Is the risk of bank vole infection with cestodes related to the population dynamics regime?

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Abstract

The bank vole (*Clethrionomys glareolus* (Schreber, 1780)) is the dominant species in the primary fir-spruce forests of the Visim State Biosphere Reserve in the Middle Urals. Here, we studied the long-term population dynamics of small mammals and infection rates with cestode larvae (Cestoida) of bank voles from 1995 to 2021. In addition to the traditionally studied risk factors of parasite infection (e.g., age and sex, phase of population cycle of the host), we assessed the possible influence of the intermediate host population dynamics by contrasting parts of the time series with regular 3-year cyclicity and noncyclic regime. The overall risk of larval cestode infections was 5.0% (95% CI: 4–6%, $N_{infected}$ = 97, N_{total} = 1938). The infection rate was associated with the animals' age and, unexpectedly, with the intermediate host population dynamics regime. The odds of finding cestode larvae in overwintered individuals were 4.3 times (2.8–6.6) higher than in young of the year, and in the noncyclic regime, the odds were 2.3 times (1.5–3.5) higher than in the 3-year cyclicity regime. No statistically significant higher risk of infection was found for males compared to females as the infection rate was only 1.4 times (0.9–2.1, ≈ 1) higher. The higher infection rates of overwintered individuals were as expected for individuals associated with longer exposure to the invasive parasite stages. We hypothesised that the noncyclic regime in long-term fluctuations of rodent numbers better resonates with the characteristic period of the cestodes' life cycle, resulting in higher infection rates.

Introduction

Parasitic systems involving small mammals that serve as parasite hosts are convenient models for studying coupled host-parasite dynamics. The high abundance and short lifespan of rodents and insectivores make it possible to estimate the parameters of fluctuation in parasite prevalence/abundance over several successive host generations (Haukisalmi *et al.* 1988; Stanko *et al.* 2002).

The relationship between the dynamics and structure of small mammal populations and the prevalence/abundance of parasitic infections has been studied in detail for many host-parasite groups. Moreover, observations of the dynamics of a host-parasite system can be long-term; for example, a *Clethrionomys glareolus* population was surveyed for 12 years (Haukisalmi and Henttonen 1990; Ieshko *et al.* 2009), while *Microtus arvalis* had a 14-year study (Fichet-Calvet *et al.* 2003), and a population of *Apodemus sylvaticus* was studied for 26 years (Behnke *et al.* 2021). These long-term datasets are valuable in aiding the understanding of host-parasite cycles and periodicity, which are the foundations of population ecology.

Our observations of small mammal populations in the southern taiga of the Middle Urals were conducted over 25 years. Throughout this period, cases of rodent liver infection were recorded with tapeworm larvae, a numerous group of parasitic flatworms (Plathelminthes: Neodermata: Cercomeromorpha: Cestoda) (Westheide and Rieger 2008). Many flatworms are dangerous parasites of animals and humans, causing pathology in various organs. The ontogenetic development of cestodes occurs with the participation of one or more hosts, so fluctuations in parasite numbers can be expected to depend less on abiotic environmental conditions (temperature, humidity, etc.) affecting the persistence of different parasite life stages and more on the dynamics, abundance, and infection of hosts (Mackiewicz 1988).

The long-term periodicity of small mammal population dynamics in the study area, from 1995 until 2006/2007, was described as a simple 3-year cycle with a regular sequence of three phases: 'trough', 'increase', and 'peak'. The phases of the population cycle differed not only in abundance level but also in specific seasonal dynamics and reproductive-age structure of the population. During the 'peak' years, the young of the year in the population of the dominant species (bank vole) did not mature (Kshnyasev and Davydova 2005, 2021). In 2006/2007, the 3-year cyclical regime was replaced by a quasi-2-year (or noncyclic) one. It differed from the 3-year cyclic regime by having a more pronounced seasonal component and the absence of the total blocking of maturation of young of the year bank voles. The prefix 'quasi' is added because spectral analysis

(used by us to analyse density dynamics) does not distinguish between a two-point cycle and its doubling (Kshnyasev and Davydova 2021). In 2017/2018, the 3-year cycle came back again. The reasons for this regime change are not clear, but we rather adhere to the hypothesis of endogenous population chaos, which describes the behaviour of nonlinear dynamic systems. These systems (e.g., populations) are subject to dynamic chaos under certain conditions and their behavior appears random (Frisman *et al.* 2015).

The observed change in the population dynamics regime made it possible to quantitatively assess its possible influence on the infection rate of rodents with cestode larvae. We also evaluated the effects of traditionally studied factors, such as age and sex of the intermediate host and the phase of the long-term population cycle.

Materials and methods

The study was based on the results of long-term observations (1995–2021) on the population dynamics of small mammals inhabiting primary fir-spruce forests of the Visim State Biosphere Reserve (southern dark conifer taiga, the Middle Urals; 57°22′ N, 59°46′ E, 538 m a.s.l.). Animal censuses were taken in permanent plots by the trap line method (with snap traps and wooden live traps; 200 traps/day per round) three times a year: in spring, summer, and autumn. Beginning in 2004, winter censuses were also performed. The bank vole (*Clethrionomys glareolus* (Schreber, 1780)) (Kryštufek and Shenbrot 2022) was the dominant species (the proportion of bank voles caught in relation to the total capture of all small mammals – p = 0.7). The sex and age of the bank voles were determined. Based on a set of exterior characteristics (body mass and body length), interior characteristics (mass of internal organs and the presence/absence of thymus), odontological traits, and capture date, two age groups were distinguished: young of the year (YY) and overwintered individuals (OW). The lifespan of young of the year is 3–6 months, in contrast to overwintered animals (12–15 months) (Olenev 2009). Young of the year, as a rule, have a thymus and are smaller in size and body weight compared to overwintered individuals, but they do not have tooth roots. Cestode larvae were detected during incomplete animal dissection (not for helminthological purposes) and complete dissection of the liver (Anikanova *et al.* 2007).

Diagnostics of larvae and metacestodes (postlarval parasite stage) were based on their localisation (liver tissue) and in some cases on morphological features of the head (number of scoleces and suckers), and they were evaluated selectively. These parasites were identified as cysticerci of Taenia (*Taenia* Linnaeus, 1758, Family Taeniidae). However, the old concepts of larval species diagnosis based on the tissue niche they occupy can now be revised. Currently, accurate diagnosis of larvae and metacestodes is only possible from comprehensive morphological and genetic analysis (Martini *et al.* 2022; Nakao *et al.* 2013). Since we cannot conclusively state that all the larvae found belong to Taenia, we therefore used the taxonomic designation 'larval cestodes' with caution. A common characteristic of taxon members is ontogenetic development involving an intermediate host harbouring the larval stage and a definitive host harbouring the adult stage. Intermediate hosts (rodents) become infected by ingesting oncospheres or mature proglottids. Definitive hosts become infected by ingesting infected organs and tissues of intermediate hosts. The parasites can complete their development in diurnal birds of prey and owls, and predatory mammals.

The probability (or risk) of infection with cestode larvae was modelled using multiple logit regression, which relates the log-odds of infection to the predictor variables. The model is expressed as: $LogOdds = Ln[N_{infected}/(N_{total} - N_{infected})] = b_0 + \Sigma b_i X_i$, where b_0 is the intercept (the baseline risk of infection when all predictors are zero), and the $b_i X_i$ terms represent the effects of the predictor variables on the risk of infection. To select the optimal model, we used the consistent Akaike information criterion: $CAIC = -2LL + K[1 + Ln(N)]$, where the model that minimized the criterion was considered the best among competing non-hierarchical models (using runs with alternative parameterizations). The predictors were categorical variables: year of capture, animal sex, and age, while the dynamics regime and phases of the 3-year cycle ('trough', 'increase', 'peak', 'noncyclic regime') were coded as four levels of another rank predictor. Log-odds ratios (LOR) and their 95% confidence intervals (CI) are given after back transformation: $OR = exp(b_i)$ or $OR = 1/exp(b_i)$, where b_i are parameters of logit regression (logarithms of the odds ratio). For rare events (less than 10% frequency), odds ratios can be directly interpreted as risk ratios (Agresti 2007).

To evaluate the lagged relationship between the two-time series (infected young of the year and overwintered animals), we employed cross-correlation. The correlation coefficients (CC) were used to measure the degree of similarity between the time series. Due to the presence of observed zeros in the data, we applied the arcsine transformation (arcsin(2p–1)) to normalize it. Additionally, given the sparsity of our data (Table S1), we performed power analysis to estimate the sample size necessary (N) for the effect to be comparable to the sex effect observed in our data. Statistical analysis was conducted using the software package Statistica (StatSoft, Inc. 2007).

Results and discussion

The overall risk of larval cestode infections was 5.0% (95% CI: 4–6%, $N_{infected} = 97$, $N_{total} = 1938$) (Table S1). The dynamics of small mammal numbers and fluctuations in the infection risk of bank voles with cestode larvae are shown in Figure 1. Since the number of small mammals in spring most clearly demonstrates a cyclic pattern (low densities guarantee no significant saturation effect of traps), Figure 1A presents data from spring captures. The 3-year cyclicity regime of host abundance (1995–2006/2007) corresponds to a lower long-term average value and low-amplitude fluctuations in infection risk compared to the drastic fluctuations on the eve of the transition to the noncyclic population dynamics regime.

It is perhaps no coincidence that the local maximum of infection occurred during the failure of the maintenance of the 3-year cyclic regime (2006). The breakdown of the cycle was also preceded by a maximum number of specialised predators (for example, 5 weasels, *Mustela nivalis* were caught in 4 traps/day).

The informative predictors of vole infection with cestode larvae were the 'age' and 'regime' (Table 1). The average age difference between overwintered individuals and young of the year is about one year, and the odds of diagnosing an invasion in overwintered individuals are 4.3 times (95% CI: 2.8–6.6) higher than in young of the year (Figure 2). The higher infection of adults compared to young is explained by the host's longer exposure to the invasive parasite stages (proportional to the total amount of food consumed), accumulation of parasites in the host body from earlier infection events, an increase in the visited area, and subsequently a
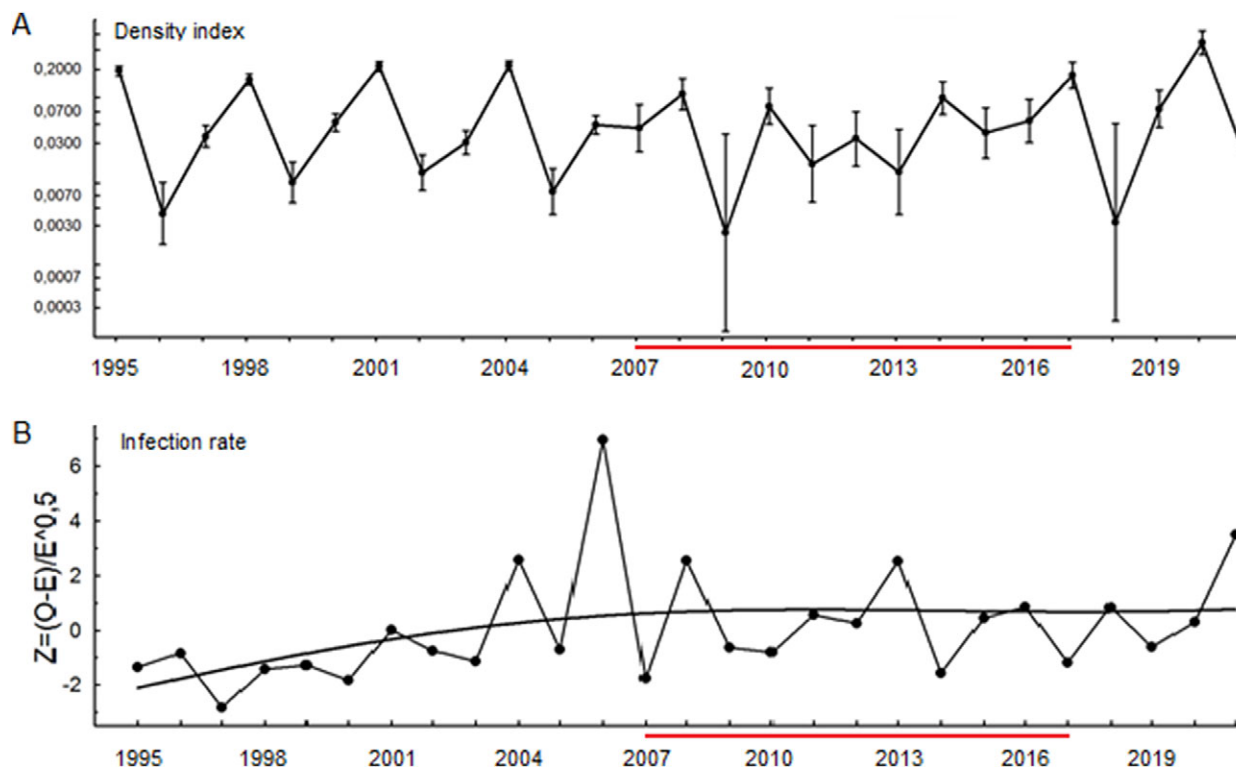
Figure 1. Long-term dynamics: (A) small mammal abundance (Density index = N_{catch}/N_{total}, log-transformed to logit scale) in spring (2007–2017, noncyclic regime shown by the red line); (B) infection rates of *Clethrionomys glareolus* with cestode larvae. The lower plot presents standardised deviations of observed (O) frequencies from the 'equilibrium' or expected (E) infection rate under the null hypothesis: $E_{ij} = N_{\bullet j} * N_{i \bullet} / N_{\bullet \bullet}$, where • denotes the marginal sum. Pearson X^2 statistic = $\Sigma[(O - E)^2/E]$ = 115.97, df = 26, p < 0.0001.

Table 1. Selection of the best model (minCAIC) to describe *Clethrionomys glareolus* infection with cestode larvae, $N_{infected}$ = 97, N_{total} = 1938

| Model rank	Predictors	K	−2LL	LR	CAIC	Δ	w
1	Age, Regime	3	718.22	59.86	743.96	0	0.802
2	Age, Phase + Regime	3	721.55	56.53	747.29	3.33	0.151
3	Age	2	732.49	45.59	749.65	5.69	0.047
4	Phase + Regime	2	762.70	15.38	779.86	35.91	0.000
5	Regime	2	765.08	13.00	782.24	38.28	0.000
6	H_0	1	778.08		786.66	42.70	0.000
7	Age, Year	21	642.42	135.66	822.60	78.65	0.000
8	Year	20	679.95	98.12	851.56	107.60	0.000

The predictors considered were three phases of dynamics ('trough', 'increase', 'peak'), two regimes of dynamics (cyclic and noncyclic), the age of the animals, and the year of animal capture. K – number of predictors, including b_0 (intercept); -2LL – negative twice the log-likelihood of the current model, a measure of model fit (lower values indicate better fit); LR(df = K – 1) – Likelihood Ratio statistic, used to compare models by testing the null hypothesis (H_0) that the simpler model is as good as the more complex one. It follows a chi-square distribution X^2(df); Δ – difference in CAIC between the current and best model (model with the lowest CAIC value); w – model weight, indicating the relative likelihood of the model given the data (higher values indicate more likely models).

greater number of contacts with parasites (Fichet-Calvet *et al.* 2003; Kisielewska 1971; Kirillova and Kirillov 2012).

The next important predictor was the dynamics regime: the infection odds in the noncyclic regime was 2.3 times higher (95% CI: 1.5–3.5) than in the 3-year cyclicity regime. It can be

hypothesised that the 2-year fluctuations in rodent numbers better 'resonate' and are thus more synchronized with the minimum duration of the cestode life cycle. That is, in the host-parasite system, literally in the 'physical' sense, the frequency of external oscillations (the number of hosts) finds a response with its own oscillations (the number of the parasite). For one of the potential *Taenia* species parasitising the bank vole (*Taenia pisiformis* Bloch, 1780; *Cysticercus pisiformis* (larval stage), the life cycle has been determined, with the duration of stages from oncosphere to invasive cysticercus being 45 days, and from cysticercus to adult stage 35–95 days, depending on the definitive host species (Shakhmatova 1963). However, the duration of viability of eggs in the environment is unknown, although it is a critically important factor for parasite persistence.

The positive zero-lag cross-correlation (CC_0 = 0.41, SE = 0.193) for the infection risk of the young of the year and overwintered animals clearly indicates synchronicity of the risk of infection in the same year (all individuals are infected from a common pool of eggs/larvae) and was expected. However, the second highest cross-correlation coefficient corresponds to a 2-year lag (CC_{+2} = 0.45, SE = 0.200) (Figure 3). Since voles do not live 2 years in the wild, this delay may correspond to the 'modal' duration of the parasite life cycle and its transit through intermediate and definitive hosts, and can be regarded as a kind of physical 'contour of enhancement/ attenuation' of invasiveness. In turn, the rapid decrease in cross-correlation coefficients at longer lags means that against the background of stochastic noise (including changes in the cyclicity regime of the intermediate host), the 'effective' duration of the parasites' life cycle will be limited by the lifespan of short-lived hosts and the finite (and short) viability persistence time of eggs,
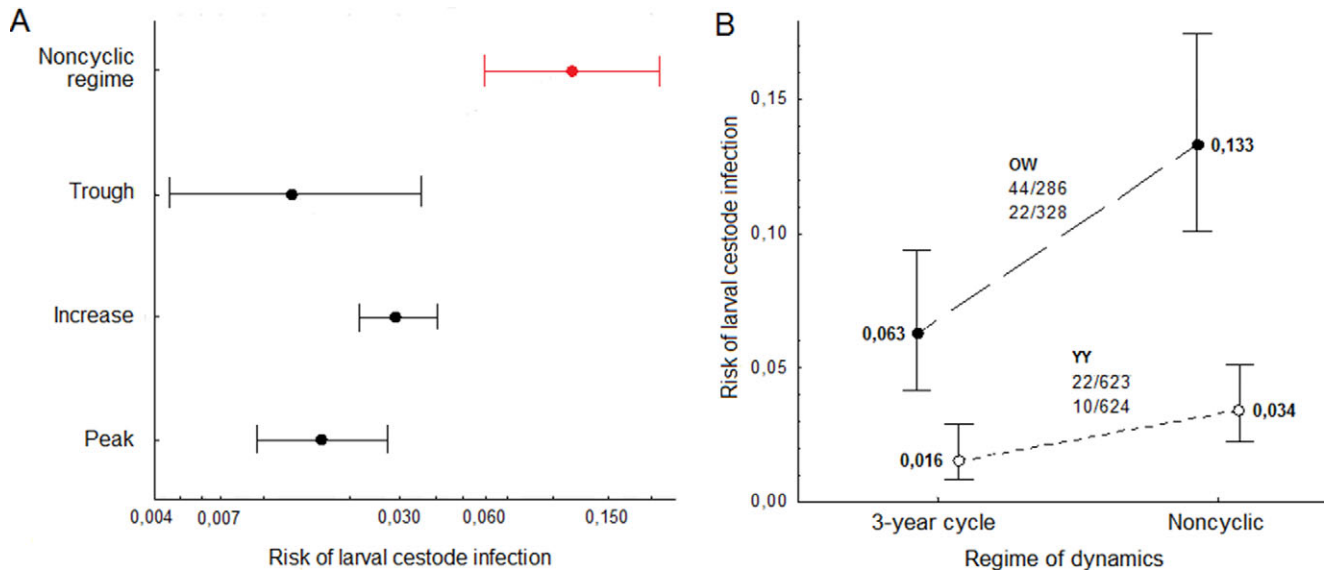
Figure 2. Risk of cestode larvae infection in *Clethrionomys glareolus*: (A) across three phases of the 3-year population cycle and during the noncyclic regime; (B) in different population groups and under two dynamic regimes. In the right-hand figure, young of the year (YY) are represented by white markers, and overwintered individuals (OW) by black markers. Numbers next to the markers indicate the proportion of infected animals, while numbers above the dashed lines (odds) show the ratio of infected to uninfected voles in YY and OW.
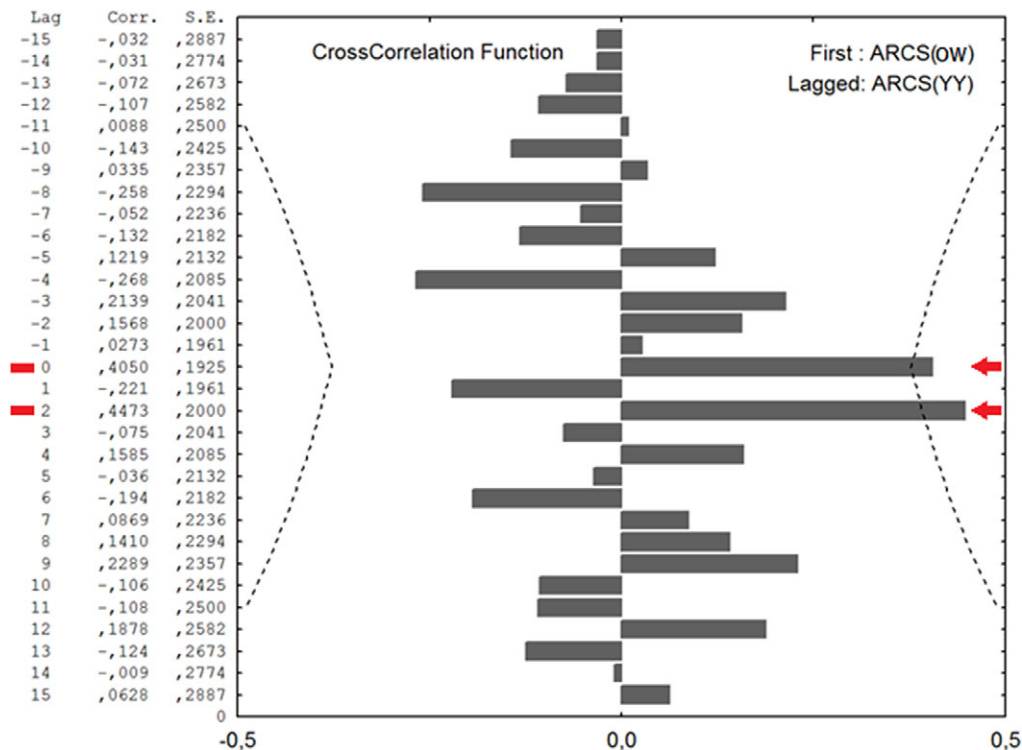
Figure 3. Cross-correlation between the arcsine-transformed infection risk of cestode larvae in young of the year (YY) and overwintered (OW) *Clethrionomys glareolus*. The first column (Lag) represents the shift in the time series relative to each other (in years). The second and third columns show the correlation coefficients and their associated errors for each lag. Red arrows and lines indicate two significant correlation coefficients: one in the year of capture (CC_0) and another at a 2-year lag (CC_{+2}).

while the definitive host serves as a long-term reservoir for adult cestodes.

The second statistical model, one that included the population cycle phase in addition to the dynamics regime, was inferior ($ER_{2/1} = w_2/w_2 = 0.188$) to the best model (see Table 1). Thus, the parasites' linkage to the 3-year cyclicity of intermediate host abundance (and its predator) cannot be considered proven. The resonance of rodent number fluctuations in the noncyclic regime

with the minimum duration of the cestodes' life cycle may also explain the lower occurrence of parasites in the bank voles in the northern part of the range where population cycles are longer (4–6 years) (Haukisalmi and Henttonen 1990).

The relationship between host and parasite abundance remains debatable. Some authors find a negative relationship between small mammal abundance (including the bank vole) and their infection rate: in 'peak' years, they recorded the minimum infection with parasites or the so-called dilution effect (see, for example, Haukisalmi and Henttonen 1990). Among the possible reasons are changes in the population structure in years of 'depression' – for example, an increase in the proportion of mature males, the more mobile and on average more heavily parasitised group. At the same time, an increase in the number of hosts and subsequently an increase in the frequency of intraspecific contacts is believed to create favourable conditions for parasite development.

Infection effects related to sex are also not always obvious (Poulin 1996; Schalk and Forbes 1997). In some cases, higher infection with adult cestode stages is found in males compared to females. The differences are explained by different consumption rates of potentially contaminated food items. The lower consumption rate in females is associated with the females' lower mobility during the offspring-rearing period (Kirillova and Kirillov 2012). In our case, infection with cestode larvae did not depend statistically on the voles' sex ($X^2(1) = 1.3$, p = 0.258); the odds of infection were only 1.4 times higher (95% CI: 0.9–2.1, ≈ 1) in males than in females. However, a posteriori power analysis showed that with a sample of 5,000 individuals, the effect could be recognised as significant. Similar results were obtained by Haukisalmi et al. (1987) for the grey red-backed vole in northern Finland; they also found no effect of sex on infection with cestode larvae (T. mustelae Gmelin, 1790).

Conclusion

For the first time, we attempted to assess the influence of the intermediate host's dynamic regime on cestode infection. Unlike the more commonly observed situation with cyclic fluctuations in the population size of intermediate or definitive hosts, this experiment could not be planned in advance.

Bank vole infection with cestode larvae predictably depends on age (overwintered individuals are more frequently infected than young of the year) and, unexpectedly, on the dynamics regime: the infection risk in the noncyclic regime is 2.3 times higher than in the 3-year cyclicity regime. The characteristic (or natural) oscillation frequencies of the parasites' life cycles may be reflected in the observed infection dynamics of intermediate or definitive hosts.

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