Germany.

### 4.1. Adults

Adult ticks of both species exhibited prolonged survival under outdoor conditions. In spring, summer, and autumn, survival times at both outdoor sites were significantly longer than indoors. Despite substantial fluctuations in temperature (–7 °C to 50 °C) and relative humidity (17–100 %) at outdoor sites, *R. sanguineus* s.s. consistently demonstrated extended survival, with 44 weeks maximum after placement in February and 4 weeks minimum after placement in November. *R. innaei* survived 37 weeks maximum after placements in February, showing the same pattern as *R. sanguineus* s.s. to survive longer outdoors than indoors. The assumption by Labruna et al. (2017) that *R. linnaei* exhibits only half the survival time of *R. sanguineus* s.s. under identical conditions (24 °C in laboratory experiments) could not be confirmed in our study (Table 8) as this study revealed that *R. linnaei* reached approximately 80 % of the survival time of *R. sanguineus* s.s. held under same conditions (Table 3).

The prolonged outdoor survival of adults corresponds with findings by Tian et al. (2023), who demonstrated increased mortality at elevated temperatures (≥30 °C) and reduced relative humidity (≤75 %) for *R. sanguineus* s.s. and *R. linnaei*. At Co2, where relative humidity rarely exceeded 70 %, *R. sanguineus* s.s. was able to survive for 24 weeks only (Table 3). In contrast, survival of *R. sanguineus* s.s. under laboratory conditions reported by Dantas-Torres et al., (2012) reached up to 83 weeks at 26 ± 1 °C and 70 ± 10 % rH, highlighting the significant influence of stable conditions and constant high humidity levels for long survival (Table 8). The average humidity at Co2 of around 50 % caused reduced survival times for both species, with bigger impact on *R. linnaei*. It can therefore be assumed that an average low humidity of 50 % has a negative influence on the survival time, like it was verified by Tian et al., (2023). In contrast, the survival rates of the adults at Co 1, the shelter without temperature regulation, demonstrated combined results of outdoor and indoor sites characterized by lower humidity and a temperature adapted to outdoor areas with reduced variations. This combination of reduced indoor humidity and delayed outdoor temperatures in Co1 resulted in a significantly reduced lifespan of adult ticks for both species after placements in February and June compared to outdoor sites. However, adult *R. sanguineus* s.s. placed in November in Co 1 exhibited a significantly increased survival time, demonstrating more suitable conditions for survival under these protective conditions

(Fig. 4). Nevertheless, individuals died during the colder period with sub-zero temperatures. Therefore, garden sheds like Co 1 are not considered a suitable overwintering habitat except for insulated sheds or kennels where temperatures stay above freezing. This suggests that in addition to low humidity, sub-zero temperatures also have a strong negative impact on the survival time of the adults. Accordingly, a protected environment that is regularly supplied with moisture and prevents sub-zero temperatures, such as a greenhouse or a doghouse, could be a suitable location outside of permanent buildings that would enable a population to survive or establish.

The outdoor placements in November, with average temperatures of 4.6 °C and relative humidity near 95 %, resulted in rapid mortality in both species. Fluctuating temperatures that also reached a constant sub-zero level over weeks resulted in ice crystal formation and exposure to wintery conditions (Fig. 3). Indoors, both species showed prolonged survival in winter (Table 3). Outdoors in winter, none of the tick individuals survived until spring, indicating that current winter conditions in southern Germany are still unsuitable for overwintering.

The time until half of the population dies ($LT_{50}$) varies notably between *R. sanguineus* s.s. and *R. linnaei*, especially in outdoor sites (Fig. 4). *R. sanguineus* s.s. populations reached half population size late, at 78–86 % of their maximum survival time outdoors, demonstrating their ability to sustain stable populations over extended periods with minimal climatic impact on survival. An exception was observed at Co 2, where adults reached half population size earlier, at 58 % of the maximum survival time. It follows that the average $LT_{50}$ of adult *R. sanguineus* s.s. at outdoor sites suggests that cold temperatures and fluctuating moisture levels are probably more limiting than low average temperatures alone.

In contrast, adult *R. innaei* populations declined rapidly both outdoors and indoors (Table 3). A likely explanation is the faster life cycle of *R. innaei* combined with higher baseline activity as seen during handling and counting by immediate response behavior (personal observation). Unlike *R. sanguineus* s.s., which often remained immobile or displayed questing behavior in elevated positions. *R. linnaei* exhibited a more vigorous activity and escape attempts during laboratory handling (personal communication Prof. Matias P.J. Szabó, April 2, 2025). It is possible that the metabolic resources of *R. linnaei* are exhausted rapidly and result in a shorter lifespan. Additionally, *R. linnaei* is more susceptible to heavy rainfall, as the mortality rate of adults increased outdoors after periods of high humidity or heavy rainfall. Individuals of *R. innaei* were frequently found dead in accumulated moisture. This is in line with reports about high mortality rates of *R. linnaei* during rainy seasons in forested areas (93–100 % rH; personal communication Prof. Matias P.J. Szabó, April 2, 2025). In contrast, *R. sanguineus* s.s. displayed clear signs of moisture avoidance and were often located in dry areas such as the cage lids, suggesting an adaptive behavioral strategy to prevent exposure to flooding. This may reflect ecological differences in microhabitat preference or a narrow range of environmental tolerance. Unfortunately, studies about the on-host and off-host ecology of *R. linnaei* have not yet been published to confirm any observation in our study.

### *4.2. Nymphs and larvae*

Like adults, juveniles survived significantly longer outdoors than indoors, except for placements in November. After placements in summer (May, June), again, humidity seems to be more important than high temperatures, which in combination with prolonged sub-zero temperatures leads to ice formation in winter (November), resulting in rapid death of all specimens. Neither nymphs nor larvae lived long enough to make a noticeable difference in survival time between the experimental sites after placement in winter. Significantly longer survival times of *R. sanguineus* s.s. compared to *R. linnaei* were also documented, especially in outdoor sites. In our study, *R. sanguineus* s.s. survived up to 2.8 times (nymphs Fig. 5,) and up to 5 times (larvae, Fig. 6) longer than *R. linnaei* in outdoor sites (Table 4 & 5) demonstrating the faster adaptation to the German climate by *R. sanguineus* s.s., which is adapted to Mediterranean and temperate climate.

*R. sanguineus* s.s. nymphs survived at outdoor sites for up to 20 weeks in summer (Table 4), with strong differences to the data of Dantas-Torres et al., (2012) where nymphs survived only 4 to 6 weeks in the environment. The authors stated that the host seeking period in summer has a negative effect on survival time on juveniles, but temperature and humidity are also important, as they recorded 55 %rH and 25 °C in Italy. Humidity levels below 80 %rH seem to be crucial for both species, as evidenced by studies of Tian et al., (2023). Compared to our studies, the humidity in the study of Dantas-Torres et al., (2012) was much lower in June, underlining the negative impact of low humidity on survival for both species. Larvae as well showed prolonged survival outdoors than indoors but both species exhibited a generally short lifespan (1 to 5 weeks, Table 5), similar to the results of the outdoor experiments of Dantas-Torres et al., (2012), (5 weeks, June to July).

Larval hatching from egg masses placed in outdoor sites allowed additional observation of the survival time compared to laboratory-bred larvae. Larvae that freshly hatched in the experimental sites in our study survived significantly longer than laboratory-bred larvae (Table 5, Table 7). Both larvae groups (freshly hatched and laboratory-bred) were counted weekly and therefore handled equally at experimental sites. These substantial differences in survival time indicate that laboratory-bred larvae probably expanded their energy reserves more rapidly due to transportation stress and handling during the experiment. Adapting to the weather after placement also seemed to consume more energy. The short survival time of laboratory-bred larvae does not allow any further analysis.

Inter-species comparison of freshly hatched larvae from egg masses (placements in July) underlines the faster adaption of *R. sanguineus* s.s. to German climate by a shorter survival of *R. linnaei*. Freshly hatched larvae of *R. sanguineus* s.s. survived for up to 12 weeks and *R. linnaei* for 10 weeks in outdoor sites. Survival in winter was also not observed, as the egg masses of both species placed in July hatched, but larvae died in November (*R. sanguineus* s.s.) and October (*R. linnaei*), with the onset of temperatures of 10 °C and lower.

### *4.3. Oviposition of engorged females and egg masses*

In order to test possible reproduction and thus the possible establishment of a population of *R. sanguineus* s.l. under German climatic conditions, engorged females were placed frequently in the experimental set-up and then observed. Under German climatic conditions the oviposition success and larval hatching was crucial. This reproductive success is essential to consider a temporary or even long-term establishment of *R. sanguineus* s.l. outdoors.

Engorged females of both species were able to survive after several placements. The survival of engorged females at outdoor sites was significantly longer in the summer months of placements than in winter, especially for *R. linnaei*. Formations of ice and periods of sub-zero temperatures ended the lifespan within one week after placements in November. After placements in May, July and September, engorged females were able to survive outdoors (Table 6) whereby females died after finishing their oviposition.

The survival time of the engorged females was long enough to lay eggs at multiple months of placement. As expected, *R. sanguineus* s.s. adapted well to the German climate outdoors. However, contrary to expectations, the oviposition of *R. linnaei* was also successful at three placements in Out 1 and Out 2 (Table 6). Simultaneous oviposition outdoors of both species was documented after placement of engorged females in May and July, but not in September. The short period in early summer provided the climatic conditions necessary for both species to lay their eggs. Especially after placements in September oviposition was documented for *R. sanguineus* s.s. at every experimental site, which indicates the fast adaptation to the German climate by the European species. Labruna et al. (2017) documented oviposition for *R. sanguineus* s.s. at 10 °C in lab studies and again for both species at low temperatures of 13-16 °C, indicating that low temperatures are not the limiting factor for oviposition success. In our study February and November covered nearly the temperature profile comparable to the study of Labruna et al., (2017) (13-16 °C) but no oviposition was documented outdoors for *R. innaei*. Strong fluctuations in temperature and humidity, also reaching sub-zero temperatures, in the outdoor area of our study disturbed oviposition of *R. linnaei*. However, none of the engorged females of *R. linnaei* were observed to oviposit after placements in September and November, both indoors and outdoors. Since the sample size is small, a lack of oviposition is not particularly significant. Besides climate factors, the lack of oviposition after February, September and November placements might be due to by other abiotic factors such as the photoperiod or biotic factors such as undetected issues within the breeding colony, as it is already the 6th generation fed on Rabbits.

As expected, only few eggs of *R. linnaei* developed under outdoor conditions. As a species adapted to tropical regions, *R. linnaei* eggs it can be assumed that development of eggs requires humidity above 60 % and permanently warm temperatures. Dantas-Torres et al., (2012) demonstrated that at temperatures around 13 °C, more than 3 % of egg clutches of both species hatched. However, in months that reached temperatures of 13 °C on average like February, September and November no hatching of larvae was observed in our study, regardless of species (Table 7). It can therefore be assumed that the consistently warm temperatures in July and August enabled the larvae to hatch (100 %), while the sometimes brief periods of low temperatures during the other months prevented hatching (Fig. 8). Even though the period of optimal weather conditions in the year 2023 was short, it can be assumed in future as well that during a short time in summer with persistent temperatures of 10-25 °C and humidity exceeding 60 %, both oviposition takes place as well as hatching of larvae.

### *4.4. Survivability of R. sanguineus s.s and R. linnaei in Germany – an outlook*

The results of our study demonstrate that all developmental stages of both species, despite the consensus of current literature (Zumpt, 1939; Chitimia-Dobler and Dobler, 2019; Rubel et al., 2022), can already survive outdoors in the South of Germany for several months and showed reproductive success in form of oviposition and hatched larvae. It can be hypothesized that the establishment of a persistent population outdoors in Germany is possible when adult individuals are introduced in spring, engorged females drop off the host in May to lay eggs, and larval hatching is finished in July. The long survival of freshly hatched larvae in this study demonstrated the survival of larvae at least until the beginning of winter in November. Therefore, especially *R. sanguineus* s.s. can persist long enough to feed on potential hosts successfully oviposit and larvae successfully hatch, which clearly demonstrates that the establishment of single outdoor populations is possible under German climate conditions, at least temporarily. However, in addition to suitable climatic conditions, outdoor establishment requires the presence of suitable hosts for blood meals as well as successful molting, which was not part of this study (Clout et al., 2000; Mata et al., 2013; Duncan et al., 2014).

For *R. sanguineus* s.s. outdoor survival is of vital importance, as this species is adapted to temperate climates and clearly shows fast adaption to German climates as well. As previously mentioned, *R. sanguineus* s.s. has been identified in the Alsace region of France (ECDC, 2023) and is reported in newly non endemic areas in long distance to the mediterranean sea (Cerný, 1989; Mihalca et al., 2012; Buczek and Buczek, 2020; Dantas-Torres et al., 2024). Additionally, dogs without travel history have been infested with *Rhipicephalus* ticks, suggesting possible established populations. The long-term survival of all developmental stages in our study supports the authenticity of these cases. In principle, it is possible *for R. sanguineus* s.s. to be spread within Germany and this has already happened (Fachet-Lehmann et al., 2025). The potential of spreading into the environment has also been proven by our study. This includes tick transfer between private gardens and non-urban areas via hosts. So far, infestations by *R. sanguineus* s.l. of wild animals that also occur in Germany, have been rarely investigated, but foxes (*Vulpes vulpes*), European hedgehogs (*Erinaceus europaeus*), Iberian lynxes (*Lynx pardinus*) and yellow-necked mice (*Apodemus flavicollis*) have been identified as possible hosts in Europe (Millán et al., 2007; Mihalca et al., 2012; Bezerra-Santos et al., 2021; Lesiczka et al., 2023; Schütte et al., 2024). These infestations rather involve *R. sanguineus* s.s. than other *Rhipicephalus* species. In Central Europe, common rodent species such as bank voles (*Myodes glareolus*) and yellow-necked mice, as well as hedgehogs could serve as viable hosts for *R. sanguineus* s.s., thereby supporting its potential establishment in outdoor environments (Obiegala et al., 2021; Schütte et al., 2024). Considering the variable landscape of Germany and the significantly different climate between the warmer south and the colder north facing the North Sea and Baltic Sea, it is more likely that populations will first establish in areas with warmer annual temperatures or shift to Germany from the Alsace region (France). However, due to the irregular introduction of ticks by dogs (through travel or vacations) (Fachet-Lehmann et al., 2025), it is not possible to make accurate predictions.

*R. innaei* showed reduced outdoor survival rates, limited oviposition, and less hatching success of larvae, demonstrating that establishment in Germany under current climatic conditions is unlikely. In endemic areas in Brazil *R. linnaei* infestations are typically restricted to rural households and close to dogs, although suitable hosts such as wild canids are present in forested areas (Szabó, pers. comm., April 2, 2025). However, given its vector competence for pathogens of veterinary and medical relevance, such as *Ehrlichia canis* in dogs (Moraes-Filho et al., 2015; Intirach et al., 2024) and *Rickettsia* spp. in humans (Marquez et al., 2021; Nieto-Cabrales et al., 2024), the prolonged survival of *R. linnaei* in Germany is a matter of concern it poses a significant health risk to both humans and animals.

Although it is generally assumed that *R. sanguineus* s.l. prefers indoor environments, as it is addressed as nidicolous and endophilous (Dantas-Torres, 2010; Gray et al., 2013), our study clearly demonstrates better outdoor survival than indoors. Indoor survival of both species appears to be dependent on continuous host availability, suggesting that a combined indoor–outdoor life cycle is possible. This poses a particular risk for dog owners whose dogs have access to a garden and can therefore spread a tick infestation between the outdoor and indoor areas resulting in long-lasting and resistant tick burden for dogs and humans then.

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Author contributions: KFL –Conceptualization, Data curation, Funding acquisition, Methodology, Investigation, Validation, Formal analysis, Visualization, Writing original draft; AL – Project administration, Conceptualization, Funding acquisition, Writing review and editing; UM – Supervision, Funding acquisition, Resources, Writing review and editing

## Ethics approval

This is an observational study about the survival of ticks, no ethical approval is necessary. Ticks were purchased from Insect Services GmbH, so no animal testing was required for this study.

**Data availability:** The datasets analyzed and included as results during the current study are available from the corresponding author on reasonable request.

## Using of AI

There is no significant use of AI.

## CRediT authorship contribution statement

**K. Fachet-Lehmann:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Data curation, Conceptualization. **A. Lindau:** Writing – review & editing, Project administration, Funding acquisition. **U. Mackenstedt:** Writing – review & editing, Supervision, Funding acquisition.

## Competing interest

There are no relevant competing interests to disclose for KFL and AL, UM declares that she repeatedly lectured for and acted as consultant for diagnostic and (veterinary) pharmaceutical companies and has previous and ongoing research collaborations with various diagnostic and (veterinary) pharmaceutical companies.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2025.102560.

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