HELMINTHS OF *RANGIFER TARANDUS* (ARTIODACTYLA, CERVIDAE) ACROSS THE SOUTHERN PART OF ITS CONTINENTAL RANGE

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Rangifer tarandus in the southern Palaearctic remains poorly documented, particularly with respect to its helminth fauna. Existing data are scarce for these small, isolated, and conservation-significant populations. As helminths influence host survival, reproduction, and population stability, and may serve as biogeographical indicators, understanding their diversity in southern regions is of clear scientific and conservation importance. A total of 242 faecal samples were collected between 2012 and 2025 from populations of *Rangifer tarandus* in China, Kazakhstan, Mongolia, and Russia and analysed using coproscopic methods. Morphological identifications were complemented by molecular analyses where possible. Taxonomic identification of larvae of some nematodes was based on sequencing the internal transcribed spacer regions of ribosomal DNA; attempts to extract DNA from the eggs of helminths failed. The study revealed trematodes of the superfamily Paramphistomatoidea, cestodes of the genus *Moniezia*, and nematodes including *Elaphostrongylus rangiferi*, *Orthostrongylus macrotis*, the dimorphic *Ostertagia gruehneri / Ostertagia arctica* species, as well as *Nematodirus*, *Capillaria*, and unidentified small strongylids. All taxa identified have previously been reported in *Rangifer tarandus* within the Palaearctic, with the exception of *Nematodirus* sp. in the southern part of the range. This study also provides the first helminth records from faecal samples of wild *Rangifer tarandus* in several Protected Areas and regions, including the State Nature Reserve «Vasyugansky» (Novosibirsk Region, Russia), Altai State Nature Reserve (Republic of Altai, Russia), Baikal State Nature Reserve (Republic of Buryatia, Russia), Irkutsk Region (Russia), Olyokminsky State Nature Sanctuary and Tokinsko-Stanovoy National Park (both – Amur Region, Russia), as well as from semiwild *Rangifer tarandus* in Zabaykalsky Krai (Russia), Khövsgöl National Park (Mongolia), and Inner Mongolia (China). The southernmost known distribution limits were established for *Elaphostrongylus rangiferi* and *Orthostrongylus macrotis*.

Key words: China, Kazakhstan, Mongolia, Palaearctic, Russia, semiwild reindeer, wild reindeer

Introduction

Rangifer tarandus Linnaeus, 1758 is widely recognised as an ecologically important species. Researchers often regard it as a flagship species that attracts considerable public attention (Kaltenborn et al., 2014). It also acts as an umbrella species, because conserving populations of *Rangifer tarandus*, which often undertake extensive migrations, requires protecting large landscapes (Mysterud et al., 2025). Globally, the IUCN Red List reclassified the species from Least Concern to Vulnerable nine years ago (Gunn, 2016). Even greater concern exists at the regional level, where authorities have included several populations of *Rangifer tarandus* in regional Red Data Books as endangered and have introduced strict protection measures (Panchenko et al., 2021). Conservationists have preserved many wild populations only by establishing Protected Areas. *Rangifer tarandus* also serves as an indicator species. Scientists can detect environmental contamination, including radionuclides, by analysing its tissues or excreta (Andersson Stavridis et al., 2024). *Rangifer tarandus* occurs in two forms: wild and semiwild (domestic) (Tryland & Kutz, 2019). Unlike conventional livestock, most semiwild *Rangifer tarandus* follow almost the same migratory lifestyle as wild popula-

tions and respond to the same environmental factors. The main difference lies in the presence of humans (indigenous nomadic herders), who accompany domestic herds and provide protection and care, including veterinary support, although not always consistently. Wild *Rangifer tarandus* may also attract individual semiwild animals into their herds, and herders can sometimes recover these animals (Klein, 1980). Thus, the boundary between wild and semiwild populations remains permeable. Consequently, studies of wild *Rangifer tarandus* biology and ecology should also consider evidence from semiwild animals. Researchers have studied domestic *Rangifer tarandus* more extensively, and these animals can therefore serve, to some extent, as a model for the species as a whole.

Rangifer tarandus is typically associated with high latitudes. This view is reflected even in common names. The Russian common name for *Rangifer tarandus*, «severnyi olen», literally means «northern deer» and refers to the north («sever»), while the North American word «caribou» derives from a term associated with snow (Guillou, 2005). However, the species' range has historically been much broader. During the Pleistocene (about 12 000 years ago), it likely formed a continuous distribution extending to approximately 45° N (Kurtén, 1968; Kurtén & Anderson, 1980). Today, this range is fragmented and has shifted northwards. Only isolated southern populations remain, and specialists know relatively little about them outside expert circles (Baskin & Danell, 2003). One of the most unexpected examples is the occurrence of *Rangifer tarandus* in the Chara Desert in Transbaikalia, Russia (Zaplatin, 1964). The global population of *Rangifer tarandus* is estimated to comprise roughly 4 000 000 animals (Baskin & Danell, 2003; Tryland & Kutz, 2019). In the Palaearctic, they are most abundant in the northern regions. Wild herds on the Taymyr Peninsula and semiwild herds in the Yamalo-Nenetsky Autonomous Okrug (Russia) number in the hundreds of thousands. Individual herds may include several thousand animals. In contrast, in the southern part of the range *Rangifer tarandus* usually occur in small groups, typically consisting of a few dozen animals (sometimes even single individuals). Only rarely do these groups reach several hundred individuals (Smirnov, 2016). Investigating parasites of *Rangifer tarandus* is important for understanding the factors that influence their populations. Helminths act as limiting factors for their host populations and at the same time may serve as indicators of population status. Helminths can impair immunity, growth, and fecundity, reduce survival, or directly cause the death of their hosts (Mizkewitsch, 1967; Tryland & Kutz, 2019). They can even influence the sex ratio of ruminant offspring (Aleuy et al., 2020). Meanwhile, stable host populations generally support a richer helminth fauna, whereas declining populations tend to harbour a depauperate parasite community (Hudson et al., 2006). Highly specialised helminths may also function as biogeographical markers for discriminating among particular host populations (MacKenzie & Abaunza, 1998).

Researchers have studied the helminths of *Rangifer tarandus* across the Holarctic relatively thoroughly, but focused primarily on northern regions and on semiwild animals (Mizkewitsch, 1967; Tryland & Kutz, 2019). By contrast, information from the southern part of the Palaearctic range remains extremely limited, especially for wild *Rangifer tarandus*, despite the high ecological and conservation value of these small, isolated populations (Machulsky, 1955; Kadenatsii, 1963; Sulimov, 1966, 1968; Zhaltsanova, 1972; Dróżdż & Namžyl, 1973; Loginova, 2024; Loginova et al., 2024). The present study represents the first attempt to examine helminths of wild *Rangifer tarandus* in the southern part of its continental Palaearctic range. To obtain a more comprehensive picture, we also included semiwild *Rangifer tarandus* in the analysis. The aim of this study was to investigate the diversity and distribution of helminths of *Rangifer tarandus* in the southern continental Palaearctic using a coprological survey.

Material and Methods

Faecal sampling

Faecal samples were collected from both wild and semiwild *Rangifer tarandus* inhabiting the southern part of the species' continental Palaearctic range. The dataset includes material from China, Kazakhstan, Mongolia, and Russia, collected between 50° N and 60° N. The sampling period comprised two components: a prospective targeted survey conducted in 2023–2025 and earlier material collected opportunistically in 2012 and 2021. Samples were collected on 12 sites (Fig. 1). Four sites were inhabited by semiwild *Rangifer tarandus* (sites 1, 4, 7, and 9; site 4 is located within a Protected Area), whereas eight sites supported wild *Rangifer tarandus* populations (sites 2, 3, 5, 8, 10, 11, and 12, all within Protected Areas, and site 6 in the wild). We sampled site 5 on four separate occasions, resulting in 15 faecal sample sets included in the study (Table 1). One faecal sample set comprises all faecal samples of *Rangifer tarandus* (1 to n) collected during a single site visit within a given season.

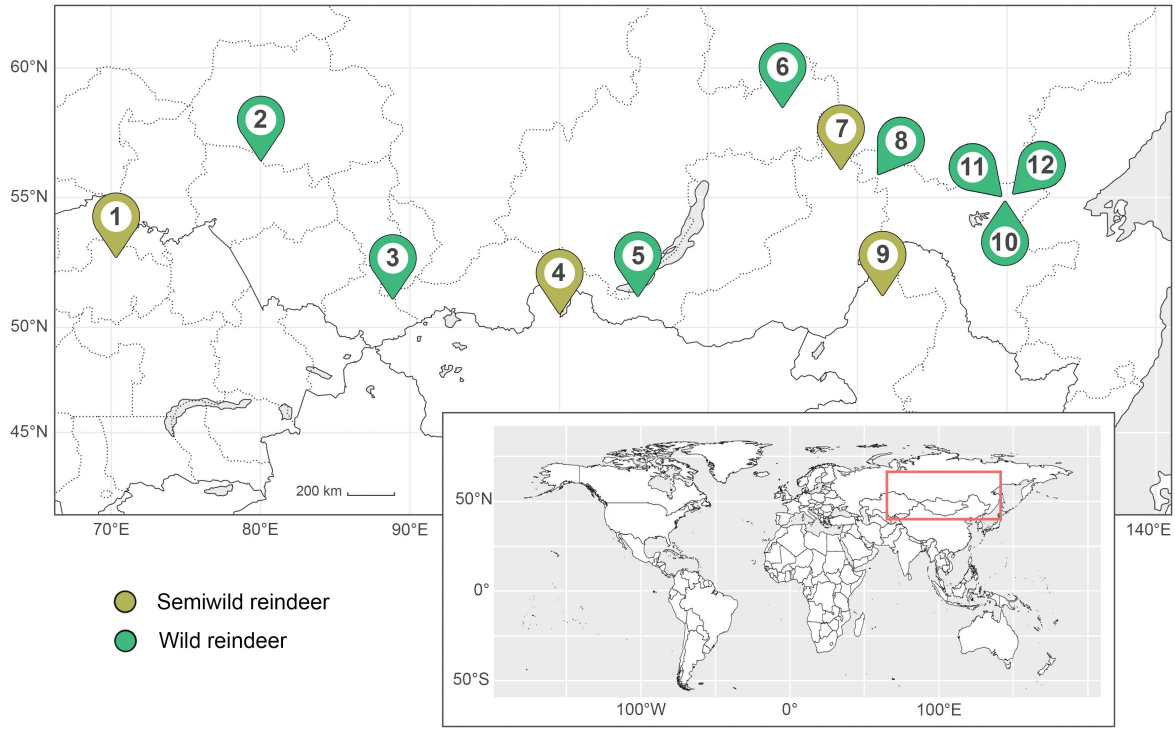

Fig. 1. Map indicating the sampling sites. Numbers correspond to identification numbers in Table 1. Sampling area is marked with a red rectangle on the world map in the insert.

Table 1. Collection data for faecal samples from *Rangifer tarandus* across the Southern continental Palaearctic

Sample set ID	Type of reindeer	Number of faecal samples	Location (country, administrative unit)	Protected Area	Co-ordinates (decimal degrees)	Date collected	Map reference
1	semiwild	2	Kazakhstan, Akmola Region	–	52.93877, 70.24527	April 2025	1
2	wild	8	Russia, Novosibirsk Region	State Nature Reserve «Vasyugansky»	56.636553, 79.981242	February 2025	2
3	wild*	3	Russia, Republic of Altai	Altai State Nature Reserve	51.38385, 88.98008	February 2024	3
4	semiwild	20	Mongolia, Khövsgöl Province	Khövsgöl National Park	50.566855, 100.127792	August 2023	4
5	wild*	20	Russia, Republic of Buryatia	Baikal State Nature Reserve	51.30777, 105.24722	February 2012	5
6	wild*	35	Russia, Republic of Buryatia	Baikal State Nature Reserve	51.30777, 105.24722	July 2023	5
7	wild*	35	Russia, Republic of Buryatia	Baikal State Nature Reserve	51.30777, 105.24722	July 2024	5
8	wild*	35	Russia, Republic of Buryatia	Baikal State Nature Reserve	51.30777, 105.24722	July 2025	5
9	wild	1	Russia, Irkutsk Region	–	58.609750, 114.980806	September 2021	6
10	semiwild	30	Russia, Zabaykalsky Krai	–	56.579214, 118.886167	February 2024	7
11	wild	7	Russia, Amur Region	Olyokminsky State Nature Sanctuary	56.19356, 121.48303	February 2023	8
12	semiwild**	10	China, Inner Mongolia	–	51.35080, 121.50146	August 2023	9
13	wild	17	Russia, Amur Region	Tokinsko-Stanovoy National Park	55.48017, 129.96444	February 2023	10
14	wild	9	Russia, Amur Region	Tokinsko-Stanovoy National Park	55.67035, 129.44511	February 2023	11
15	wild	10	Russia, Amur Region	Tokinsko-Stanovoy National Park	55.44280, 130.48006	July 2021	12

Note: * – subspecies of wild northern Siberian forest *Rangifer tarandus* listed in the Red Data Book of the Russian Federation (Panchenko et al., 2021) as an endangered population; ** – population listed in the second category of the Chinese State Key Protected Wildlife List (All these animals are listed in the IUCN Red List as Vulnerable species). Sampling sites are arranged from west to east.

We collected faecal samples from the ground or snow without disturbing the animals. Most samples were obtained immediately after defecation. Sets 5, 7, 8, and 9 constituted exceptions; in these cases, we collected samples in the habitat of *Rangifer tarandus* without directly observing defecation. Consequently, for these sets the sampling season did not necessarily correspond to the season of defecation. Each faecal sample was placed in an individual plastic container and labelled with the date and location of collection. In some cases, primarily for semiwild *Rangifer tarandus*, additional information was available, including the animal's sex and age. These supplementary data are provided in Electronic Supplement 1. Although we cannot completely exclude the possibility that some pellets originated from the same individuals, we deliberately minimised this risk. We collected pellets from distinct clusters separated by several metres. We also considered morphological differences among pellets, including size (small vs. large), shape (rounded; rounded with an elongated protrusion at one pole resembling a grape seed; angular-flattened), and spatial arrangement (scattered vs. compact conglomerate). This approach allowed us to ensure with high confidence that each sample corresponded to a single individual, indicating that the dataset represents 242 animals. Each faecal sample contained 12–15 pellets. Most sets arrived at the Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution of the RAS (Russia) in a moist state and were stored at +4°C. Sets 5, 9, and 15 dried naturally and were delivered under dry conditions. Field sampling in this region is constrained by remote and rugged mountain terrain and by the small, dispersed structure of wild groups of *Rangifer tarandus*. As a result, sampling was partly opportunistic. These limitations resulted in uneven sampling efforts and introduced a potential risk of pseudoreplication, which we explicitly acknowledge. To avoid overinterpretation, we have restricted our conclusions to presence-only patterns and refrain from drawing population-level ecological inferences.

Faecal analysis

A total of 242 faecal samples (180 from wild and 62 from semiwild species of *Rangifer tarandus*) were examined on the presence of helminths in accordance with the current Russian Federation state standard GOST R 54627-2011 (National Standard, 2013). First, we inspected all samples for adult helminths or their fragments, such as cestode proglottids. We then analysed each sample using three additional diagnostic methods.

The first method was drip larvoscopy following the technique of Vajda (1931). We placed three drops of tap water on a microscope slide at some distance from one another, and placed one faecal pellet in each drop. Then we gently rinsed the pellets with several additional drops of water to ensure that their surfaces were completely wetted. The preparation was left for 40 min.; when dry pellets were examined, the exposure time was extended to 1.5 h. Afterwards, the pellets were removed with forceps, and the remaining liquid on the slide was examined under a microscope without a coverslip to detect larvae of zooparasitic nematodes. One slide prepared in this way was examined for each faecal sample.

The second method was combined ovoscopy according to the method of Darling (Darling et al., 1920). We mixed 3 g of faeces with 60 ml of tap water, homogenised the mixture in a mortar with a pestle, filtered it into a 20-ml centrifuge tube, and centrifuged it at 1500 rpm for 5 min. Then we decanted the supernatant and added Darling's flotation solution (a pre-prepared mixture of equal parts glycerol and saturated sodium chloride solution) to the sediment until the tube was filled. We centrifuged the tube again under the same conditions. Using a 5-mm coproscopic loop, we transferred six drops from the surface layer to a microscope slide (ensuring coverage of the entire surface of the fluid column in a 15-mm-diameter tube), covered with a 24 × 24 mm coverslip, and examined microscopically for helminth eggs. One slide prepared by this method was examined for each faecal sample.

The third method was sedimentation ovoscopy using sequential washings. We mixed 3 g of faeces with 60 ml of tap water, homogenised the mixture, and filtered it into a beaker. After allowing the suspension to settle for several minutes, we carefully poured off the supernatant and replaced it with fresh tap water. This procedure was repeated until the supernatant became clear. The remaining water was then decanted by inverting the beaker, and the residual drops containing the sediment were transferred onto a slide, covered with a 24 × 24 mm coverslip, and examined microscopically for helminth eggs. One slide prepared in this manner was examined for each faecal sample.

For ovoscopy, regardless of the method, we counted the number of eggs of each taxon across the entire preparation (i.e. the whole slide). We also counted larvae across the entire slide. The use of two ovoscopic techniques was justified by their different sensitivity to light and heavy eggs. However, in practice each method occasionally enabled the detection of other developmental stages, such as eggs when us-

ing the Vajda method or larvae when using ovoscopic methods (see Electronic Supplement 1).

For each faecal sample, we applied all three methods to the same set of pellets. First, we performed larvoscopy. We then mixed these same pellets with water, after which we used part of the mixture for flotation ovoscopy and another part for sedimentation ovoscopy. During quantification of the results, we summed the helminth specimens in the egg and/or larval stages detected by all three methods for each sample. This procedure ensured that no helminths were counted more than once. Because the initial mass of the pellets was known, we first calculated the number of specimens of each helminth taxon per 3 g of faeces and then recalculated this value per 1 g. The final measure was expressed as the number of helminth eggs per 1 g of faeces (eggs/g) or the number of helminth larvae per 1 g of faeces (larvae/g).

Quantitative analysis was additionally performed using a VIGIS counting chamber from the Diapar kit (VIGIS, Moscow, USSR), which is analogous to the McMaster chamber and is conventionally used for such analyses. However, in our study the chamber method consistently produced lower counts than those obtained by directly observing and counting objects during qualitative examination. This discrepancy is methodologically expected because the chamber detects only a fraction of the total sample volume and is known to underestimate parasite abundance, particularly when egg or larval concentrations are low or unevenly distributed (Mizkewitsch, 1967; National Standard, 2013). Since we processed each sample as the complete set of pellets and knew the exact mass of the analysed material, the qualitative examination allowed us to obtain full counts of all detected developmental stages across the three diagnostic methods. This approach therefore provided a more accurate estimate of the true helminth burden than extrapolation from the subsample analysed in the chamber procedure. For this reason, we relied on quantitative values derived from the full-count qualitative analysis rather than on the lower estimates obtained with the chamber. Using chamber-derived values to calculate means would artificially reduce intensity estimates and misrepresent parasite load. The chosen approach therefore represents the most reliable method available for these samples.

Helminth identification

We examined preparations and identified helminths based on their morphological and morphometric characteristics. Morphological criteria for eggs included their shape, shell structure, the presence of an operculum or polar plugs, colour, and the type of internal contents. For larvae, diagnostic features included intestinal structure (homogeneous or with visible intestinal cells), tail morphology (including the presence of spines or spikes), and the presence of a sheath. We also considered the resting position of the larva.

Morphometric characteristics included egg length and width. For larvae, we considered the following measurements: total body length, maximum width at the level of the oesophagus, distance from the anterior end to the nerve ring, to the excretory pore, to the oesophagus-intestine junction, to the genital primordium, and to the anus, as well as tail length, the length of any spine or spike (when present), the length of the caudal portion of the sheath, and the length of the sheath filament.

We performed morphological and morphometric analyses using a Mikmed-6 light microscope (LOMO-MA, Russia) equipped with a digital Canon 5D Mark II camera (Canon, Japan) connected via an optical-mechanical C-mount adapter (LOMO-MA, Russia). We obtained photomicrographs at 400 × magnification (200 × for third-stage larvae). We took measurements from these images using Fiji/ImageJ Version 1.2.4, RRID:SCR_003070 (National Institutes of Health, USA). Prior to analysis, we calibrated the software using an officially certified OMP micrometer calibration slide (LOMO-MA, Russia). We measured the linear dimensions of eggs using the Straight Line tool, whereas larval measurements additionally required the Segmented Line tool when specimens were curved. To immobilise live larvae, we briefly heated them over a lighter flame for 3–5 s (heat shock). We also considered host specificity. We compared the obtained data with reference descriptions reported in the literature (Skrjabin, 1949; Spassky, 1951; Skrjabin et al., 1954, 1957; Mizkewitsch, 1967; Boev, 1975; Kontrimavichus et al., 1976; Tryland & Kutz, 2019).

DNA analysis

To maintain focus, we have described only those molecular procedures that successfully yielded DNA isolation and analysis from specific nematode larvae. Although we attempted to extend these methods to the eggs of nematodes, cestodes, and trematodes, we could not achieve consistent DNA recovery. Specifically, we attempted to culture miracidia from fresh trematode eggs to facilitate molecular identification; however, the low density of eggs within the coprological samples precluded successful DNA extraction. The first- or third-stage larvae (L1 or L3) of zooparasitic nematodes were

transferred into 0.5-ml Eppendorf tubes. We extracted DNA using the QIAamp DNA Accessory Set, Micro Kit (Qiagen, Netherlands) according to the manufacturer's protocol. For each nematode sample, we used 1.0 µl of extracted DNA as the template for polymerase chain reaction (PCR). We based the taxonomic identification of nematodes on sequencing the internal transcribed spacer regions of ribosomal DNA (ITS rDNA). The study used two conserved 20-base oligonucleotide primers, NC1 (5'-ACG-TCT-GGT-TCA-GGG-TTG-TT-3') and NC2 (5'-TTA-GTT-TCT-TTT-CCT-CCG-CT-3'), originally described by Gasser et al. (1993). We performed PCR on a T100 Thermal Cycler (Bio-Rad, USA). The reaction followed a standard thermocycling scheme comprising an initial denaturation step (3 min at 95°C), 35 cycles of denaturation (30 s at 95°C), primer annealing (45 s at 55°C), and elongation (1 min at 72°C), followed by a final elongation step (5 min at 72°C). We included reagent-only reactions without DNA as negative controls to monitor possible contamination. We also included positive controls containing validated reference DNA (*Elaphostrongylus rangiferi* Mitskewich, 1958, GenBank accession number OQ731722; *Varestrongylus eleguneniensis* Verocai, Kutz, Simard & Hoberg, 2014, OM743794; *Orthostrongylus macrotis* (Dikmans, 1931) Dougherty & Goble, 1945, OL700044; and *Ostertagia gruehneri* Skrjabin, 1929 / *Ostertagia arctica* Mizkewitsch, 1929, OQ726410) to verify successful amplification. We assessed amplification success by separating PCR products electrophoretically in a 1% agarose gel for 30 minutes at 100 V using the Mini-Sub Cell GT + PowerPac Basic system (Bio-Rad, USA), and then visualised the bands on an EXC-F15.M transilluminator (Vilber Lourmat, Germany). When products of the expected size were detected, based on published data or prior experience, we evaluated their yield. If only faint bands appeared, we performed an additional round of amplification. We pooled sufficient quantities of PCR product and purified them in a 0.8% agarose gel by prolonged electrophoresis (70–90 min). We excised the DNA band and extracted the PCR product using the SV Gel and PCR Clean-Up kit (Promega, USA). We further purified the eluate by ethanol precipitation with ammonium acetate. We then re-suspended the resulting pellet in high-purity autoclaved molecular-grade water (G-Biosciences, USA). The volume of water added (10–40 µl) depended on the intensity of the band in the gel. We measured the DNA concentration using a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, USA). Samples with high DNA concentrations were diluted to 15–30 ng/µl. We subsequently carried out direct sequencing at Genotech® (Moscow, Russia). We assembled and analysed forward and reverse chromatograms in ab1 format using Chromas 2.6.6 (Technelysium Pty Ltd, Australia). We identified phylogenetically related sequences in GenBank (NCBI) using the BLASTN 2.13.0+ algorithm (Zhang et al., 2000; Morgulis et al., 2008).

Statistical analysis

The numbers of eggs and larvae of each detected helminth taxon were first determined for each 3-g faecal sample collected from individuals of *Rangifer tarandus*. These values represented the results produced by the three diagnostic methods (see Electronic Supplement 1). We then recalculated these counts per gram of faeces, yielding infection-intensity estimates for each helminth taxon in every positive faecal sample (Blaker, 2000). We calculated the median intensity (among positive samples) and the interquartile range (IQR) using Python's scientific computing ecosystem: NumPy Version 2.4.0, RRID:SCR_008633 (NumPy team, USA) and the Pandas library Version 3.0.1, RRID:SCR_018214 (NumFOCUS, Inc., USA). These statistics represent the median number of eggs or larvae of a given helminth taxon per gram of the faeces in samples collected at a single site. Because sample sets 5, 6, 7, and 8 were collected at the same site in different years, we pooled their data to obtain a single estimate of mean infection intensity for Site 5.

We calculated sample prevalence as the percentage of positive faecal samples relative to the total number of examined samples within each Sample Set (Blaker, 2000; National Standard, 2013). We estimated 95% confidence intervals (CIs) for prevalence as Clopper-Pearson exact binomial intervals in R Version 4.3, RRID:SCR_001905 (R Core Team, 2025) using the built-in function binom.test and confirmed the results with the binom package to ensure numerical stability.

To quantify differences in parasite occurrence between faecal samples obtained from wild and semiwild *Rangifer tarandus*, we applied an integrated analytical framework that combined prevalence comparison, effect-size estimation, hypothesis testing, odds-ratio evaluation, and post-hoc power analysis. We conducted all statistical analyses in the R statistical environment (R Core Team, 2025) using the packages rcompanion, epiR, and pwr. We first compared prevalence between host groups by calculating absolute and relative differences in infec-

tion proportions. To assess the magnitude of these differences beyond statistical significance alone, we estimated standardised effect sizes using Cohen's h. We tested the significance of group differences using chi-square tests or Fisher's exact tests, depending on the expected cell counts. To provide an epidemiologically interpretable measure, we calculated odds ratios (ORs) with 95% confidence intervals using functions from the epiR package. We then performed post-hoc power analyses with the pwr package to evaluate the robustness of the statistical conclusions. These analyses were based on the observed effect sizes, sample sizes, and significance thresholds, allowing an assessment of whether non-significant results reflected limited statistical power or genuinely small biological effects. Together, these analytical procedures provided a robust multi-metric evaluation of parasite prevalence patterns, integrating effect magnitude, statistical confidence, epidemiological interpretability, and inferential reliability.

Attempts to identify any influence of sex or age of the host-animals on helminth infection were discontinued, as such information was largely unavailable in the dataset. We were also unable to assess reliably the effect of season on helminth infection, because, as mentioned above, the season of sample collection did not always correspond to the season when the faeces had originally been deposited by the host-animal. Consequently, the dataset did not provide sufficient structure to support the application of a General Linear Model (GLM) or similar analytical approaches. We also chose not to apply a GLM to test differences in prevalence between wild and semiwild samples, because the structure of our data did not justify a parametric modelling framework. Instead, we focused on a direct comparison of prevalence between two fixed groups, for which standard proportion-based methods already quantify both effect size and associated uncertainty without introducing additional model-based assumptions. Given that the dataset contained only a binary grouping variable and a binary outcome, a logistic GLM would yield results mathematically equivalent to the odds ratio already reported.

It is important to emphasise that our comparisons between faecal samples from wild and semiwild *Rangifer tarandus* are based on datasets that are not fully standardised across time, location, or demographic structure. Each group includes samples collected in different years and seasons, across multiple geographic sites, and from populations with differing age and sex compositions. These factors may influence parasite prevalence independently of the form of *Rangifer tarandus* and therefore constrain the generalisability of our conclusions, a limitation that we explicitly acknowledge.

Results

In the faecal samples, external examination revealed no intact helminths or helminth fragments. Eggs of trematodes of the superfamily Paramphistomatoidea Stiles & Goldberger, 1910 were detected using sedimentation. Eggs of cestodes of the genus *Moniezia* Blanchard, 1891 were detected by both flotation and sedimentation methods. Eggs and L3 larvae of small strongylid nematodes, eggs of *Nematodirus* Ransom, 1907, eggs of *Capillaria* Zeder, 1800, and L1 larvae of Protostrongylidae Leiper, 1926 were likewise recorded (see Electronic Supplement 1).

These Protostrongylidae L1 larvae comprised both dorsal-spined larvae (DSL) and morphotypes corresponding to *Protostrongylus* Kamensky, 1905. We identified the DSL as *Elaphostrongylus rangiferi*, and identified the *Protostrongylus*-morphotype as *Orthostrongylus macrotis*. For *Elaphostrongylus rangiferi* larvae from sample set 12 (site 9), DNA analysis confirmed the initial morphological identification. DNA amplification failed for four additional DSL pools from sites 2, 5, 8, and 12; therefore, we based their identification on morphology, expected host specificity, geographic distribution, and published taxonomic descriptions. For *Orthostrongylus macrotis*, DNA analysis successfully confirmed the identification. In sample set 15 (site 12), we identified the L3 larvae as *Ostertagia gruehneri* using both morphological characters and DNA analysis. The nucleotide sequences obtained in this study were deposited in GenBank (Table 2). The appearance of the helminths found in the faeces is shown in Fig. 2. In the faecal samples collected on site 1, 3, 6, and 11, no helminths were detected. The data on sample prevalence and intensity (among positives) are presented in Table 3. The intensity of infection by all detected helminth taxa in all positive samples is interpreted as low according to GOST R 54627-2011 terminology (National Standard, 2013). The ranges from minimum to maximum values for each helminth taxon are presented in Table 4. Nematodes of the species *Orthostrongylus macrotis* occurred exclusively in faecal samples from wild *Rangifer tarandus*, whereas *Capillaria* nematodes were detected only in samples from semiwild *Rangifer tarandus*. All remaining helminth taxa were present in material from both wild and semiwild *Rangifer tarandus*. Fig. 3 illustrates the comparative distribution of helminth taxa across sites corresponding to habitats of wild and semiwild *Rangifer tarandus*.

Table 2. Parasitic nematode species detected in the faeces of *Rangifer tarandus* and identified by their ITS region

Sample set ID	Helminth Species	GenBank*	Voucher**
12	*Elaphostrongylus rangiferi* Mitskewich, 1958	PX720411	IPEE_Parasites 14460
15	*Orthostrongylus macrotis* (Dikmans, 1931) Dougherty & Goble	PX720450	IPEE_Parasites 14459
15	*Ostertagia gruehneri* Skrjabin, 1929	PX716654	IPEE_Parasites 14458

Note: * – GenBank accession numbers are provided for sequences obtained from individual larvae at the first (L1) or third (L3) developmental stage, each representing its respective species; ** – voucher specimens with definitive identifications and accession numbers are archived in the Museum of Helminthological Collections, Parasitology Center, A.N. Severtsov Institute of Ecology and Evolution of the RAS (Russia).

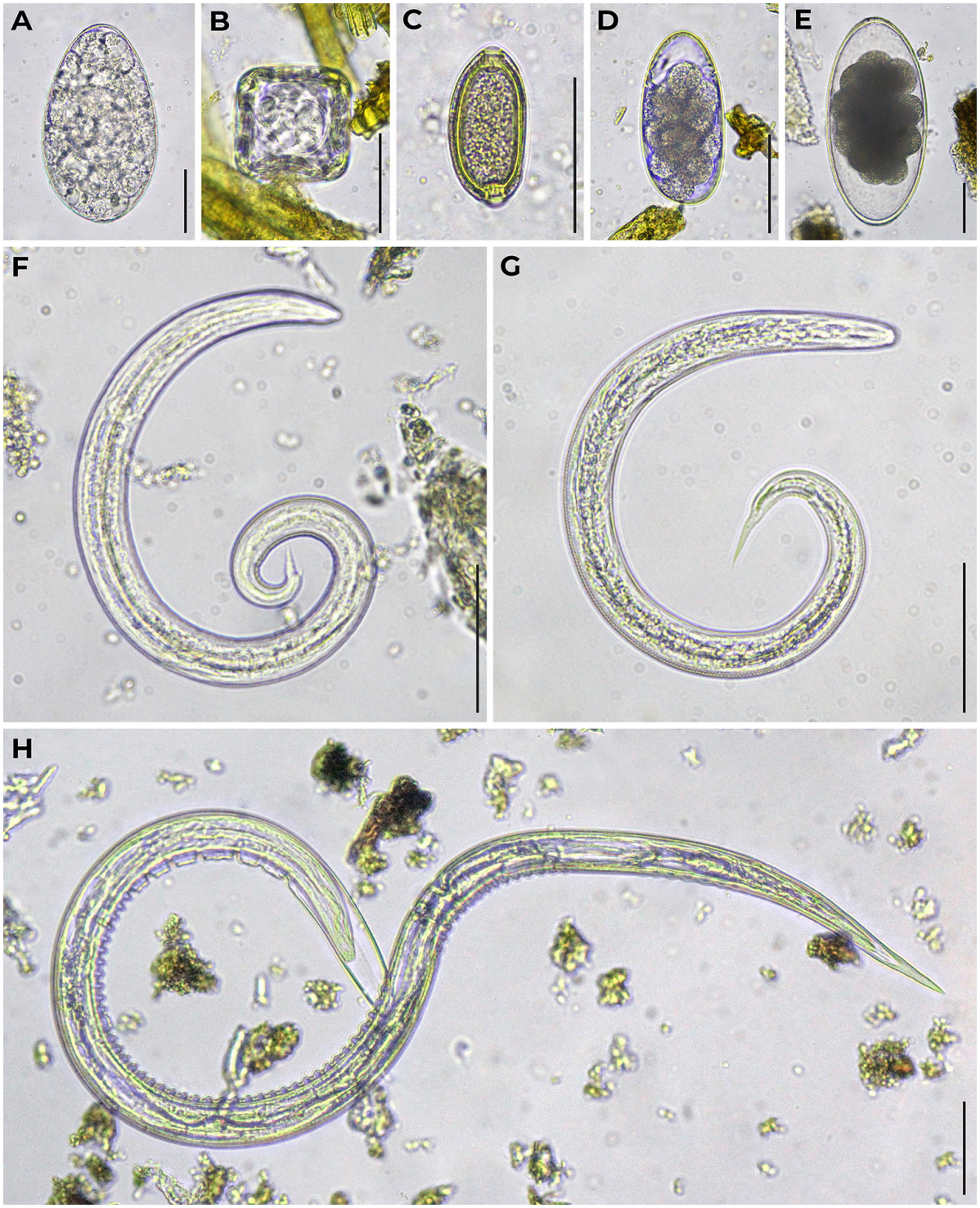

Fig. 2. Appearance of the helminths found in the faeces. Designations: A – Paramphistomatoidea sp. egg; B – *Moniezia* sp. egg; C – *Capillaria* sp. egg; D – Strongyle-type egg; E – *Nematodirus* sp. egg; F – *Elaphostrongylus rangiferi* L1; G – *Orthostrongylus macrotis* L1; H – *Ostertagia gruehneri* L3 (dead). Bright field microscopy. A to G magnification: 400 ×, H magnification: 200 ×. A, E, F, G, H – helminths in water; B, C, D – helminths in Darling' solution. Cover slips used. No staining added. Scale bars = 50 μm.

able 3. Helminths found in faeces of *Rangifer tarandus*

Map site	Trematodes	Cestodes	Nematodes				
	Paramphistomatoidea	*Moniezia*	Strongyle-type	*Nematodirus*	*Elaphostrongylus rangiferi*	*Orthostrongylus macrotis*	*Capillaria*
1	–	–	–	–	–	–	–
2	–	5/8 (63%) 0.245; 0.910; 1.0 (1.15)	1/8 (13%) 0.003; 0.530; 0.3 (0)	–	6/8 (75%) 0.349; 0.969; 0.5 (0.4)	–	–
3	–	–	–	–	–	–	–
4	2/20 (10%) 0.012; 0.326; 0.5 (0.4)	1/20 (5%) 0.001; 0.249; 0.3 (0)	9/20 (45%) 0.232; 0.687; 0.7 (1.35)	–	–	–	2/20 (10%) 0.012; 0.326; 0.3 (0)
5	2/125 (2%) 0.002; 0.057; 0.3 (0)	7/125 (6%) 0.023; 0.114; 0.7 (0.4)	–	–	1/125 (1%) 0.0002; 0.044; 2.0 (0)	–	–
6	–	–	–	–	–	–	–
7	–	–	–	3/30 (10%) 0.021; 0.266; 0.3 (1)	–	–	–
8	–	1/7 (14%) 0.004; 0.577; 0.3 (0)	–	–	3/7 (43%) 0.116; 0.748; 0.7 (1)	–	–
9	–	–	3/10 (30%) 0.066; 0.652; 1.0 (1.7)	–	2/10 (20%) 0.025; 0.556; 26.3 (68.3)	–	1/10 (10%) 0.003; 0.445; 0.7 (0)
10	–	5/17 (29%) 0.104; 0.569; 0.7 (0.7)	–	–	–	–	–
11	–	–	–	–	–	–	–
12	3/10 (30%) 0.066; 0.652; 0.7 (0.4)	–	5/10 (50%)* 0.187; 0.813; 2.7 (4.55)	1/10 (10%) 0.003; 0.445; 0.3 (0)	1/10 (10%) 0.003; 0.445; 1.3 (0)	1/10 (10%) 0.003; 0.445; 4.0 (0)	–

Note: % – number of positive samples/number of studied samples (sample prevalence), confidence interval (CI) is 95%, lower bound and upper bound are given; sample intensity (among positives) is shown as median with Interquartile range (IQR).

Table 4. Sample intensity (among positives) of infection according to National Standard (2013) with quantitative values clarifying the intensity categories established in the standard, supplemented by data from our study to indicate the corresponding classification

Helminths	Intensity of infection depending on the number of found helminth eggs and larvae, specimens per 1 g of faeces			
	Low	Medium	High	Very High
NEMATODES	1–100	101–500*	501–1000	> 1000
GINs** (eggs + L3s)***	0.3–6.7 (sites 2, 4 ,9, 12)	–	–	–
Nematodirus (eggs)	0.3–1.3 (sites 7, 12)	–	–	–
Elaphostrongylus rangiferi (L1s)	0.3–75.3 (sites 2, 5, 8, 9, 12)	–	–	–
Orthostrongylus macrotis (L1s)	4.0 (site 12)	–	–	–
Capillaria (eggs)	0.3–0.7 (sites 4, 9)	–	–	–
CESTODES	1–100	101–500*	501–1000	> 1000
Moniezia (eggs)	0.3–2.0 (sites)	–	–	–
TREMATODES	1–10	11–100	> 100	–
Paramphistomatoidea (eggs)	0.3–0.7 (sites 4, 5, 12)	–	–	–

Note: * – low intensity in case of adult animals; ** – gastrointestinal nematodes (small strongylides); *** – including *Ostertagia gruehneri*.

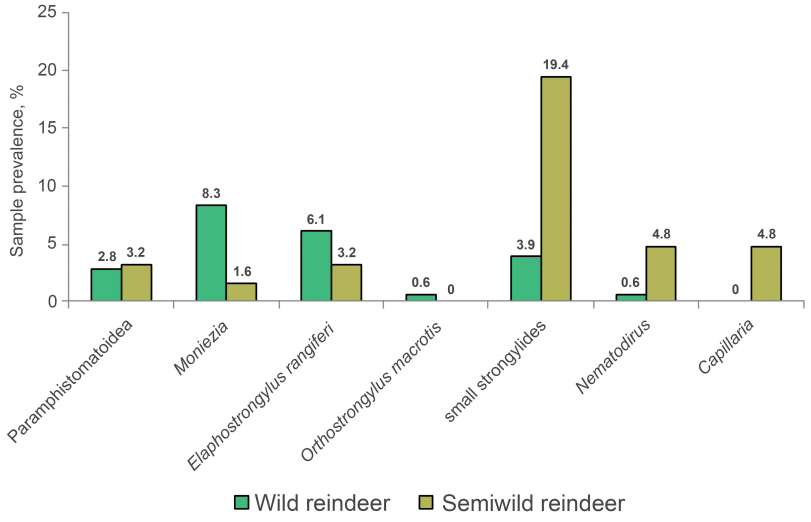

Fig. 3. Sample prevalence for 242 fecal samples collected from wild (180 samples) and semiwild (62 samples) reindeer (*Rangifer tarandus*).

We emphasise that this comparison is descriptive only, and several limitations must be acknowledged. The sample sizes are small, with less than ten positive sites in each group. In addition, the number of samples per positive site is uneven, ranging from eight samples to 90 samples. The data represent frequencies in samples rather than in individual animals, as a single sample cannot always be confidently attributed to an individual animal when defecation was not directly observed. Accordingly, these data should not be interpreted as estimates of population-level prevalence but rather as a presence-only baseline survey.

Across parasite groups, the integrated analysis (combining prevalence differences, effect-size estimation (Cohen's h), significance testing, odds-ratio evaluation, and power analysis) revealed considerable heterogeneity in both effect magnitude and statistical support. For gastrointestinal nematodes (GINs), we observed a large prevalence difference (≈ 15.5%), with a medium-to-large effect size (h ≈ 0.51), a highly significant result (p = 0.0004), and a strong odds ratio (OR = 5.9). Statistical power exceeded 0.95, indicating a robust and methodologically reliable result, with clearly higher prevalence in faecal samples from semiwild *Rangifer tarandus*. For *Nematodirus*, the prevalence difference was moderate (≈ 4.3%), with a small-to-medium effect size (h ≈ 0.29). Although the odds ratio was high (OR = 8.9), the p-value was marginal (p = 0.06), and statistical power remained limited (≈ 0.65), suggesting a plausible but weakly supported effect likely constrained by sample size. *Elaphostrongylus rangiferi* showed a small negative prevalence difference (≈ -2.9%) and a negligible effect size, with no statistical support for group differences (p = 0.54, OR = 0.50) and very low statistical power (≈ 0.2). This pattern indicates no detectable difference under the current sampling conditions. For *Orthostrongylus macrotis*, the prevalence difference was minimal (≈ -0.6%), with an effect size close to zero. The p-value equaled 1.0, and the odds ratio could not be interpreted reliably owing to a zero cell. The statistical power was extremely low (< 0.1), indicating insufficient data and no evidence of a meaningful difference between groups. *Capillaria* showed a moderate prevalence difference (≈ 4.8%) and a medium effect size (h ≈ 0.44). The association was statistically significant (p = 0.01), although the odds ratio could not be calculated owing to a zero cell. The statistical power was moderate (≈ 0.75), supporting a higher prevalence in faecal samples from semiwild *Rangifer tarandus*. For *Moniezia*, the prevalence difference was moderately negative (≈ -6.7%), with a medium effect size (h ≈ -0.33). However, the association was not statistically significant (p = 0.12), the odds ratio was low (OR = 0.18), and the statistical power remained weak (≈ 0.45–0.50), indicating a non-significant trend towards higher prevalence in faecal samples from wild *Rangifer tarandus*. Paramphistomatoidea showed an almost negligible prevalence difference (≈ 0.5%) and an effect size close to zero. The p-value equaled 1.0, the odds ratio was approximately 1.15, and the statistical power was extremely low (< 0.1), indicating no detectable difference and very low analytical sensitivity.

Discussion

The limited available sources indicate that during the XX century researchers studied helminths of *Rangifer tarandus* in the Palaearctic between 50° N and 60° N only within the former USSR and Mongolia. Published records are available for *Rangifer tarandus* from Khabarovsky Krai, present-day Republic of Buryatia, Republic of Tuva (Russia) (Machulsky, 1955; Sulimov, 1966, 1968; Kadenatsii, 1963; Zhaltsanova, 1972; Skrjabin, 1930), and Khövsgöl Province (Mongolia) (as «Chubsugul Aymak» in Dróżdż & Namžyl, 1973). In most of these studies, researchers used the Skrjabin's helminthological dissection method (Skrjabin, 1928), and they examined domestic *Rangifer tarandus* as the study animals. In the XXI century, only two relevant studies were published. One addressed *Rangifer tarandus* in Kazakhstan, and the other focused on the Magadan Region of Russia (Loginova, 2024; Loginova et al., 2024). Loginova, a co-author of the present study, conducted both investigations. Consequently, no site included in the present study has previously been examined using the same methodological approach and the same type of *Rangifer tarandus*. This circumstance restricts direct comparisons among sites and between studies. However, within the broader region surveyed, earlier studies have already documented the helminth fauna detected here, with the exception of a representative of the family Molineidae.

Machulsky (1955), Sulimov (1968), and Kadenatsii (1963) reported *Nematodirella longissimespiculata* (Romanovitsch, 1915) Skrjabin & Schikhobalova, 1952, whereas our material contained *Nematodirus*. Mizkewitsch (1967) noted

that these two genera frequently occur in *Rangifer tarandus* together. Given the low intensity of infection among positive samples (< 1 egg per 1 g of faeces) and the detection of eggs in only four of 242 samples, it is plausible that such mixed infections were simply not captured in the present dataset.

Eggs of rumen flukes belonging to the superfamily Paramphistomatoidea, detected in our material, may belong to species of the genus *Paramphistomum* Fischoeder, 1901 (Paramphistomatidae Fischoeder, 1901), such as *Paramphistomum cervi* (Zeder, 1790), which has been widely reported for *Rangifer tarandus* (Kadenatsii, 1963; Mizkewitsch, 1967; Tryland & Kutz, 2019). Alternatively, they may correspond to *Calicophoron daubneyi* Dinnik, 1962 (Paramphistomatidae), reported from Cervidae in the Palaearctic (Rehbein et al., 2024), or to *Fischoederius elongatus* (Poirier, 1883) Stiles & Goldberger, 1910 (Gastrothylacidae Stiles & Goldberger, 1910), which Zhaltsanova (1972) recorded in *Rangifer tarandus* from the Republic of Buryatia. The eggs of these trematodes are morphologically highly similar, and their size ranges overlap (Skrjabin, 1949). Moreover, this group still requires comprehensive taxonomic revision (Eduardo, 1982). For these reasons, we restricted identification to the superfamily level.

Moniezia species reported for *Rangifer tarandus* in the south were identified either as *Moniezia expansa* (Rudolphi, 1810) Blanchard, 1891 in semiwild *Rangifer tarandus* in the Republic of Buryatia (Machulsky, 1955), *M. baeri* Skrjabin, 1931 in semiwild *Rangifer tarandus* in the Republic of Tuva (Sulimov, 1966), or *M. benedeni* (Moniez, 1879) Blanchard, 1891 in wild *Rangifer tarandus* in the Republic of Tuva (Sulimov, 1968) and semiwild *Rangifer tarandus* in Khabarovsky Krai (Kadenatsii, 1963). The *Moniezia* eggs observed in our material tended to appear square in two-dimensional projection. On this basis, we excluded *Moniezia expansa* from the diagnosis, as this species is characterised by triangular eggs. Nevertheless, we retained identification at the genus level, because a recent revision indicates that the taxonomy of this group requires further development (Haukisalmi et al., 2018).

The small strongylid eggs detected in the material showed considerable variation in both size and shape. This variation suggests the presence of several species belonging to different genera, including, for instance, *Cooperia* Ransom, 1907, *Haemonchus* Cobb, 1898, *Ostertagia* (Ransom, 1907) Orloff, 1933, *Spiculopteragia* (Orloff, 1933) Travassos, 1937, *Teladorsagia* Andreeva & Satubaldin, 1954, *Trichostrongylus* Looss, 1905. Species-level identification cannot be achieved without molecular-genetic analysis, because these nematodes exhibit egg polymorphism and egg size may depend on the host species and its body size. Furthermore, interspecific hybridisation, together with other influencing factors, cannot be excluded (Skrjabin et al., 1954).

Material obtained from wild *Rangifer tarandus* at site 12 enabled us to determine the species identity of the small strongylid through molecular-genetic analysis. The analysis identified the species as *Ostertagia gruehneri*. This species is currently regarded as dimorphic, with the major morph corresponding to *Ostertagia gruehneri* and the minor morph to *Ostertagia arctica* (Dróżdż, 1995). Notably, Skrjabin (1930) originally described *Ostertagia gruehneri* in 1929 from domestic *Rangifer tarandus* in the southern part of the species range (Khabarovsky Krai). In the same year, Mizkewitsch described the minor morph (*Ostertagia arctica*) from material collected in Arkhangelsk (Skrjabin, 1930; Mizkewitsch, 1967). Sulimov (1966, 1968) later reported findings of *Ostertagia gruehneri* and *Ostertagia arctica* in both domestic and wild *Rangifer tarandus* in the Republic of Tuva, whereas Kadenatsii (1963) documented *Ostertagia gruehneri* in domestic *Rangifer tarandus* from Khabarovsky Krai, and Dróżdż & Namžyl (1973) reported both *Ostertagia gruehneri* and *Ostertagia arctica* in domestic *Rangifer tarandus* from Mongolia.

Palaearctic *Rangifer tarandus* can host two known protostrongylid species with the DSL larval morphotype: *Elaphostrongylus rangiferi* and *Varestrongylus eleguneniensis* (Mizkewitsch, 1967; Tryland & Kutz, 2019). Although precise identification of larvae requires DNA analysis, certain morphological differences exist between the larvae of these two species. For domestic *Rangifer tarandus* from China (site 9), we supported the morphological diagnosis with molecular-genetic confirmation. In all other cases, identification relied on morphological characters together with the well-documented wide distribution of *Elaphostrongylus rangiferi*. By contrast, *Varestrongylus eleguneniensis* has been recorded only once from wild *Rangifer tarandus* in the Palaearctic (Loginova et al., 2023b). An unidentified species of *Elaphostrongylus* Cameron, 1931 was also reported from semiwild *Rangifer tarandus* in

the Republic of Tuva in the XX century (Sulimov, 1966). Therefore, the assignment to *Elaphostrongylus rangiferi* is based on an integrative approach, including morphological characters, host specificity, geographic distribution data, and the available taxonomic literature for this group, and should be confirmed by molecular data whenever such data become available.

Another protostrongylid detected in the faeces was *Orthostrongylus macrotis*. This species is primarily known from the Nearctic region (Boev, 1975). In the Palaearctic, it has been reported so far only twice: first, through genetic identification from wild faeces of *Rangifer tarandus* collected at 71.18833° N, 98.07083° E in Taimyr (Russia) in 2022 (Loginova et al., 2023a), and through morphological identification from the faeces of the wild *Rangifer tarandus* collected at 63.72640° N, 158.07980° E in Magadan Region (Russia) in 2024 (Loginova et al., 2024). In our study, we again detected *Orthostrongylus macrotis* genetically in faecal samples from wild *Rangifer tarandus* (site 12). Given the very limited number of observations and the restricted geographic coverage of available records, these findings do not permit robust biogeographical conclusions. However, they suggest the tentative hypothesis that *Orthostrongylus macrotis* may occur in parts of Eastern Siberia and may potentially serve as an indicator of certain wild populations of *Rangifer tarandus*. At present, these suggestions remain speculative and require systematic testing through broader and targeted sampling programmes.

In contrast, we detected eggs of *Capillaria* sp. only in faeces of semiwild *Rangifer tarandus* in our dataset (site 4 and site 9: Mongolia and China). Previous studies from the southern part of the range of *Rangifer tarandus* also reported *Capillaria* exclusively from semiwild animals, including in the Republic of Tuva (Sulimov, 1966) and in Khabarovsky Krai (Kadenatsii, 1963). Across published Palaearctic data (Skrjabin et al., 1957; Mizkewitsch, 1967; Tryland & Kutz, 2019; Loginova et al., 2023b), researchers have likewise recorded *Capillaria* only in semiwild *Rangifer tarandus*. While this recurring pattern is noteworthy, it should still be regarded as a working hypothesis suggesting a possible association between *Capillaria* and semiwild *Rangifer tarandus*. This assumption also requires formal testing through larger and geographically broader sampling efforts.

Paramphistomatoidea are rumen flukes that can affect digestive system. *Moniezia* is a tapeworm inhabiting small intestine. Once numerous it can be life threatening. GINs, *Nematodirus* and *Capillaria* inhabit mostly small intestine also. Their impact varies. The brainworm *Elaphostrongylus rangiferi* inhabits central nervous system and muscles. Its presence can either cause no symptoms or be lethal. The lungworm *Orthostrongylus macrotis*, due to its localisation, can compromise the health of the host (Mizkewitsch, 1967; Tryland & Kutz, 2019).

It should be noted that Kazakhstan does not host natural populations of *Rangifer tarandus*. In both documented cases (Loginova, 2024; present study), owners kept the animals in two private menageries, where several individuals had been imported from Russia during the XXI century. However, these private introduction attempts still require monitoring, and we therefore consider their inclusion in the present study important.

Across all examined parasite groups in this research, only GINs and *Capillaria* showed consistent and statistically supported differences between the two host categories. In both cases, faecal samples from semiwild *Rangifer tarandus* exhibited a noticeably higher prevalence. For GINs, the effect was strong and robust and was supported by high statistical power. For *Capillaria*, the observed differences were moderate but remained consistent across analytical approaches. For all other parasite taxa, differences between groups were either minimal or statistically unreliable. In several cases, small sample sizes, rare detections, and zero-inflated datasets substantially limited inferential precision. These methodological limitations suggest that some real patterns may remain undetected because of insufficient statistical power rather than a true biological absence of differences.

In all cases where samples tested positive, infection intensity (among positives) was low (Table 4). This observation may be consistent with, but does not in itself demonstrate, the assumption that the animals producing these faeces were in generally adequate physiological condition.

The authors acknowledge that coproscopy captures only a partial picture of the helminth fauna. Several important limitations are inherent in this method. Egg counts do not always correlate directly with the number of mature helminths present. Helminth reproductive output also fluctuates daily and seasonally. Another limitation arises from pooling samples across multiple years, although parasite patterns may vary with year and climatic conditions. In addition, DNA extraction and analysis

failed for four DSL larval pools (and for all eggs); consequently, we based their identification on morphology and host specificity. Coproscopy does not detect tissue-dwelling or body-cavity helminths, including larval Taeniidae Ludwig, 1886 and adult *Setaria* Viborg, 1795, *Onchocerca* Diesing, 1841, and related parasites. Coproscopic results may also appear falsely negative when helminths remain immature and have not yet begun producing eggs or larvae. Animals carrying extremely heavy infections may also be under-represented in samples because they die in remote areas and therefore remain unsampled. However, we selected coproscopy because it is a non-invasive approach, unlike the lethal sampling required for Skrjabin's helminthological dissection method (Skrjabin, 1928). This approach allows researchers to study live, protected wild *Rangifer tarandus* and enables reliable comparison with data obtained from semiwild animals. Accordingly, we interpret the results of this study strictly within these methodological constraints and do not treat them as a complete representation of the helminth community.

The impact of heterogeneity within the collected sample sets varied among parasite groups. For parasites, for which we detected strong and statistically well-supported differences, such as GINs and, to a lesser extent, *Capillaria*, the magnitude and consistency of the observed effects reduce the likelihood that sampling structure alone explains the detected patterns, although some degree of effect inflation or attenuation cannot be excluded. In contrast, parasite groups showing weak, non-significant, or highly uncertain differences are much more sensitive to the non-representative nature of the sampling design. For these taxa, variation in seasonality, habitat, or host demography may either obscure genuine differences or create the appearance of minor effects. Consequently, biological interpretations concerning *Nematodirus*, *Moniezia*, *Elaphostrongylus rangiferi*, *Orthostrongylus macrotis*, and Paramphistomatoidea should be considered tentative.

At the population level, our data may cautiously support the view that a relatively greater helminth diversity and higher helminth burdens are associated with stability of the host population. Thus, the known groups of wild northern Siberian forest *Rangifer tarandus* (*R. t. valentinae* Flerov, 1932) that persist in the Altai (site 3) and Baikal State Nature Reserves (site 5) are extremely small, often comprising only a few dozen individuals. This subspecies is included in the Red Data Book of the Russian Federation (Panchenko et al., 2021) as an endangered population. Among the 128 samples collected from this population, we detected only three helminth taxa, occurring in just ten samples. In contrast, in Tokinsko-Stanovoy National Park (sites 10, 11, 12), where wild *Rangifer tarandus* is also present, we detected six helminth taxa in 26 samples, with sample prevalence reaching 50%, while the local population of *Rangifer tarandus* is estimated at approximately 700–800 individuals.

Looking ahead, several considerations could improve the reliability and interpretability of future studies. Larger sample sizes, particularly for rare parasite groups (such as *Orthostrongylus macrotis*), would increase the statistical power and reduce the frequency of zero-count cells. More balanced sampling between wild and semi-domesticated populations would further strengthen comparative analyses. Incorporating ecological and behavioural variables, such as habitat type, host density, seasonal dynamics, and grazing practices, may help explain the observed host-parasite differences. Analytical approaches robust to sparse data, including Bayesian methods and mixed-effects models, could also yield more stable estimates. Finally, repeated sampling across seasons and years would help determine whether the patterns identified here represent persistent ecological processes or short-term fluctuations.

Conclusions

In our coprological survey, aimed at detecting helminths in *Rangifer tarandus* in the southern part of its Palaearctic range, we identified trematodes of the superfamily Paramphistomatoidea, cestodes of the genus *Moniezia*, nematodes including *Elaphostrongylus rangiferi*, *Orthostrongylus macrotis*, and the dimorphic species *Ostertagia gruehneri* / *Ostertagia arctica*, as well as representatives of the genera *Nematodirus* and *Capillaria*, together with small strongylids that we could not identify to genus level. All helminths recorded in this study have previously been reported from *Rangifer tarandus* and from the Palaearctic region, with the exception of *Nematodirus* sp. in the southern part of the range. However, this study provides the first examination of helminths in the faeces of wild *Rangifer tarandus* from the State Nature Reserve «Vasyugansky» (Novosibirsk Region, Russia), Altai State Nature Reserve (Republic of Altai, Russia), Baikal State Nature Reserve (Republic of Buryatia,

Russia), Irkutsk Region (Russia), Olyokminsky State Nature Sanctuary (Amur Region, Russia), Tokinsko-Stanovoy National Park (Amur Region, Russia), as well as from the faeces of semiwild *Rangifer tarandus* in Zabaykalsky Krai (Russia), Mongolia, and Inner Mongolia (China). We established the southernmost known range limits for *Elaphostrongylus rangiferi* (51.35080° N, 121.50146° E; China) and for *Orthostrongylus macrotis* (55.44280° N, 130.48006° E; Russia).

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Supporting Information

Additional data for the paper by Loginova et al. (2026) may be found in the **Supporting Information**.

References

Aleuy O.A., Serrano E., Ruckstuhl K.E., Hoberg E.P., Kutz S. 2020. Parasite intensity drives fetal development and sex allocation in a wild ungulate. *Scientific Reports* 10: 15626. DOI: 10.1038/s41598-020-72376-x

Andersson Stavridis M., Røed S.B., Hansen B.B., Mikkelsen Ø., Ciesielski T.M., Jenssen B.M. 2024. Tracing the footprints of Arctic pollution: Spatial variations in toxic and essential elements in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) faeces. *Science of the Total Environment* 906: 167562. DOI: 10.1016/j.scitotenv.2023.167562

Baskin L., Danell K. 2003. *Ecology of Ungulates: A Handbook of Species in Eastern Europe and Northern and Central Asia*. Berlin/Heidelberg, New York: Springer. 434 p.

Blaker H. 2000. Confidence curves and improved exact confidence intervals for discrete distributions. *Canadian Journal of Statistics* 28(4): 783–798. DOI: 10.2307/3315916

Boev S.N. 1975. *Protostrongylides. Principles of Nematodology*. Vol. 25. Moscow: Nauka. 267 p. [In Russian]

Darling S.T., Barber M.A., Hacker H.P. 1920. *Hookworm and Malaria. Research in Malaya, Java, and the Fiji Islands (Report of Uncinariasis Commission to the Orient 1915–1917)*. New York: Rockefeller Foundation International Health Board. 191 p.

Dróżdż J. 1995. Polymorphism in the Ostertagiinae Lopez-Neyra, 1947 and Comments on the Systematics of These Nematodes. *Systematic Parasitology* 32(2): 91–99. DOI: 10.1007/BF00009507

Dróżdż J., Namžyl G. 1973. On Trichostrongylidae (Nematoda) of cervid ruminants in Mongolia, with reference to some more data concerning the historical formation of the helminth fauna of this host group. *Acta Parasitologica Polonica* 30: 475–479.

Eduardo S.L. 1982. The taxonomy of the family Paramphistomidae Fischoeder, 1901 with special reference to the morphology of species occurring in ruminants. I. General considerations. *Systematic Parasitology* 4(1): 7–57. DOI: 10.1007/BF00012228

Gasser R.B., Chilton N.B., Hoste H., Beveridge I. 1993. Rapid sequencing of rDNA from single worms and eggs of parasitic helminths. *Nucleic Acids Research* 21(10): 2525–2526. DOI: 10.1093/nar/21.10.2525

Guillou S. 2005. *Reindeer: Inhabitant of cold regions*. Paris: Éd. Atlas jeunesse. 29 p.

Gunn A. 2016. *Rangifer tarandus*. In: *The IUCN Red List of Threatened Species 2016: e.T29742A22167140*. Available from https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T29742A22167140.en

Haukisalmi V., Laaksonen S., Oksanen A., Beckmen K., Halajian A., Yanagida T., Nakao M. 2018. Molecular taxonomy and subgeneric classification of tapeworms of the genus *Moniezia* Blanchard, 1891 (Cestoda, Anoplocephalidae) in northern cervids (*Alces* and *Rangifer*). *Parasitology International* 67(2): 218–224. DOI: 10.1016/j.parint.2017.12.006

Hudson P.J., Dobson A.P., Lafferty K.D. 2006. Is a healthy ecosystem one that is rich in parasites?. *Trends in Ecology and Evolution* 21(7): 381–385. DOI: 10.1016/j.tree.2006.04.007

Kadenatsii A.N. 1963. Helminths of Reindeer in Khabarovsk Krai. In: *Proceedings of the All-Union Scientific Conference dedicated to the 90th anniversary of the Kazan Veterinary Institute*. Kazan: KVI. P. 146–147. [In Russian]

Kaltenborn B.P., Andersen O., Gundersen V. 2014. The role of wild reindeer as a flagship species in new management models in Norway. *Norwegian Journal of Geography* 68(3): 168–177. DOI: 10.1080/00291951.2014.904400

Klein D.R. 1980. Conflict Between Domestic Reindeer and Their Wild Counterparts: A Review of Eurasian and North American Experience. *Arctic* 33(4): 739–756. DOI: 10.14430/arctic2593

Kontrimavichus V.L., Delyamure S.L., Boev S.N. 1976. *Metastrongyliodeas of Animals and Man. Principles of Nematodology.* Vol. 26. Moscow: Nauka. 239 p. [In Russian]

Kurtén B. 1968. *Pleistocene mammals in Europe*. London: Weidenfeld and Nicolson. 317 p.

Kurtén B., Anderson E. 1980. *Pleistocene mammals in North America*. New York: Columbia University Press. 442 p.

Loginova O.A. 2024. Helminths of Reindeer in Kazakhstan. In: *Modern Problems of General and Applied Parasitology*. Voronezh: Tsifrovaya poligrafiya. P. 90–95. [In Russian]

Loginova O.A., Kolpashchikov L.A., Spiridonov S.E. 2023a. First report of *Orthostrongylus* sp. (Nematoda: Protostrongylidae) in wild reindeer (*Rangifer tarandus*) from the Taimyr, Russia: Nearctic parasites in a Palearctic host. *Parasitology Research* 122(2): 685–689. DOI: 10.1007/s00436-022-07754-7

Loginova O.A., Rozenfeld S.B., Sipko T.P., Mizin I.A., Panchenko D.V., Laishev K.A., Bondar M.G., Kolpashchikov L.A., Gruzdev A.R., Kulemeev P.S., Litovka D.I., Semerikova M.N., Mamontov V.N., Mamaev E.G., Spiridonov S.E. 2023b. Diversity and Distribution of Helminths in Wild Ruminants of the Russian Arctic: Reindeer (*Rangifer tarandus*), Muskoxen (*Ovibos moschatus*), and Snow Sheep (*Ovis nivicola*). *Diversity* 15(5): 672. DOI: 10.3390/d15050672

Loginova O.A., Sipko T.P., Hernandez-Blanco J.A., Plotnikova Iu.K. 2024. Helminthocoproscopy of Wild Reindeer and Muskoxen in the Magadan Region. In: *Biological problems of the North*. Magadan: Znanie-M. P. 167–168. [In Russian]

Machulsky S.N. 1955. Wild ungulates as reservoirs of Helminthic Diseases for Farm Animals of the Buryat-Mongolian ASSR. *Proceedings of the Buryat-Mongolian Zoological Veterinary Institute* 9: 163–172. [In Russian]

MacKenzie K., Abaunza P. 1998. Parasites as Biological Tags for Stock Discrimination of Marine Fish: a Guide to Procedures and Methods. *Fisheries Research* 38(1): 45–56. DOI: 10.1016/S0165-7836(98)00116-7

Mizkewitsch V.Y. 1967. *Reindeer Helminths and the Diseases They Cause.* Leningrad: Kolos. 308 p. [In Russian]

Morgulis A., Coulouris G., Raytselis Y., Madden T.L., Agarwala R., Schäffer A.A. 2008. Database indexing for production MegaBLAST searches. *Bioinformatics* 24(16): 1757–1764. DOI: 10.1093/bioinformatics/btn322

Mysterud A., Tveraa T., Hansen B.B., Gundersen V., Tømmervik H., Erlandsson R., Røed K.H., Våge J., Andersen R., Brænd E., Bøthun S.W., Elgaaen M., Holand Ø., Kjørstad M., Kvie K., Mossing A., Myren I.S., Panzacchi M., Peeters B., Punsvik T., Romtveit L., Skarin A., Moorter B.V., Veiberg V., Jaren V., Strand O., Rolandsen C.M. 2025. A quality standard for conservation of wild reindeer. *Wildlife Monographs* 219(1): e70005. DOI: 10.1002/wmon.70005

National Standard. 2013. *National Standard of the Russian Federation GOST R 54627-2011: Agricultural Ruminant Animals. Methods of Laboratory Helminthological Diagnostics*. Moscow: Standartinform. 20 p. [In Russian]

Panchenko D.V., Mizin I.A., Rozhnov V.V. 2021. Reindeer *Rangifer tarandus* Linnaeus, 1758. In: *Red Data Book of the Russian Federation. Animals*, 2nd ed. Moscow: VNII Ekologiya. P. 1020–1025. [In Russian]

R Core Team. 2025. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from https://www.R-project.org

Rehbein S., Vymyslická P.J., Peterka T., Strube C., Visser M., Mayr S., Lackerschmid J. 2024. *Calicophoron daubneyi* (Paramphistomidae) in deer of the Šumava National Park, Czech Republic – Consequence of Prevalent Rumen Fluke Infection in Cattle. *Veterinary Parasitology: Regional Studies and Reports* 50: 101012. DOI: 10.1016/j.vprsr.2024.101012

Skrjabin K.I. 1928. *Method of complete helminthological dissections of vertebrates, including humans.* Moscow: First Moscow State University. 45 p. [In Russian]

Skrjabin K.I. 1930. *Worm infections in reindeer.* Moscow, Lenindrad: Selkhozgiz. 88 p. [In Russian]

Skrjabin K.I. 1949. *Trematodes of Animals and Man. Principles of Trematodology.* Vol. 3. Moscow: AS USSR. 623 p. [In Russian]

Skrjabin K.I., Shikhobalova N.P., Schulz R.S. 1954. *Trichostrongylides of Animals and Man. Principles of Nematodology.* Vol. 3. Moscow: AS USSR. 683 p. [In Russian]

Skrjabin K.I., Shikhobalova N.P., Orloff I.W. 1957. *Trichocephalides and Capillariides of Animals and Man and the Diseases They Cause. Principles of Nematodology*. Vol. 6. Moscow: AS USSR. 587 p. [In Russian]

Smirnov M.N. 2016. *Reindeer in the South of Siberia.* Krasnoyarsk: Siberian Federal University. 230 p. [In Russian]

Spassky A.A. 1951. *Fundamentals of Cestodology. Anoplocephalates – tapeworms of domestic and wild animals.* Vol. 1. Moscow: AS USSR. 735 p. [In Russian]

Sulimov A.D. 1966. Helminths of Reindeer in Tuva. *Proceedings of the Omsk Veterinary Institute* 24: 135–141. [In Russian]

Sulimov A.D. 1968. On the Helminth Fauna of Wild Ruminants of Tuva. *Proceedings of the Omsk Veterinary Institute* 25: 238–242. [In Russian]

Tryland M., Kutz S.J. (Eds.). 2019. *Reindeer and Caribou. Health and Disease*. Boca Raton, London, New York: CRC Press. 533 p.

Vajda T. 1931. Rapid method for diagnosing lung helminths in sheep. *Állatorvosi Lapok* 54: 187–190.

Zaplatin M.A. 1964. *Chara: With a movie camera across Transbaikalia*. Moscow: Mysl. 142 p. [In Russian]

Zhaltsanova D.S.D. 1972. Detection of *Fischoederius elongatus* (Poirier, 1883) in the Buryat ASSR. In: *Epizootiology, Epidemiology, and Prophylaxis of Helminthiases*. Vol. 24. Moscow: All-Union Society of Helminthologists. P. 49–50. [In Russian]

Zhang Z., Schwartz S., Wagner L., Miller W. 2000. A greedy algorithm for aligning DNA sequences. *Journal of Computational Biology* 7(1–2): 203–214. DOI: 10.1089/10665270050081478

ГЕЛЬМИНТЫ *RANGIFER TARANDUS* (ARTIODACTYLA, CERVIDAE) В ЮЖНОЙ ЧАСТИ ЕГО МАТЕРИКОВОГО АРЕАЛА

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Rangifer tarandus в южной Палеарктике остается малоизученным, особенно в отношении его гельминтофауны. Существующие данные по этим небольшим, изолированным и имеющим важное природоохранное значение популяциям скудны. Поскольку гельминты влияют на выживаемость, размножение и стабильность популяции хозяев, а также могут служить биогеографическими индикаторами, понимание их разнообразия в южных регионах имеет очевидное научное и природоохранное значение. В период с 2012 по 2025 гг. было собрано 242 образца фекалий от популяций *Rangifer tarandus* в Китае, Казахстане, Монголии и России, которые были проанализированы с использованием копроскопических методов. Морфологическая идентификация гельминтов была дополнена молекулярным анализом (там, где это было возможно). Таксономическая идентификация некоторых личинок нематод основывалась на секвенировании внутренних транскрибируемых спейсерных областей рибосомной ДНК (выделить ДНК из яиц гельминтов не удалось). Исследование выявило трематод надсемейства Paramphistomatoidea, цестод рода *Moniezia* и нематод, включая *Elaphostrongylus rangiferi*, *Orthostrongylus macrotis*, диморфный вид *Ostertagia gruehneri / Ostertagia arctica*, а также *Nematodirus*, *Capillaria* и неидентифицированных малых стронгилид. Все идентифицированные таксоны ранее были зарегистрированы у *Rangifer tarandus* и в пределах Палеарктики, за исключением *Nematodirus* sp. в южной части ареала. Данное исследование впервые предоставляет данные об обнаружении гельминтов в образцах фекалий диких *Rangifer tarandus* на нескольких охраняемых территориях и регионах, включая государственный природный заповедник «Васюганский» (Новосибирская область, Россия), Алтайский государственный природный заповедник (Республика Алтай, Россия), Байкальский государственный природный заповедник (Республика Бурятия, Россия), Иркутскую область (Россия), государственный природный заказник «Олекминский» (Амурская область, Россия), Токинско-Становой национальный парк (Амурская область, Россия), а также у полудиких *Rangifer tarandus* в Забайкальском крае (Россия), национальном парке Хубсугул (Монголия) и на территории Внутренней Монголии (Китай). Установлены самые южные границы распространения для *Elaphostrongylus rangiferi* и *Orthostrongylus macrotis*.

Ключевые слова: дикий северный олень, Казахстан, Китай, Монголия, Палеарктика, полудикий северный олень, Россия