Age, season and spatio-temporal factors affecting the prevalence of Echinococcus multilocularis and Taenia taeniaeformis in Arvicola terrestris

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Abstract: Background: Taenia taeniaeformis and the related zoonotic cestode Echinococcus multilocularis both infect the water vole Arvicola terrestris. We investigated the effect of age, spatio-temporal and season-related factors on the prevalence of these parasites in their shared intermediate host. The absolute age of the voles was calculated based on their eye lens weights, and we included the mean day temperature and mean precipitation experienced by each individual as independent factors. Results: Overall prevalences of E. multilocularis and T. taeniaeformis were 15.1% and 23.4%, respectively, in 856 A. terrestris trapped in the canton Zürich, Switzerland. Prevalences were lower in young (≤3 months: E. multilocularis 7.6%, T. taeniaeformis 17.9%) than in older animals (>7 months: 32.6% and 34.8%). Only 12 of 129 E. multilocularis-infected voles harboured protoscoleces. Similar proportions of animals with several strobilocerci were found in T. taeniaeformis infected voles of <5 months and ≤5 months of age (12.8% and 11.9%). Multivariate analyses revealed strong spatio-temporal variations in prevalences of E. multilocularis. In one trapping area, prevalences varied on an exceptional high level of 40.6-78.5% during the whole study period. Low temperatures significantly correlated with the infection rate whereas precipitation was of lower importance. Significant spatial variations in prevalences were also identified for Taenia taeniaeformis. Although the trapping period and the meteorological factors temperature and precipitation were included in the best models for explaining the infection risk, their effects were not significant for this parasite. Conclusions: Our results demonstrate that, besides temporal and spatial factors, low temperatures contribute to the risk of infection with E. multilocularis. This suggests that the enhanced survival of E. multilocularis eggs under cold weather conditions determines the level of infection pressure on the intermediate hosts and possibly also the infection risk for human alveolar echinoccosis (AE). Therefore, interventions against the zoonotic cestode E. multilocularis by deworming foxes may be most efficient if conducted just before and during winter.

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Age, season and spatio-temporal factors affecting the prevalence of *Echinococcus multilocularis* and *Taenia taeniaeformis* in *Arvicola terrestris*

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**Abstract**

**Background:** *Taenia taeniaeformis* and the related zoonotic cestode *Echinococcus multilocularis* both infect the water vole *Arvicola terrestris*. We investigated the effect of age, spatio-temporal and season-related factors on the prevalence of these parasites in their shared intermediate host. The absolute age of the voles was calculated based on their eye lens weights, and we included the mean day temperature and mean precipitation experienced by each individual as independent factors.

**Results:** Overall prevalences of *E. multilocularis* and *T. taeniaeformis* were 15.1% and 23.4%, respectively, in 856 *A. terrestris* trapped in the canton Zürich, Switzerland. Prevalences were lower in young (≤ 3 months: 7.6%, *T. taeniaeformis* 17.9%) than in older animals (>7 months: 32.6% and 34.8%). Only 12 of 129 *E. multilocularis*-infected voles harboured protoscoleces. Similar proportions of animals with several strobilocerci were found in *T. taeniaeformis* infected voles of <5 months and ≥ 5 months of age (12.8% and 11.9%). Multivariate analyses revealed strong spatio-temporal variations in prevalences of *E. multilocularis*. In one trapping area, prevalences varied on an exceptional high level of 40.6-78.5% during the whole study period. Low temperatures significantly correlated with the infection rate whereas precipitation was of lower importance. Significant spatial variations in prevalences were also identified for *Taenia taeniaeformis*. Although the trapping period and the meteorological factors temperature and precipitation were included in the best models for explaining the infection risk, their effects were not significant for this parasite.

**Conclusions:** Our results demonstrate that, besides temporal and spatial factors, low temperatures contribute to the risk of infection with *E. multilocularis*. This suggests that the enhanced survival of *E. multilocularis* eggs under cold weather conditions determines the level of infection pressure on the intermediate hosts and possibly also the infection risk for human alveolar echinococcosis (AE). Therefore, interventions against the zoonotic cestode *E. multilocularis* by deworming foxes may be most efficient if conducted just before and during winter.

**Background**

Population dynamics of organisms in temperate zones are generally shaped by seasonal variations. Parasites living within their hosts are protected from the direct impact of season-related factors like temperature or humidity but they usually have free living stages that can directly be affected by adverse environmental conditions. The understanding of how meteorological factors and seasonal changes affect the population dynamics of zoonotic parasites can contribute to better understand their epidemiology and to develop efficient control strategies.

In many parts of Europe, the zoonotic fox tapeworm *Echinococcus multilocularis* has benefited from increasing fox (*Vulpes vulpes*) populations and the invasion of foxes into urbanized areas during the last two decades [1-4]. In many cities of Switzerland, Germany and France, the life cycle of *E. multilocularis* is established in urban settings [2,5-7]. As a consequence, the incidence of human alveolar echinococcosis (AE) has increased in Switzerland by a factor of 2.6 during the first five years of the 21st century as compared with the preceding five year period [8]. Human AE is an expensive disease to manage [9] and the
frequently life-long treatment is very demanding for the affected patients. Therefore, there is a need to better understand the factors which affect the transmission dynamics of this parasite.

In experimental studies, it has been shown that the eggs of *E. multilocularis* can survive several months in a cold and humid environment, which is typical for winters in central Europe, but only a few days when exposed to dry and hot conditions prevailing in summers [10]. It therefore could be expected that *E. multilocularis* eggs excreted by foxes can accumulate during winter resulting in a higher infection pressure during this period compared to the rest of the year.

In Europe, the natural life cycle of *E. multilocularis* depends on the predator-prey relationship between foxes as the most important definitive hosts and *Arvicola* (voles), mainly the species *Microtus arvalis* and *Arvicola terrestris*, as intermediate hosts [11]. *Arvicola terrestris* and *M. arvalis* have a short life expectancy ranging from several months to rarely over 1 year [12]. Their population densities and structures are strongly affected by perennial cycles [13,14] and seasonal changes. Population densities of voles are generally highest in autumn and lowest in spring when the age structure of populations is strongly shaped by a higher proportion of old animals due to reduced reproduction during winter [15-17]. To understand the seasonal variation in the epidemiology of *E. multilocularis*, it is therefore important to know to what extent different age classes of the intermediate hosts develop the infective stages (protoscoleces) for the final hosts.

We investigated the influence of temporal and spatial factors on the prevalence of *E. multilocularis* in *A. terrestris*, the most abundant intermediate host in the city of Zürich, Switzerland. Furthermore, we analysed how age affects the prevalence and the development of protoscoleces and whether low temperatures (as a proxy for the winter season) and high humidity correlate with infection risk. The same analyses were undertaken for *Taenia taeniaeformis*, another taeniid species with domestic cats as principal definitive host and *A. terrestris* as a frequent intermediate host. Eggs of *Taenia* species have a similar resistance to freezing [18] and desiccation [19] as those of *E. multilocularis*, suggesting similarities concerning seasonal variations in the infection pressure on intermediate hosts.

**Materials and methods**

**Study area and animals**

The study was conducted in the periphery of the city of Zurich, Switzerland, and in the nearby municipality of Rifferswil (Figure 1). From March 2007 to June 2008, a total of 856 *A. terrestris*, 252 animals in Zurich and 604 in Rifferswil, were collected. These animals were not trapped for the purpose of this study but rather in the framework of a continuous control program to avoid agricultural damages on grassland areas. Field workers used unbaited Topcat traps (Topcat GmBH, L’Auberson; Switzerland) and tongue traps (Hauptner Instrumente GmbH, Dietlikon, Switzerland), which were placed in vole galleries.

The voles were either dissected immediately after trapping or stored in a chest freezer at a constant temperature of -20°C prior to dissection. Careful examination was performed at the opening of thoracic and peritoneal cavities, and organs, in particular the liver, were attentively examined for lesions. Metacestodes were collected and identified after morphological characteristics. *Taenia taeniaeformis* was determined by counting all lucent, round-shaped vesicles of 3-10 mm size. All other lesions with a diameter of > 3 mm were cut into small pieces and investigated for the presence of protoscoleces of *E. multilocularis*. If protoscoleces were present, the metacestode material was squashed in a sieve with 1 mm mesh size and washed with PBS. Protoscoleces were counted under a binocular microscope in a petri
dish. If more than 100 protoscoleces were present, 3
diluted subsamples of 100 μl were counted microscopi-
cally and the total number was calculated. Visually uni-
dentifiable lesions were further investigated after
proteinase K digestion by a PCR specific for *E. multilo-
cularis* [20].

**Age determination of rodents**
The absolute age was calculated by measuring the
weight of dry crystalline lenses [21,22] according to Bur-
let et al. [23]. In short, after dissection, eyes were put
directly into formalin (10%) for fixation over a period of
4 weeks. Lenses were then removed from the eye, air-
dried at +80°C over a period of 48 hours and immedi-
ately weighted. The age of individual voles was calcu-
lated by the formula

$$
\hat{x} = x - 0.58(1.80x)^{1/2},
$$

where $x$ is the age in
months and $y$ the eye lens weight in mg. As freezing
increases lens weights of *A. terrestris* by 3.3%, lens
weights of frozen lenses were divided by 1.033 to obtain
a correct age estimate [23].

**Determination of seasonal and climatic factors**
The date of birth of each vole was calculated based on
its age and trapping day. To analyse the influence of
meteorological factors, the means of day temperature
(measured 5 cm above ground) and of precipitation
experienced by each individual was calculated (data
source: Swiss Meteorological Institute MeteoSwiss;
weather station Zürich Fluntern, 8°34′/47°23′).

**Statistical analyses**
Prevalences of *E. multilocularis* and *T. taeniaeformis*
were analysed using logistic regression models. The vari-
ables age (age of individuals expressed in months), per-
iod (time when an individual was trapped: March -June
2007, July - October 2007, November 2007 - February
2008, March - June 2008), area (trapping areas 1-4,
Figure 1), mean day temperature [°C] and mean precipi-
tation per day of living [mm] were selected as indepen-
dent variables for the modelling procedure.

Models were fitted using all possible combinations of
the selected predictor variables. Best models were
selected using Akaike’s information criterion (AIC, [24])
corrected for small samples sizes. Only models with
$\Delta$AICc < 2 compared to the model with the lowest
AICc were selected. Akaike model weights were calcu-
lated [25] to determine the degree by which a model
was supported by the data.

Logistic regressions were calculated using SPSS 17.0
[24]. Maximum likelihood estimate of $k$ was used to cal-
culate the degree of overdispersion of the number of proto-
scoleces in infected rodents. This parameter of negative
binomial distribution tends towards 0 with increasing
accumulation of parasites [26].

**Results**
Age determination revealed strong shifts in the age
structure of the *A. terrestris* population over time
(Figure 2). During the first period (March-June 2007)
the portion of animals older than 5 months (48.6%, CI
95% 36.9%-60.6%) was significantly higher than in the
same period one year later (March-June 2008: 26.8%,
21.7%-32.5%). Mean day temperatures per month during
the second year of the study (July 07 - June 08) were
consistently (unless August 2007 and May 2008) higher
than during the preceding year (in average 2.0°C).

Liver lesions were observed in 270 of 856 dissected
*A. terrestris* (31.5%, CI 95% 28.4%-34.8%). The overall
prevalence rate of *E. multilocularis* was 15.1% (12.7%-17.6%), and protoscoleces were found in 12 animals cor-
responding to 1.4% (0.7%-2.4%) of all studied animals or
9.3% (4.9%-15.7%) of the *E. multilocularis*-positive ani-
mals. Animals older than 7 months were more than
4-times more frequently infected than animals ≤ 3
months. Furthermore, none of the animals under 3
months of age harboured protoscoleces (Table 1), and
the youngest animal with protoscoleces was 3.2 months
of age. In 10 animals the protoscolex burden was deter-
mined. The maximum likelihood estimate of $k = 0.16$
indicates a heavily overdispersed protoscolex burden.
Four animals (40%) harbouring between 61 and 568 pro-
toscoleces (together 1057 protoscoleces), representing
0.2% of the total number, five animals had between
2492 and 67'550 protoscoleces, and the extrapolated
number of protoscoleces was 451’540 in one animal,
representing 73.8% of this parasite stage identified in
this study. However, no relation between age and the
number of protoscoleces was identified (Spearman R =
-0.52, p = 0.12; Figure 3).

The overall prevalence of *T. taeniaeformis* was 23.4%
(20.6%-26.3%). Animals older than 5 months were
roughly 2-times more frequently infected than animals ≤
3 months (Table 1). Most infected animals harbouring
one *T. taeniaeformis* strobilocercus but 25 out of 200
infected animals had 2-10 strobilocerci (Figure 3). The
proportion of multiple infections was not dependent on
the age of the animals (Spearman R = 0.02, p = 0.82):
Seventeen of 133 (12.8%) infected animals of <5 months
of age and 8 of 67 (11.9%) infected animals of ≥ 5
months of age had more than one strobilocercus. In
total, five of the ten animals with known *E. multilocu-
laris* protoscoleces burden were simultaneously infected
with *T. taeniaeformis*, which is a significant higher pro-
portion than expected by chance (Actus randomization
test, p<0.05). Three of these five animals harboured 2, 8
and 10 strobilocerci and, interestingly, the animal with
10 strobilocerci also had the highest protoscoleces bur-
den. In addition, 1.9% (1.1%-3.0%) of all animals were
infected with *T. crassiceps*. Scoleces of this species were mostly found in subcutaneous cysts but also pleural cavities.

The model selection procedure for *E. multilocularis* infections revealed two best models (ΔAICc < 2; Table 2), containing ‘age’, ‘period’, ‘area’, ‘mean day temperature’ and ‘mean precipitation’ as factors for explaining the prevalence (Table 3). Prevalence rates of *E. multilocularis* differed strongly between the four trapping areas (Figure 4a) and ranged between 11.2% (95% CI 12.7-27.2, area 3) and 60.7% (CI 40.6-78.5%, area 2). Furthermore, low temperatures significantly increased the infection risk (Table 3). The second best model suggests that higher precipitation is associated with a higher infection risk but this effect was not significant (Table 3).

The model selection procedure for *T. taeniaeformis* revealed 4 best models (ΔAICc < 2; Table 2) which include the factors ‘age’, ‘period’, ‘area’, ‘mean day temperature’ and ‘mean precipitation’ as factors explaining parasite prevalence (Table 3). In animals with ages of 5 months or higher, the prevalence was significantly higher than in juvenile animals (Table 1), and prevalences were lower in area 1 than in area 4 (Table 3 and Figure 4b). Although each of the three factors ‘period’, ‘mean temperature’ and ‘mean precipitation’ entered one of the four best models, the 95% confidence intervals of the odds ratios strongly overlapped the value 1 for all three factors.

**Discussion**

**Prevalence of *E. multilocularis***

This study shows that the transmission dynamics of the two taeniid species *E. multilocularis* and *T. taeniaeformis* are significantly affected by spatial factors. The prevalence rates of *E. multilocularis* in *A. terrestris* were significantly higher (95% CI: 40.6-78.5%) in one study area as compared to the others and surpassed, to our knowledge, the highest ever reported prevalence of 39% in intermediate hosts in Central Europe [27]. This finding confirms the occurrence of micro-foci [28-30] with exceptional high *E. multilocularis* infection pressure in densely populated areas and possibly reflects the high fox densities in urban and periurban areas [2,3,31].

Transmission dynamics of the two investigated taenid species can be affected by various host-related factors. In addition to the densities of final (foxes for *E. multilocularis* and domestic cats for *T. taeniaeformis*) and intermediate hosts [32-34], the predation activity of final hosts [17,35] can play an important role in transmission [7,36]. Furthermore, temporal fluctuations of prevalences can origin from shifts in the age structure of populations [37]. Once a metacestode has established, it can be detected for the

![Figure 2 Age pyramids of *Arvicola terrestris* in the canton of Zurich, Switzerland, in different seasons. The single pyramid segments represent the percentage of the population trapped during the corresponding period. Dark grey: males, light grey: females.](image)

**Table 1 Prevalence rates of taeniid infections in trapped *Arvicola terrestris* of different age classes**

| age class in months (N animals) | ≤ 3 (N = 436) | >3-5 (N = 227) | >5-7 (N = 101) | >7 (N = 92) |
|-------------------------------|---------------|---------------|---------------|------------|
| *E. multilocularis*            | 7.6 (5.3-10.5)| 19.4 (14.5-25.1)| 21.8 (14.2-31.1)| 32.6 (23.2-43.2) |
| *E. multilocularis* protoscolec | 0.0 (0.0-0.7) | 1.3 (0.3-3.8)  | 3.0 (0.6-8.4)  | 6.5 (2.4-13.7)  |
| *T. taeniaeformis*            | 17.9 (14.4-21.8)| 24.2 (18.8-30.5)| 34.7 (25.5-48.8)| 34.8 (25.1-45.4) |
| *T. crassiceps*               | 0.9 (0.3-2.3)  | 2.6 (1.0-5.7)  | 5.0 (1.6-11.2) | 0.0 (0.0-3.2)  |

95% confidence intervals are shown in brackets (N total = 856).
rest of the rodent’s life. Therefore, infections accumulate with increasing age in single vole generations and prevalences increase. In previous studies done in Zurich and the city of Geneva, *E. multilocularis* prevalences were 10.7 and 9.2%, in adult voles respectively, and 1.3% in subadults and juveniles [20,38]. In this study, we also recorded a higher prevalence in adult voles. Furthermore, we documented an increase of prevalence rates over several age classes (Table 1).

The age structure of voles is closely related to seasonal factors. In early spring, old animals predominate as reproduction is low in winter [16,17,37]. Nevertheless, season-related age structure can vary considerably from year to year, as shown by our data with a higher proportion of old overwintering voles in spring 2007 (Figure 2) after an extraordinary mild winter [39,40]. As age strongly affects parasite prevalence, such temporal variations in the age structure over years can hamper the detection of seasonal variation in the infection pressure.

As shown in this study, the determination of the absolute age of intermediate hosts can help to overcome such methodological limitations. Based on this data, it was possible to calculate for each individual rodent to which temperatures it was exposed during its live. Hence, it could be demonstrated that low day temperatures typical for the winter season correlate with a

### Figure 3

Numbers of *Echinococcus multilocularis* protoscoleces and *Taenia taeniaeformis* strobilocerci in trapped *Arvicola terrestris*.

### Table 2

Factors affecting prevalences of *Echinococcus multilocularis* and *Taenia taeniaeformis*

| Factors included in best models | ΔAICc | AICc weight |
|--------------------------------|-------|-------------|
| **a) E. multilocularis***       |       |             |
| age, period, area, mean day temperature | -244.04  | 0.57         |
| age, period, area, mean day temperature, mean precipitation | -243.45  | 0.43         |
| **b) T. taeniaeformis***       |       |             |
| age, area                        | 51.08  | 0.00 0.42   |
| age, area, mean day temperature  | 52.22  | 1.14 0.24   |
| age, area, period, mean day temperature | 52.75  | 1.67 0.18   |
| age, area, mean precipitation   | 52.94  | 1.87 0.16   |

* Null model AICc = -131.22.

** Null model AICc = 83.73.

All factors are shown that were included in the best models (ΔAICc<2, N = 856).
higher infection rate. Absolute age estimates were also considered in the only study we are aware of that also described a clear season-related infection pattern of *E. multilocularis* [37]. As in our study for *A. terrestris*, seasonal patterns of infection were found for *M. arvalis* with highest prevalences of *E. multilocularis* in spring in old over-wintered animals which had acquired their infections in winter (from October to April).

Staubach et al. [41] demonstrated that *E. multilocularis*-infected foxes are more frequently found in areas with high soil moisture. Correspondingly, our second best model explaining the prevalence of *E. multilocularis* in *A. terrestris* included the factor precipitation. However, the effect size of this factor alone was too small to demonstrate a clear relationship with the infection risk. Soil moisture is not only affected by precipitation but also by many other factors (e.g. temperature, vegetation growth and sun exposition [Hagan 1955]) and a direct measure of soil moisture could be a better predictor than the amount of precipitation to explain the infection pressure.

The fact that living during periods with low temperatures contributed significantly to the infection risk with *E. multilocularis* underlines the epidemiological relevance of the experimental study of Veit and colleagues [10] showing that *E. multilocularis* eggs survive for months under cold conditions but die within a few hot and dry days. Another aspect that possibly contributes to seasonal patterns in the parasite’s transmission dynamics is a seasonal pattern of the predation on *A. terrestris* and other rodents by foxes [7,17,36]. These studies revealed higher predation rates in autumn with a larger availability of voles than in spring, when rodent density are generally considerably lower [7,42].

The higher consumption possibly explains higher prevalence rates in foxes during winter months as revealed by several studies in high endemic areas [43,44] and consequently, a higher contamination of the environment with *E. multilocularis* eggs.

The presence of protoscoleces was clearly related to the age of the investigated animals. The low number of animals with protoscoleces made it impossible to perform multivariable analyses in order to investigate seasonal effects on the prevalence of protoscoleces harbouring animals. However, it is expected that season-related changes in the age structure of the intermediate host population cause that there is a higher proportion of animals harbouring protoscoleces during winter and early spring, before the start of reproduction. This does not necessarily mean that foxes are exposed to a higher infection pressure during this period, as absolute density of voles and predation on rodents by foxes is considerably lower during spring and early summer [17,36,45].

### Prevalences of *T. taeniaeformis*

Similar to *E. multilocularis*, *T. taeniaeformis* causes lifelong infections in intermediate hosts and is more prevalent in older animals [20,38,46-48]. Furthermore, eggs of different taenid species have a similar resistance to environmental conditions as those of *E. multilocularis* [10,19]. Accordingly, two other studies reported higher prevalence rates in overwintered intermediate hosts [15,47]. In contrast, we found no clear association of low temperatures and high precipitation with higher prevalence rates of *T. taeniaeformis*. The eggs of this parasite might be less sensitive to hot and dry weather conditions due to the special defecation behavior of domestic cats which usually bury their droppings into loose soil where taenid eggs

**Table 3** Odds ratios of factors explaining prevalences of *Echinococcus multilocularis* and *Taenia taeniaeformis* in *Arvicola terrestris*

| Model factors   | *E. multilocularis* | *T. taeniaeformis* strobilocerci |
|-----------------|---------------------|----------------------------------|
| Age             | 1.13 (1.06-1.20)    | 1.39 (1.09-1.80)                 |
| Period          | 0.95 (0.91-1.00)    | 0.88 (0.86-0.90)                 |
| Area            | 0.94 (0.91-0.97)    | 0.92 (0.90-0.95)                 |
| Mean day temperature | 0.90 (0.86-0.93)  | 0.92 (0.89-0.95)                 |
| Mean precipitation | 1.13 (1.10-1.16)  | 0.98 (0.96-1.00)                 |

Shown are all odds ratios (OR) and 95% confidence intervals (95% CI) for the factors of the best models (ΔAICc < 2, N = 856).
are less exposed to adverse weather conditions. Further, the loose ground of the burrows of *A. terrestris* could be a good substrate for cats to defecate.

Contrary to Reperant and colleagues [38], we found significant spatial variations in the prevalence of *T. taeniaeformis*. However, in contrast to Le Pesteur [15], the observed pattern did not correspond to the spatial variation of *E. multilocularis* prevalence rates. Probably, these different spatial patterns are caused by different distributions of fox and cat densities. Interestingly, the lowest prevalence rates for *T. taeniaeformis* were found in an area (area 1) where many people walk their dogs and this might contribute to a lower presence of domestic cats.

Although 23% of all investigated animals were infected with *T. taeniaeformis*, only 13% of these 200 animals harbored more than one strobilocercus. Furthermore, increasing age was not linked to a higher amount of

**Figure 4** Temporal prevalences of *Echinococcus multilocularis* and *Taenia taeniaeformis* strobilocerci in 4 study areas. a) Prevalences and 95% confidence intervals of *Echinococcus multilocularis* (undifferentiated and protoscoleces-containing metacestodes), b) prevalences and 95% confidence intervals of *Taenia taeniaeformis* strobilocerci. Overall prevalence rates per area are symbolised by circles. For *E. multilocularis*, the number of voles with protoscoleces and the total number of studied individuals are given above the associated bars (N total = 856 *Arvicola terrestris*). Study areas are shown in Figure 1.
animals with more than one strobilocercus and the prevalences were similar in animals >7 months and those of 5 to ≤7 months (Table 1). This parasite has not a proliferative growth like E. multilocularis [49] and it is unlikely that it caused an increase of the mortality of infected intermediate hosts which could explain such an asymptotic increase of prevalence along the age classes. Possibly T. taeniaeformis was hyperendemic in A. terrestris and regulated by a concomitant immunity. Such regulations have been demonstrated with experimental T. taeniaeformis infections of rats [50,51] and by epidemiological investigations of sheep and goats infected with T. hydatigena [52]. Interestingly, the fact that heavily E. multilocularis-infected voles had more T. taeniaeformis strobilocerci than expected indicates an immune-suppression driven by E. multilocularis metacestode [53], which counter-acts the protective immune mechanisms against super-infections with T. taeniaeformis.

Conclusions
Our results demonstrate that the availability of absolute age estimates of intermediate hosts can be crucial to detect season-related variations in the infection pressure by taeniid species. As shown for E. multilocularis, infection pressure on voles can vary considerably within a small spatial scale and along different seasons. This knowledge possibly can also contribute to model spatial and temporal variation of the infection risk for human. Based on the presented results, we suggest that reducing the infection pressure on intermediate host and presumably as well on humans by the delivery of anthelmintic baits for foxes is more effective during the cold and humid winter season than during the rest of the year.

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Authors’ contributions
PB did the laboratory work, analyzed the data, participated in the statistical analyses and drafted the manuscript. PD and DH designed and supervised the study and critically revised the manuscript. Additionally, DH contributed to data analyses and statistics. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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