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Epidemiology and treatment of respiratory nematode infections in western European hedgehogs (*Erinaceus europaeus*)

Catarina Jota Baptista [a,b,*], Inês Gama [c,d], Julia Serena [e], Petr Heneberg [f,**], María Cásero [e], Luís Madeira de Carvalho [c,d]

[a] Egas Moniz Center for Interdisciplinary Research (CiiEM), Egas Moniz School of Health & Science, Caparica, 2829-511, Portugal
[b] Center for the Research and Technology of Agro-Environmental and Biological Sciences (CITAB-Inov4Agro), UTAD, Vila Real, 5000-801, Portugal
[c] CIISA—Center of Interdisciplinary Research in Animal Health, Faculty of Veterinary Medicine, University of Lisbon, Avenida da Universidade Técnica, Lisbon, 1300-477, Portugal
[d] Laboratory for Animal and Veterinary Sciences (AL4AnimalS), Avenida da Universidade Técnica, Lisbon, 1300-477, Portugal
[e] RIAS-ALDEIA - Wildlife Rehabilitation and Research Center, Ria Formosa Natural Park, Olhão, Portugal
[f] Charles University, Third Faculty of Medicine, Prague, Czech Republic

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ABSTRACT

Respiratory nematodes are common in rescued western European hedgehogs (*Erinaceus europaeus*), but their epidemiology and treatment in rehabilitation settings remain poorly defined. We investigated respiratory nematode infections in 78 fecal samples of 30 hedgehogs admitted to a wildlife rehabilitation center in southern Portugal and in putative gastropod intermediate hosts. Outcomes after subcutaneous levamisole (10–20 mg/kg) and ivermectin (3 mg/kg) treatments, monitored by the Baermann technique, were compared. Respiratory nematode infections were highly prevalent in rescued hedgehogs and may be sustained within rehabilitation facilities by infected gastropod intermediate hosts. At the animal level, *Crenosoma striatum* was detected in 63% of hedgehogs and *Capillaria* spp. in 7% of hedgehogs, including a mixed infection in one hedgehog. The Baermann technique was the most sensitive method for detecting *C. striatum*. Samples from outdoor enclosures were more often positive for *C. striatum* than those from indoor enclosures (55% vs. 29%). All the examined gastropods (10/10) were positive for *C. striatum* larvae, supporting active transmission within the rehabilitation center. Outcomes were better with levamisole than with ivermectin, although persistence and relapses were frequent. Neither treatment resulted in consistent clearance. These findings support the need for integrated parasite management and standardized treatment protocols in wildlife rehabilitation centers.

1. Introduction

The western European hedgehog (*Erinaceus europaeus*) is a small mammal widely distributed across Western and Central Europe. The conservation status of *E. europaeus* was revised to near-threatened in 2023, reflecting concerns about population declines reported in several European countries, including the United Kingdom and Denmark (Rasmussen et al., 2020, 2024). Several zoonotic agents have been reported in hedgehogs, and their proximity to humans also exposes them to multiple anthropogenic threats, including poisoning, vehicle collisions, injuries from lawn mowers or garden netting, and predation by companion animals, particularly dogs (Rautio et al., 2016). Among the diseases affecting rescued hedgehogs, verminous pneumonia caused by *Crenosoma striatum* is among the most commonly reported respiratory parasitoses and one of the most prevalent lung lesions described in rehabilitation settings (Lehmann et al., 2024). Adult worms inhabit the bronchi and trachea (Taylor et al., 2016; Lehmann et al., 2024). Eggs produced by females hatch into larvae, usually within the respiratory tract; these larvae are then swallowed and pass through the gastrointestinal tract, which explains their detection in feces, although excretion may be inconsistent (Taylor et al., 2016). Gastropods, including shelled and shell-less snails and slugs such as *Succinea* spp. and *Agriolimax* spp., act as intermediate hosts and harbor infective third-stage larvae (Lange et al., 2018; van de Sanden et al., 2025). Following ingestion, the larvae

* Corresponding author. Egas Moniz Center for Interdisciplinary Research (CiiEM), Egas Moniz School of Health & Science, 2829-511, Caparica, Portugal.
** Corresponding author. Charles University, Third Faculty of Medicine, Ruská 87, CZ-100 00 Prague, Czech Republic.
E-mail addresses: catabap@hotmail.com (C. Jota Baptista), petr.heneberg@lf3.cuni.cz (P. Heneberg).

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migrate from the intestine to the lungs, presumably via vascular or lymphatic pathways (Carreno and Nadler, 2003; Taylor et al., 2016).

Clinical signs associated with *C. striatum* infection include dry cough, abnormal respiratory sounds, choking episodes, pneumonia, anemia, and, in severe cases, death. Parasitic bronchopneumonia is especially frequent in juvenile hedgehogs. Other respiratory nematodes have also been reported in hedgehogs. In particular, *Capillaria* spp., especially *Eucoleus aerophilus* (syn. *Capillaria aerophila*), are commonly identified at necropsy either alone or in mixed infections with *C. striatum* (Majeed et al., 1989; Beck, 2007; Hoseini et al., 2014; Alfaia et al., 2024). However, the clinical relevance of these infections is not uniformly interpreted in the literature. Severe or persistent respiratory parasitism may adversely affect morbidity, rehabilitation, recovery, and eventual reintroduction. The indication for antiparasitic treatment or prophylaxis in hedgehogs remains debated. Levamisole is often considered the treatment of choice, particularly in severe clinical cases and debilitated animals, but protocols based on ivermectin or moxidectin have also been described, with variable and often inconclusive outcomes (Cousquer, 2004; Mariacher et al., 2021; Van De Weyer et al., 2023; Lehmann et al., 2024). A summary of published reports on the use of ivermectin and levamisole for treating respiratory nematode infections in hedgehogs is presented in Table 1.

In the present study, we investigated the pathology, epidemiology, and treatment of respiratory nematode infection in *E. europaeus* admitted to a wildlife rehabilitation center in southern Portugal. The specific aims were to: (i) semiquantitatively assess respiratory nematode infection in admitted hedgehogs; (ii) explore whether temporal variation in rainfall and the presence of gastropod intermediate hosts were associated with reinfection risk and delayed coprological positivity in the rehabilitation setting; and (iii) compare the outcomes of two subcutaneous treatment protocols commonly used for treating verminous pneumonia, namely levamisole and ivermectin.

2. Materials and methods

2.1. Sampling

Between September 2021 and February 2022, 78 fecal samples were collected from 30 *E. europaeus* admitted to the Wildlife Rehabilitation and Research Center of Ria Formosa (RIAS), Portugal. Samples were collected from the bottom of transport boxes or cardboard containers with a spatula, taking care to avoid soil contamination and minimize handling stress. In animals housed individually indoors, feces could be collected directly over three consecutive days. In shared outdoor enclosures, the animals were temporarily separated into transport boxes or cardboard containers and monitored for up to 2 h until defecation. The samples were stored at 4 °C until analysis. Fecal samples were stored at 4 °C until analysis to preserve larval viability for Baermann examination. Freezing may damage larvae and compromise the recovery of motile first-stage larvae. Hedgehogs admitted dead, or those that were euthanized or dying during rehabilitation, underwent routine necropsy as part of the RIAS protocol. Lungs showing gross lesions compatible with verminous pneumonia were examined in detail. Nematodes were manually recovered from one lung, preserved in 70% ethanol in Eppendorf tubes, and used for molecular confirmation of *C. striatum* infection. Sex information was unavailable for several individuals and was therefore excluded from the analyses.

2.2. Study site and climatic variables

RIAS is located in Ria Formosa Natural Park (Olhão, Faro, Portugal) and receives wild animals from the Algarve and Baixo Alentejo regions, the southernmost areas of Portugal. The center has more than 15 years of experience in wildlife rehabilitation and is part of the Portuguese wildlife rescue center network (ALDEIA Association). In recent years, hedgehog admissions have increased markedly, from approximately 10 individuals per year at the beginning of the twenty-first century to approximately 150 individuals per year at present. Housing conditions (Fig. 1a–d) reflected routine practices in rehabilitation-center management. Hedgehogs could therefore be maintained indoors, outdoors, or sequentially in both settings during treatment and follow-up. Juveniles and debilitated animals were generally housed indoors initially and transferred to outdoor rehabilitation enclosures once clinically stable or above approximately 300 g body weight.

The Algarve region has a temperate Mediterranean climate characterized by rainy winters and hot, dry summers. The mean temperatures are approximately 25 °C in summer and 15 °C in winter, with most rainfall occurring between October and May and an average annual

Table 1
Summary of published reports on the use of ivermectin and levamisole for treating respiratory nematode infections in hedgehogs.

Drug	Reference	Hedgehog species	Parasite(s)	Dose regimen	Route	Main reported outcome
Ivermectin	Van De Weyer et al. (2023)	*E. europaeus*	*Capillaria* spp.	0.4 mg/kg weekly for 2 doses	Oral	Approximately 60% efficacy
	Cousquer (2004)	*E. europaeus*	*C. striatum*	0.2–0.4 mg/kg weekly for 2–3 doses	Oral/ subcutaneous	Partial efficacy; less effective than levamisole
	Mariacher et al. (2021)	*E. europaeus*	Mixed infections (*C. striatum*, *Capillaria* spp.)	Not specified	Not specified	Levamisole was considered more effective
	Pfäffle (2010)	*E. europaeus*	Multiple helminths	0.3–0.5 mg/kg, single dose	Subcutaneous	Not consistently effective against lungworms
	Naem et al. (2015)	*E. concolor*	*C. striatum*, *Capillaria* spp.	0.2 mg/kg, single dose	Oral	Limited efficacy; relapses reported
	Soll (1989)	Exotic mammals	Metastrongyles	0.2–0.4 mg/kg, 1–3 doses	Oral/ subcutaneous	Variable efficacy among species
Levamisole	Van De Weyer et al. (2023)	*E. europaeus*	*Capillaria* spp., *C. striatum*	10 mg/kg every 48 h for 3 doses	Subcutaneous	Highest efficacy among tested drugs; approximately 90% against *Capillaria* spp.
	Cousquer (2004)	*E. europaeus*	*C. striatum*	10 mg/kg every 48 h for 3 doses	Subcutaneous	Effective in clinical cases; preferred over ivermectin
	Bexton (2016)	*E. europaeus*	*C. striatum*	10 mg/kg every other day	Subcutaneous	Recommended for verminous pneumonia
	Pfäffle (2010)	*E. europaeus*	Mixed lungworm infections	10 mg/kg	Subcutaneous	Reported as effective; resistance not described
	Naem et al. (2015)	*E. concolor*	*C. striatum*, *Capillaria* spp.	Not specified	Not specified	Preferred over ivermectin, especially in mixed infections
	Beck (2007)	*E. europaeus*	Lung nematodes	10 mg/kg	Subcutaneous	Reported as effective; considered the best option for *C. striatum* infection
	Mariacher et al. (2021)	*E. europaeus*	Mixed infections	Not specified	Not specified	Levamisole was listed among the effective options

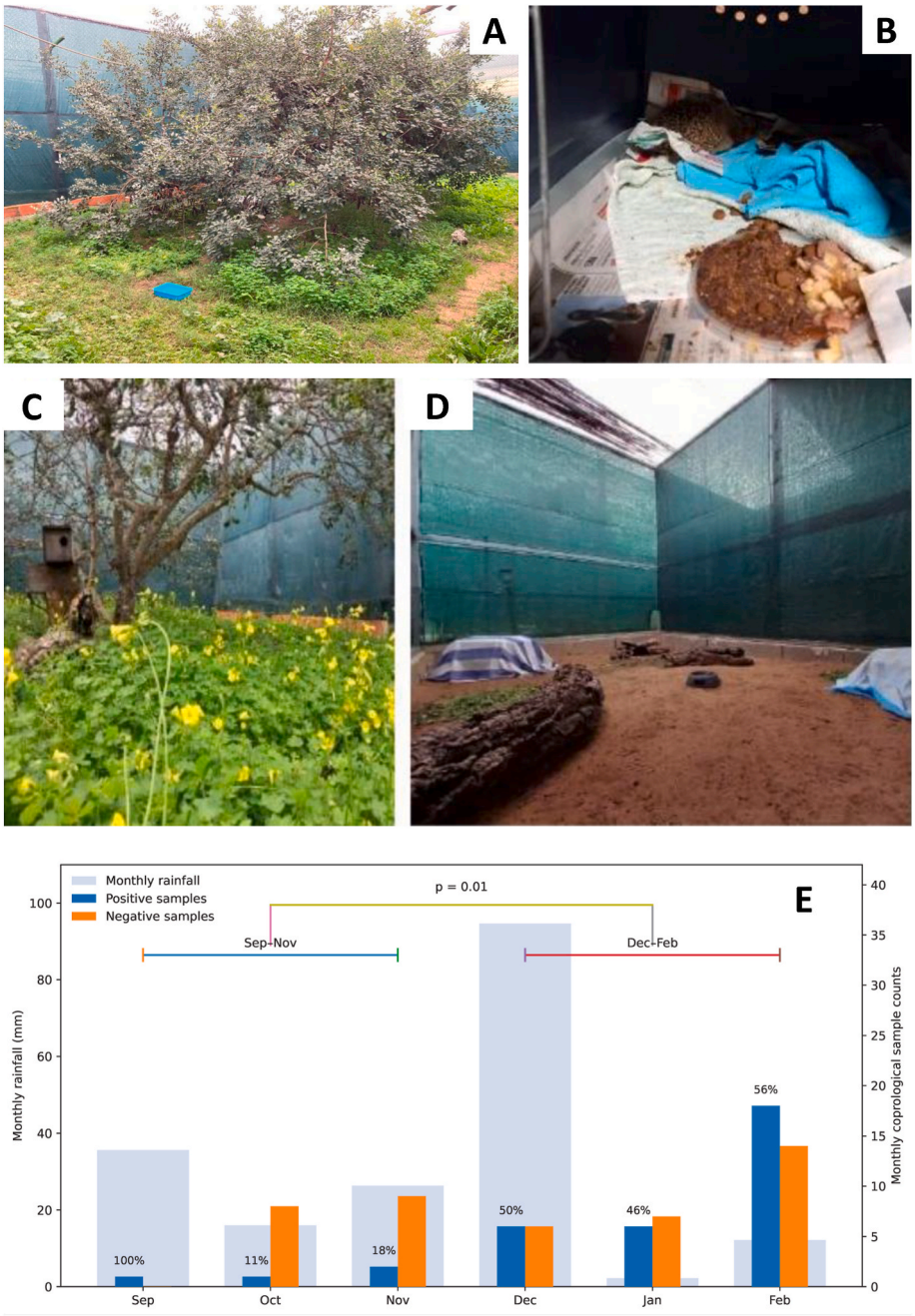

Fig. 1. Environmental context and intermediate hosts of *Crenosoma striatum* infection in rescued western European hedgehogs. **(a–d)** CM10 facility in RIAS, including exterior **(a,c,d)** and interior **(b)** parts. **(e)** Monthly trends in the positive and negative coprology results during the study period. The azure columns represents positive results, the orange columns represent negative results, and the Hawkes blue columns show monthly rainfall precipitation totals in the Faro/Olhão region (in mm). Percents of positive samples are indicated above the azure columns.

precipitation of 509 mm. The relative humidity generally ranges from 55% to 81% and remains above 70% from September to April (Portal do clima - IPMA et al., 2016). Although regional relative humidity remains relatively stable during much of the year, rainfall during the study period differed markedly between the dry early-autumn period and the wetter late-autumn/winter months.

Daily precipitation data for the Faro/Olhão region were obtained from the NASA POWER database using coordinates corresponding to the RIAS region. The corrected daily precipitation variable, PRECTOTCORR, was used. Monthly precipitation totals were calculated by summing daily precipitation values for each calendar month. Monthly coprological prevalence was calculated as the number of positive coprological examinations divided by the total number of coprological examinations in that month.

To evaluate delayed associations between precipitation and subsequent coprological positivity, cumulative precipitation was calculated for rolling 30-day exposure windows. Each window was anchored to the last day of the sampling month and shifted backward in 10-day increments from 0 to 70 days. Thus, the 0-day delay represented precipitation during the 30 days ending on the last day of the sampling month, whereas the 40-day delay represented precipitation during the 30-day period ending 40 days before the end of the sampling month. September was excluded from lag-correlation analysis because only one coprological examination was available. Pearson correlation coefficients were calculated between monthly prevalence and lagged 30-day precipitation totals. In addition, grouped binomial generalized linear

models were fitted using the counts of positive and negative coprological examinations per month. One-sided p-values were used because the a priori hypothesis was that increased precipitation would increase subsequent infection risk by promoting gastropod activity and larval development.

2.3. Coprological examination

Four parasitological methods commonly used in routine coprology were applied: direct fecal smear, Willis flotation, natural sedimentation, and the Baermann technique. For the direct smears, a small amount of feces was mixed with a few drops of saline, placed between a microscope slide and a coverslip, and examined under a microscope (Taylor et al., 2016). For the Willis flotation method, fecal samples were weighed and homogenized with 15–20 mL of saturated sucrose solution using a glass rod (Taylor et al., 2016). The suspension was filtered through a funnel fitted with a metal mesh strainer into a test tube until a convex meniscus formed, after which a coverslip was placed on top. After 15–20 min, the coverslip was transferred to a microscope slide for examination. Passive flotation using the Willis method was selected because centrifugal flotation was unavailable under the routine diagnostic conditions at the rehabilitation center during the study period. Natural sedimentation was performed in parallel with the flotation method. After the coverslip used for flotation was removed, the supernatant was discarded, while the sediment at the bottom of the tube was retained. A few drops of sediment were collected with a Pasteur pipette, placed on a slide, and examined under a microscope (Bowman, 2020). For the Baermann technique, fecal samples were homogenized and weighed, and 10–15 g of feces were wrapped in gauze to form a pouch. The pouch was placed in a conical cup filled with water, ensuring that the sample was completely submerged for 8–24 h. After the gauze was removed, 2 mL of sediment was collected and transferred to a Falcon tube. After vortexing, a 100-µL aliquot was placed between a slide and a coverslip for microscopic examination. *C. striatum* larvae were counted, and the number of larvae per gram of feces (LPG) was calculated as follows: LPG = (n × 2 mL/0.1 mL)/sample weight (Alho et al., 2013). All the slides were examined at 4×, 10×, and 40× magnifications.

A fecal sample was considered positive when respiratory nematode larvae or eggs were detected by at least one of the coprological methods performed. At the individual level, hedgehogs were considered positive if parasites were detected in at least one fecal sample by any coprological method during the study period; animals were considered negative if parasites were never detected. Because some hedgehogs underwent repeated coprological examinations during rehabilitation, temporal comparisons between the early and late study periods were based on coprological observations rather than fully independent host-level prevalence estimates.

2.4. Examination of gastropod intermediate hosts

Because gastropods (slugs) were visually abundant in the RIAS facilities during the wet season, they were collected from one enclosure (CM10; Fig. 1a) to assess the presence of nematode larvae. Gastropods were observed throughout the study period, but appeared less abundant during the dry season and became visibly more common during wetter periods. In January 2023, 10 gastropods were collected and examined using an adapted Baermann technique, as previously described (Mozzer et al., 2011; Coaglio et al., 2016).

2.5. DNA extraction, amplification, and sequencing

DNA was extracted from whole adult nematodes morphologically compatible with *C. striatum*, which were recovered from lungs during necropsy and preserved in 70% ethanol before molecular analysis. DNA extraction and amplification were performed as previously described using primers targeting the nuclear ITS2 and 28S rDNA loci and the mitochondrial CO1 locus (Heneberg et al., 2014) (Table 2). PCR amplicons were purified using the GenElute PCR Clean-Up Kit (Merck, Darmstadt, Germany) and subjected to bidirectional Sanger sequencing with the same primers on an ABI 3130 DNA analyzer (Applied Biosystems, Foster City, CA, USA). The resulting sequences were deposited in the NCBI Nucleotide database under the accession numbers OQ568208-OQ568209 (partial CO1), OQ568210-OQ568213 (partial 5.8S rDNA and ITS2), and OQ572232-OQ572235 (partial 28S rDNA), and were analyzed using NCBI BLAST.

2.6. Evaluation of treatment protocols

Before January 2023, RIAS had used a commercially available oral levamisole formulation (Tabernil Vermicida) without satisfactory clinical or parasitological response, as treated hedgehogs frequently remained positive by fecal examination and continued to show respiratory symptoms of infection. Tabernil Vermicida is a commercially available oral levamisole formulation for birds containing levamisole hydrochloride 75 mg/mL. In accordance with the product information, we administered it orally in drinking water at 2 mL/L for one day, equivalent to approximately 20–25 mg levamisole/kg body weight, with repeat administration after 2–3 weeks in heavily infested animals or where reinfection risk exists. However, this formulation was not developed for hedgehogs, and complete retrospective records of the exact amount consumed by individual hedgehogs were not recorded. Therefore, alternative protocols described in the literature, including subcutaneous levamisole and ivermectin administration (Soll, 1989), were evaluated.

2.7. Levamisole protocol

Levamisole (Anthelmin, 75 mg/mL) was administered subcutaneously at dosages of 10 or 20 mg/kg. All the animals initially received three administrations on Days 0, 2, and 4. Animals showing respiratory signs compatible with verminous pneumonia received an additional treatment on Day 6. Hoglets and juveniles weighing <300 g received 10 mg/kg, whereas animals weighing >300 g received 20 mg/kg. A total of 41 hedgehogs meeting the inclusion criteria received subcutaneous levamisole treatment and were monitored using repeated Baermann examinations. Admission body weight ranged from 74 to 552 g, with a median of 120 g (IQR: 98–196 g). Most animals were hoglets (78%), whereas juveniles and adults represented 17% and 5% of the cohort, respectively.

Treatment response was monitored using the Baermann technique every 7 days, and the results were recorded as positive (1) or negative (0). Animals that remained positive after the first treatment course could receive a second identical course. Hedgehogs presenting with concomitant disease were excluded from the trial. Weekly Baermann monitoring was used because levamisole was administered in a short treatment

Table 2
Primers used for the amplification and sequencing of mitochondrial and nuclear DNA loci of *Crenosoma striatum*.

Locus	Primer name	Sequence (5′–3′)	Reference
ITS2	NC13 (ITS2)/F	ATCGATGAAGAACGCAGC	Jacobs et al. (1997)
	Dd28SR1	ACAAACAACCCGACTCCAAG	Otranto et al. (2007)
28S rDNA	C1	ACCCGCTGAATTTAAGCAT	Chisholm et al. (2001)
	28S-1270R/22	CAGCTATCCTGAGGGAAACTTC	Sato et al. (2010)
CO1	JB3	TTTTTTGGGCATCCTGAGGTTTAT	Bowles et al. (1992)
	JB4.5	TAAAGAAAGAACATAATGAAAATG	Bowles et al. (1992)

course, and early post-treatment assessment was needed to identify persistent larval shedding or recurrence and to guide retreatment decisions during rehabilitation.

2.8. Ivermectin protocol

Fifteen hedgehogs infected with *C. striatum* were included in the ivermectin trial. Admission body weight ranged from 58 to 460 g, with a median of 126 g (IQR: 99–146 g). Most animals were hoglets (86.7%), whereas juveniles represented 13% of the cohort. The animals received ivermectin (Vectimax, 10 mg/mL) subcutaneously at 3 mg/kg body weight at 21-day intervals for three treatment rounds on Days 0, 21, and 42. Follow-up coprological evaluation using the Baermann technique was performed immediately before each subsequent treatment and 21 days after the final treatment, corresponding to Days 21, 42, and 63. The 21-day retesting interval was used because it coincided with the rehabilitation center's routine ivermectin treatment schedule. The results were recorded as positive (1) or negative (0). Hedgehogs presenting with concomitant disease were excluded from the trial. Because hedgehogs were admitted and released during the ivermectin protocol, the ivermectin group represented a dynamic treatment-monitoring cohort rather than a fixed cohort followed through all three treatment rounds. Consequently, denominators refer to the number of animals present and evaluable at each assessment.

2.9. Statistical analysis

The data were analyzed using R version 4.2.2 with the R Commander extension. Normality was assessed using the Shapiro–Wilk test. Associations between categorical variables were evaluated using the chi-square test or Fisher's exact test when expected cell counts were small. For nonnormally distributed continuous variables, the Mann–Whitney *U* test was used, whereas normally distributed variables were compared using Student's *t*-test.

3. Results

3.1. Coprological findings

Among the 78 fecal samples analyzed, 33 (42%) were positive for *C. striatum*, and two (3%) were positive for *Capillaria* spp. Considering infection categories, 32/78 samples (41%) were positive only for *C. striatum*, 1/78 (1%) was positive only for *Capillaria* spp., and 1/78 (1%) had a mixed infection with both parasites. At the animal level, *C. striatum* was detected in 63% of hedgehogs, and *Capillaria* spp. in 7% of hedgehogs, including a mixed infection in one hedgehog.

Owing to the limited sample volume, only 43 samples could be analyzed using all four coprological methods. Among these, the direct smear method identified *C. striatum* in 7/43 samples (16%), Willis flotation in 3/43 (7%), including one mixed infection, natural sedimentation in 6/43 (14%), plus one sample positive for *Capillaria* spp., and the Baermann technique in 12/43 samples (28%). Thus, the Baermann technique yielded the highest detection rate for *C. striatum*, followed by direct smear, natural sedimentation, and Willis flotation. No significant difference was found between flotation and natural sedimentation for the detection of *Capillaria* spp. (Fisher's exact test, $p = 0.30$). In contrast, significant differences were observed among direct smear, natural sedimentation, and Baermann techniques for the detection of *C. striatum* (chi-square test, $p \leq 0.001$ each). Among the hedgehogs positive for *C. striatum*, juveniles represented the largest age category, followed by hoglets. Both adult hedgehogs included in the study were positive. However, no statistically significant association between age class and infection status was detected.

3.2. Molecular confirmation

Sequences obtained from adult nematodes recovered from lungs during necropsy confirmed the presence of *C. striatum*. Molecular identification was based on >99% similarity at the ITS2 locus for all four analyzed specimens relative to the *C. striatum* larval sequence KT257661 from hedgehogs in Germany (Lange et al., 2018). Analysis of the partial 28S rDNA locus supported identification as *Crenosoma* sp. However, because the corresponding *C. striatum* 28S rDNA sequence was not available in the NCBI database, the closest match (96–97% similarity) was *Crenosoma mephitidis* AY292793 (Carreno and Nadler, 2003). A CO1 sequence was also obtained, but no comparable *Crenosoma* spp. CO1 sequences were available in the NCBI Nucleotide database.

3.3. Environmental and meteorological findings

Coprological positivity varied significantly by housing type. The samples collected from the indoor enclosures were positive in 10/34 cases (29%), whereas those from the outdoor enclosures were positive in 24/44 cases (54.5%) (chi-square test, $p = 0.03$).

During the study period, negative coprological results were more frequent at the beginning of sampling (September – November 2021). Monthly prevalence increased from 11% in October and 18% in November to 50% in December, 46% in January, and 56% in February (Fig. 1e). The relative distributions of positive and negative results differed significantly between the early (September–November 2021) and late (December 2021–February 2022) periods of the study (Fisher's exact test, $p = 0.004$).

During the September 2021–February 2022 study period, mean daily maximum temperatures ranged from 16.3 °C to 25.5 °C, whereas mean daily minimum temperatures ranged from 11.6 °C to 18.7 °C, and mean relative humidity ranged from 71.6% to 85.5% in the Faro/Olhão region. In the outdoor enclosures, no significant associations were found between coprological positivity and maximum temperature (Welch two sample t-test, $p = 0.08$), minimum temperature (Welch two sample t-test, $p = 0.19$), or relative humidity (Welch two sample t-test, $p = 0.60$). Relative humidity exceeded 86% throughout this period. Same-month precipitation not significantly associated with coprological status (Pearson correlation, $r = -0.14$, one-sided$p = 0.41$). However, delayed precipitation analysis suggested stronger associations with rainfall occurring several weeks before infection detection. The strongest association was observed for the 40-day delayed 30-day precipitation window (Pearson $r = 0.783$, one-sided $p = 0.059$; grouped-binomial GLM one-sided $p = 0.007$). Positive associations were also observed for 50- and 60-day delays (Fig. 2).

3.4. Gastropod intermediate hosts

All gastropods examined (10/10) were positive for *C. striatum* larvae, indicating that the parasite life cycle was being maintained within the RIAS facilities. The gastropods examined were not identified to species level, which limited assessment of species-specific intermediate-host involvement.

3.5. Treatment outcomes

Subcutaneous levamisole reduced the proportion of Baermann-positive hedgehogs after the first treatment course, although persistence and relapse remained frequent. Seven days after completion of the first treatment course, following three or four administrations given at 48-h intervals, 10/41 hedgehogs (24%) remained Baermann-positive. Among the 31 hedgehogs that initially tested negative after treatment, 12 (39%) became positive again two to five weeks later. These 12 hedgehogs subsequently received a second levamisole course, after which 1/12 (8%) remained Baermann-positive at the next 7-day follow-up examination.

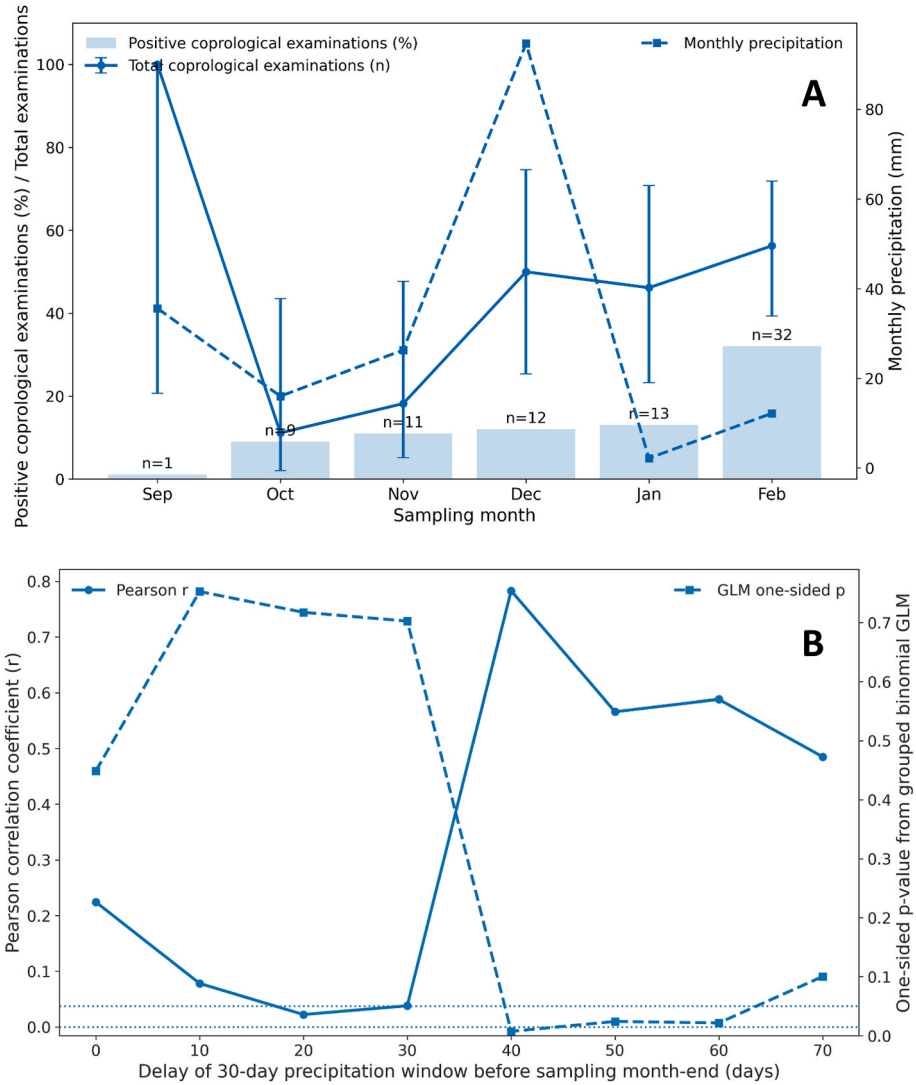

Fig. 2. Temporal patterns of *Crenosoma striatum* infection in rescued western European hedgehogs. **(a)** Monthly prevalence of positive coprological findings in rescued western European hedgehogs and monthly precipitation in the Faro/Olhão region. Points indicate prevalence with Wilson 95% confidence intervals, bars indicate the number of coprological examinations per month, and the dashed line indicates monthly precipitation from NASA POWER. **(b)** Delayed precipitation analysis. Pearson correlation coefficients between monthly prevalence and lagged 30-day precipitation totals are shown together with one-sided p-values from grouped-binomial generalized linear models. Precipitation windows were shifted backward by 0–70 days relative to the end of each sampling month.

Subcutaneous ivermectin treatment resulted in incomplete parasitological clearance across all treatment rounds. The ivermectin cohort was dynamic, as hedgehogs were admitted and released during the protocol. At the first post-treatment assessment, 6/12 hedgehogs (50%) were Baermann-positive, and 6/12 were negative. All six animals that were negative after the first treatment remained negative at the next assessment; therefore, relapse after the first negative result was 0/6. Three hedgehogs entered the protocol after the first ivermectin administration and were first evaluated at the second assessment. At the second assessment, 4/15 hedgehogs (27%) were Baermann-positive. Thirteen hedgehogs were evaluable at the third assessment because two animals had been released, and 6/13 (46%) were Baermann-positive.

The proportion of Baermann-positive hedgehogs was numerically lower after levamisole treatment than after ivermectin treatment after the first treatment course (24% vs. 50%) and after repeated treatment (8% after the second levamisole course vs. 27% after the second ivermectin course). When all post-treatment evaluations were pooled, Baermann-positive follow-up examinations were less frequent after levamisole treatment than after ivermectin treatment (21% vs. 40%; one-sided Fisher exact test $p = 0.04$). Persistent or recurrent infection was observed with both protocols. Relapses after an initial negative result were frequent in the levamisole group (39%), whereas this outcome was not directly comparable in the ivermectin group because of differences in follow-up structure. A summary comparison of both treatment strategies is presented in Table 3.

Table 3
Comparison of treatment outcomes between levamisole and ivermectin in *Crenosoma striatum*-infected hedgehogs. * Three hedgehogs entered follow-up after the first ivermectin assessment and therefore were not evaluable after the first treatment round. N/A: Data not available or not applicable because of the study design (e.g., no third course for the levamisole group).

Metric	Levamisole	Ivermectin
Animals treated (total)	41	15 *
Positive after 1st treatment (%)	24% (10/41)	50% (6/12)
Relapsed after 1st negative (%)	39% (12/31)	N/A
Positive after 2nd treatment (%)	8% (2/24)	27% (4/15)
Positive after 3rd treatment (%)	N/A	46% (6/13)

4. Discussion

4.1. Main findings and epidemiological context

This study revealed a high prevalence of respiratory nematode infection among rescued western European hedgehogs admitted to a wildlife rehabilitation center in southern Portugal. The prevalence observed for *C. striatum* was comparable to that in previous reports from Portugal, including 46% (Barradas et al., 2020) and 38% (Lobo, 2021), and to that in several studies from other European countries (Majeed et al., 1989; Gaglio et al., 2010; Liatis et al., 2017; Mariacher et al., 2021; Rasmussen et al., 2021). In contrast, higher prevalences, exceeding 70%, have been reported in Italy, Great Britain, and Finland (Giannetto et al., 1993; South and Haynes, 2018; Rautio et al., 2016). Such variation is unsurprising, given differences across studies in geography, host age structure, diagnostic approach, and study population.

The low frequency of *Capillaria* spp. detection in the present study was similar to the low prevalence reported by Naem et al. (2015), who detected *Capillaria* spp. in 4% of examined hedgehogs. In contrast, higher prevalences have been reported in other studies, including 24% by Lobo (2021), 52% by Rasmussen et al. (2021), and 62% by Gaglio et al. (2010). Mixed respiratory parasite infections are often described in hedgehogs (Bexton and Robinson, 2003). Rasmussen et al. (2021) and Naem et al. (2015) reported that 38% and 43% of hedgehogs, respectively, harbored more than one parasite species. Rasmussen et al. (2021) noted that 35.1% of the hedgehogs were coinfected with *C. striatum* and *Capillaria* spp. In contrast, Majeed et al. (1989) reported mixed infection with *C. striatum* and *Eucoleus aerophilus* in 16% of animals. Associations with coccidia, *Cryptosporidium* spp., and *Physaloptera clausa* infection have also been documented (Liatis et al., 2017; Mariacher et al., 2021; Rasmussen et al., 2021; Naem et al., 2015). The relatively low detection of *Capillaria* spp. in the present study may reflect true epidemiological differences, but it may also reflect differences in sampling and diagnostic methodology, particularly the use of passive rather than centrifugal flotation.

Methodological heterogeneity likely accounts for some of the variation in prevalence across studies. Some authors relied primarily on coprological examination (Gaglio et al., 2010; South and Haynes, 2018; Lobo, 2021; Mariacher et al., 2021), whereas others used necropsy or pulmonary histopathology (Boag and Fowler, 1988; Majeed et al., 1989; Pfäffle, 2010; Naem et al., 2015; Rautio et al., 2016; Liatis et al., 2017; Barradas et al., 2020; Rasmussen et al., 2021). Study populations also differed with respect to age classes, with some studies including only adults (Poglayen et al., 2003), others including adults and juveniles (Mariacher et al., 2021), and others including neonates as well (Majeed et al., 1989; Naem et al., 2015; Rautio et al., 2016). Taken together, these differences complicate direct comparison and reinforce the need for standardized diagnostic and reporting approaches in hedgehog parasitology.

4.2. Diagnostic performance of the coprological methods

The present results support the use of the Baermann technique as the most useful coprological method for the detection of *C. striatum* in live hedgehogs. Observations of motile first-stage larvae provide a direct parasitological diagnosis, and Baermann examination is widely regarded as the reference coprological method for lungworm detection (Beck, 2007). The eggs of pulmonary nematodes are fragile, and the interval between oviposition and hatching is short, reducing the sensitivity of methods designed primarily for egg detection, such as flotation, sedimentation, or direct smear (Alho et al., 2013).

The practical limitations of the Baermann technique should not be overlooked. Compared with some other methods, the Baermann technique requires more fecal material and usually takes at least 8 h before the larvae can be recovered and visualized (Alho et al., 2013). These constraints are particularly relevant in wildlife rehabilitation settings, where sample quantity may be limited and rapid clinical decisions are often needed. In this context, direct smear remains a useful, rapid, and inexpensive bedside test, especially in animals with a high parasite burden and compatible respiratory signs. South and Haynes (2018) considered direct fecal smears a reliable and cost-effective approach and suggested that even two smears may provide a useful estimate of endoparasite burden. In the present study, the Baermann examination detected more positive samples than the direct smear.

The performance of the flotation and sedimentation methods in this study was also lower than that of the Baermann technique. These findings are consistent with reports indicating that fecal analysis may miss a substantial proportion of lungworm infections confirmed by histology or necropsy (Majeed et al., 1989; Cousquer, 2004). Nevertheless, flotation and direct smearing may still be useful for detecting *Capillaria* spp., whose characteristic barrel-shaped, bipolar eggs can be visualized microscopically. Species-level differentiation remains difficult, however. *Capillaria erinacei* eggs are generally described as larger, darker, and more parallel-sided, whereas *Eucoleus aerophilus* eggs tend to be lighter, with more convex lateral walls and flatter opercula (Pfäffle, 2010). For animals with marked respiratory signs, tracheal lavage may provide an alternative diagnostic approach with potentially increased sensitivity and the added advantage of identifying concurrent bacterial pneumonia. The need for anesthesia and intubation limits its routine use in wildlife rehabilitation (Cousquer, 2004).

The treatment results indicate that both subcutaneous levamisole and subcutaneous ivermectin achieved only partial parasitological clearance under the conditions of this study, and persistent or recurrent positivity was observed with both protocols. Although Baermann-positive follow-up examinations were numerically less frequent after levamisole treatment, the small sample size limits strong conclusions regarding comparative efficacy. These findings are in line with previous reports suggesting that levamisole remains commonly recommended or reported as useful for respiratory nematodes in hedgehogs, whereas ivermectin may produce more variable outcomes (Cousquer, 2004; Bexton, 2016; Mariacher et al., 2021; Van De Weyer et al., 2023).

Several factors may explain ivermectin's variable performance. The 21-day ivermectin interval used here reflected the routine rehabilitation-center protocol at the time rather than an experimentally optimized treatment schedule. This interval may not have been optimal compared with the shorter or weekly intervals described elsewhere (Cousquer, 2004; Van De Weyer et al., 2023). In addition, intermittent larval shedding, incomplete clearance of adult worms, reinfection during rehabilitation, and possibly reduced drug susceptibility may contribute to persistent or recurrent infection. Because the prepatent period of *C. striatum* may extend for several weeks, recurrent positivity shortly after treatment cannot be attributed confidently to reinfection alone. However, reinfection remains likely under the conditions of this study, as some hedgehogs that previously tested negative later tested positive, and infected gastropods were confirmed within the facility. Similar uncertainty has been reported for ivermectin efficacy against *C. striatum* and other lungworms (Pfäffle, 2010; Xu et al., 1998). The mechanisms underlying reduced or inconsistent ivermectin efficacy remain incompletely understood but may include limited drug exposure of parasites located within the respiratory tract, incomplete activity against some developmental stages, host-specific pharmacokinetic differences affecting drug absorption or tissue distribution, and possible P-glycoprotein-mediated drug tolerance mechanisms described in other nematodes (Xu et al., 1998). However, reinfection remains difficult to separate from true treatment failure under rehabilitation-center conditions.

From a practical perspective, subcutaneous ivermectin administration is simpler than repeated oral dosing in wildlife rehabilitation settings. Oral levamisole can be difficult to administer consistently to stressed, anorectic, or group-housed hedgehogs. However, in the present study, subcutaneous levamisole was also feasible and appeared to be the most useful protocol. These results therefore support levamisole as the

preferred treatment option in this setting and emphasize that treatment alone is unlikely to be sufficient unless environmental sources of infection are also addressed.

4.3. Environmental transmission and risk of reinfection

One of the most important findings of this study was the demonstration that all the examined gastropods from one enclosure were positive for *C. striatum* larvae. This strongly supports the presence of an active transmission cycle within the rehabilitation center and provides a likely explanation for persistent or recurrent infection after treatment. These findings are epidemiologically important because they show that hedgehogs may not only be infected but also reexposed after admission, especially when housed in outdoor enclosures under conditions favorable for infection.

The biology of *C. striatum* makes such a scenario possible. Transmission depends on an obligatory gastropod intermediate host, and environmental conditions closely influence the abundance and activity of these hosts. Temperature, humidity, and rainfall may affect both the survival of the larval stages and the activity of snails and slugs, thereby shaping transmission intensity (Morand, 2015; Beck, 2007; Cameron, 1970). The delayed association between precipitation and coprological positivity found in the present study is biologically relevant. Rainfall may increase gastropod activity and survival, thereby increasing the probability of exposure to infective larvae. Detectable Baermann positivity would be expected only after transmission, parasite maturation, and larval shedding. The strongest exploratory associations were observed for precipitation occurring approximately 40–60 days before detection, consistent with a delayed transmission process rather than an immediate rainfall effect.

To our knowledge, few studies have examined respiratory nematode infection in hedgehogs alongside local environmental conditions and intermediate hosts in a rehabilitation setting. This makes the present observations particularly relevant, even if still preliminary. They suggest that treatment efficacy in rescue centers cannot be interpreted independently of exposure risk within the facility. Shorter treatment intervals, improved enclosure hygiene, reducing food residues and fecal contamination, and measures to limit gastropod access may all improve parasite control. These environmental components are often underemphasized in clinical treatment studies, yet they may be critical determinants of apparent anthelmintic success.

4.4. Clinical relevance, rehabilitation, and conservation implications

Infection with *C. striatum* may be subclinical or may cause clinically important respiratory disease. Clinical signs described in the literature include cough, weakness, weight loss, and exercise intolerance, and complications may include bacterial pneumonia, pulmonary emphysema, and heart failure (Pfäffle, 2010; Bexton, 2016; Beck, 2007). Hoseini et al. (2014) and Nematollahi et al. (2014) described microabscess formation around parasites, which may reduce drug access to the site of infection and thereby compromise treatment efficacy. In the present study, however, overt clinical disease was not universal despite the relatively high infection prevalence, suggesting that parasite detection alone should not automatically be equated with severe clinical impact.

This has implications for both rehabilitation medicine and conservation. Some authors recommend prophylactic deworming of all hedgehogs entering rescue centers (Bexton, 2016), but blanket treatment may not always be justified. Parasites are part of natural ecosystems, and host–parasite relationships reflect long-term coevolution. Antiparasitic treatment in wildlife may have ecological costs and may contribute to selection for resistance (Irvine, 2006; Pedersen and Fenton, 2015). On the other hand, antihelmintic treatment can also improve host fitness or population performance in some wildlife systems. For example, experimental reduction of *Trichostrongylus tenuis* in red grouse increased breeding production and winter survival, and parasite removal helped prevent population crashes (Hudson et al., 1992, 1998). More recently, landscape-scale fenbendazole treatment reduced helminth burdens in northern bobwhite and was associated with improved population responses (Henry et al., 2024; Leach et al., 2024). Therefore, treatment decisions in wildlife rehabilitation should balance individual welfare, parasite burden, conservation context, reinfection risk, and potential ecological consequences. In practical terms, regular monitoring, good nutrition, stress minimization, appropriate stocking density, enclosure hygiene, and timely diagnostic testing are likely to be as important as drug choice in reducing the impact of respiratory parasitism during rehabilitation.

4.5. Limitations

The present study reflects the practical realities of wildlife rehabilitation medicine, where controlled housing conditions, standardized exposure histories, and fixed treatment cohorts are often difficult to maintain. The sample size was relatively small, particularly for some subgroup analyses, limiting the statistical power and potentially obscuring associations with climatic variables. Not all fecal samples could be examined with all diagnostic methods due to insufficient sample volume, limiting the ability to compare techniques under fully standardized conditions. The Baermann technique, although the most informative method used here, is itself imperfect. It depends on the quantity of feces and larval excretion at the time of sampling, and intermittent shedding may have produced false-negative results (Alho et al., 2013). This is especially relevant when Baermann positivity is used as the main endpoint in treatment trials. The use of passive flotation rather than centrifugal flotation may have reduced the sensitivity for detecting *Capillaria* spp. eggs and could partly explain the lower prevalence observed relative to some previous studies. Future investigations should ideally incorporate centrifugal flotation techniques to improve egg recovery. The treatment comparison was pragmatic rather than experimental. The levamisole and ivermectin groups were not randomized, did not follow identical monitoring schedules, and were exposed to real-world rehabilitation conditions, including potential reinfection. As a result, the apparent superiority of levamisole should be interpreted cautiously as an observation under field conditions rather than as definitive evidence from a controlled efficacy trial.

Environmental reinfection was likely an important confounder. The detection of *C. striatum* larvae in all examined gastropods supports the presence of an active transmission cycle within the rehabilitation center. Consequently, reinfection should be considered an important confounding factor when interpreting treatment outcomes, because persistent or recurrent Baermann positivity may reflect treatment failure, intermittent larval shedding, reinfection, or a combination of these processes. The hedgehogs in the present study could not be maintained in fully controlled, parasite-free conditions, and infected gastropods were confirmed within the facility. Gastropods were sampled from only one enclosure at a single time point, limiting the generalizability of the extent and seasonal dynamics of intermediate host infection across the entire rescue center. Because housing conditions changed during rehabilitation and animals could move between indoor and outdoor environments, environmental exposure risk was not constant throughout follow-up.

The study was conducted at a single rehabilitation center in southern Portugal. Although this setting provided valuable ecological and clinical insight, the findings may not be directly generalizable to other centers, climates, or management systems. Multicentric studies using standardized diagnostic methods, longer follow-up, controlled housing conditions, and formal treatment comparisons would be valuable next steps.

5. Conclusions

Respiratory nematode infection was common in rescued western

European hedgehogs admitted to this rehabilitation center in southern Portugal, with *C. striatum* detected far more frequently than *Capillaria* spp. The Baermann technique was the most useful coprological method for detecting *C. striatum* in live animals. Under the conditions evaluated, subcutaneous levamisole performed better than ivermectin did, although neither protocol achieved consistent parasitological clearance, and recurrence was frequent. The detection of *C. striatum* larvae in all the examined gastropods from one enclosure indicates that transmission can be maintained within rehabilitation facilities, likely contributing to reinfection and complicating treatment assessment. Although climatic variables were not significantly associated with infection status in this dataset, the observed temporal pattern was consistent with the possible influence of rainfall and humidity on transmission dynamics. Overall, these findings highlight that the management of respiratory nematodes in hedgehog rehabilitation centers requires an integrated approach combining appropriate diagnostics, targeted treatment, and environmental control, and support the need for larger, standardized studies to optimize treatment protocols and clarify the roles of reinfection and environmental factors.

Ethical standards

Ethical review and approval were waived for the present trial due to the absence of interference with the normal animal management of the rescue center, as designed by the veterinary team. This study and its procedures followed the daily activity and preventive protocols of the rescue center, and are aligned with the Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes. None of the animals were subjected to monitoring procedures or treatments solely for experimental purposes.

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CRediT authorship contribution statement

Catarina Jota Baptista: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Validation, Writing – original draft. **Inês Gama:** Investigation, Methodology, Writing – review & editing. **Julia Serena:** Investigation, Methodology, Writing – review & editing. **Petr Heneberg:** Formal analysis, Investigation, Writing – review & editing. **María Cásero:** Investigation, Writing – review & editing. **Luís Madeira de Carvalho:** Investigation, Supervision, Writing – review & editing.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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