Commentary

Population dynamics of *Taenia polyacantha* metacestodes in the bank vole *Clethrionomys glareolus*

Voitto Haukisalmi & Heikki Henttonen

Haukisalmi, V., Department of Zoology, Division of Ecology, P.O. Box 17, FIN-00014 University of Helsinki, Finland

Henttonen, H., Department of Forest Ecology, Finnish Forest Research Institute, P.O. Box 18, FIN-01301, Vantaa, Finland

Received 1 February 1993, accepted 16 February 1993

Taenia polyacantha is a holarctic tapeworm of canids, especially the foxes, *Vulpes* spp. The larval stage of *Taenia polyacantha* is a relatively rare parasite of rodents, the highest prevalence reported being 12% (Wiger et al. 1974). Adult tapeworms inhabit the small intestine of the final host, producing eggs to be expelled in faeces. When the intermediate rodent hosts ingest food contaminated with tapeworm eggs, embryos migrate into the body cavity and develop there into larvae, or metacestodes (Rausch 1985). A metacestode of *T. polyacantha* is readily identified by the number of rostellar hooks (52–62) and by the distinctive "tail" (Verster 1969, Wiger et al. 1974).

We have continuously collected data on metacestodes of microtine rodents at Pallasjärvi, western Finnish Lapland, since 1970. Despite the examination of thousands of voles belonging to six species (Clethrionomys glareolus, C. rutilus, C. rufocanus, Microtus agrestis, M. oeconomus and Lemmus lemmus), T. polyacantha remained absent until 1987, when a single infected vole was found. Thereafter it has been

regularly present at Pallasjärvi. We here analyse the age and sex relations and population dynamics of *T. polyacantha* in the most abundant species of the microtine community, the bank vole *Clethrionomys glareolus*, in 1988–1992.

Materials and study sites

The voles (n = 1229) were obtained from three main study sites: 1) a trapping site on the upper part of a forested mountain slope (n = 825), 2) several permanent study grids at lower elevations (n = 274), and 3) three low elevation live trapping grids (n = 55), where vole densities have constantly been higher than in the surrounding areas due to the provision of supplemental food (Henttonen et al. 1987 and Henttonen unpubl.). In addition, we have included data (n = 75) from several other forest sites nearby. The habitat of all study sites is fairly similar, i.e. spruce- $(Picea\ abies)$ dominated taiga forest with a thick moss layer; blueberry $(Vaccinium\ myrtillus)$ is the dominant forb species.

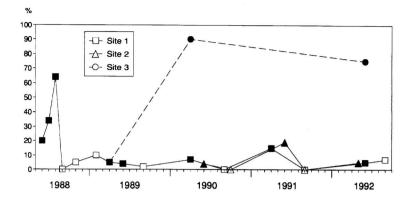


Fig. 1. Population dynamics (percent of voles infected, %) of *Taenia polyacantha* metacestodes in overwintering cohorts of the bank vole *Clethrionomys glareolus* at Pallasjärvi. Open symbols = immature voles, closed symbols = mature voles.

Infection levels in relation to sex and functional groups of voles

The best log-linear model (Fienberg 1970) for association between vole sex (S), functional group (F), and presence/absence of metacestodes (M) was SF,MF (fit to the observed data: $G^2 = 1.52$, df = 3, P = 0.68). This model indicates that the sample sex ratio and prevalence of metacestodes depend on the functional group, but there is no association between the prevalence and sex of the vole (Table 1).

The prevalence of *T. polyacantha* was very low in immature, subadult voles (age 1–2.5 months), but clearly higher in overwintered voles (age 8–12 months), which represent the same cohort (Table 1). Data from site 1 in 1988 show that the prevalence in overwintered voles continues to increase during the summer (Fig. 1). The mature summer-born voles (those already breeding during the summer of their birth and disappearing before the winter, age 2–3 months), show intermediate prevalence compared to that of subadult and overwintered voles. The number of

metacestodes per infected host did not vary markedly between host sexes (Mann-Whitney test for overwintered voles: U = 856.0, P = 0.43) and functional groups (Table 1).

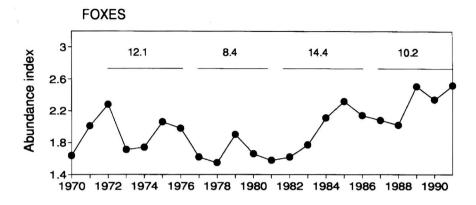
These patterns suggest that the probability of a vole's acquiring a *T. polyacantha* infection increases with increasing exposure time, i.e., host age. There is no indication, however, that infections by *T. polyacantha* metacestodes would increase vole mortality, e.g., by increasing vulnerability to (fox) predation. Mortality due to heavy infections is expected to lead to a decrease in prevalence (Lester 1984) and mean abundance (Anderson & Gordon 1982) of parasites in the older age groups of hosts; these phenomena were not observed in *T. polyacantha*.

Long-term population dynamics

Data for male and female voles have been combined in the following description of long-term population changes, because host sex does not affect occurrence of *T. polyacantha* (Table 1). At

Table 1. Percent of bank voles *Clethrionomys glareolus* infected by *Taenia polyacantha* metacestodes by sex and functional group at Pallasjärvi (1987–1992), and median number and range of metacestodes in infected hosts.

		Males				Females		
Functional groups	n	%	median	range	n %	median	range	
Immature	351	1	20.0	20–27	312 2	24.0	5–24	
Mature, summer-born	31	6	20.5	5-36	55 5	36.0	25-36	
Mature, overwintered	479	11	22.0	1–121	359 13	21.0	1–60	



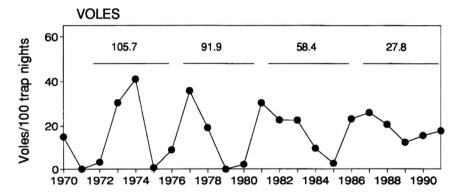


Fig. 2. Long-term changes in abundance index of foxes (*Vulpes vulpes*) in Lapland (source: Finnish Game and Fisheries Research Institute) and autumnal density of all voles at Pallasjärvi (source: Henttonen et al. 1987 and Henttonen unpubl.). Inserted are coefficients of variation, calculated for 5-year periods.

sites 1 and 2, the prevalence of *T. polyacantha* remained at a low level throughout the study period (Fig. 1). The apparent infection peak in overwintered voles later in the summer of 1988 at site 1 is due to the fact that these voles were older (age 10–12 months) than the overwintered voles in the spring samples (late May, age 8–10 months). In 1989, the prevalence of overwintered voles in the extra food grids (site 3) was low, comparable to that at other sites, but thereafter their prevalence reached a high level (75–90%). The high frequency of infected bank voles in the food grids indicates that foxes foraged intensively on these high-density prey patches.

The colonization and persistence of *T. polyacantha* at Pallasjärvi suggest that vole or fox densities have changed leading to an enhancement in the transmission of cestodes. We

used game inquiries from Lapland as a source for a fox (*Vulpes vulpes*) abundance index; these inquiries are made each year in March (Finnish Game and Fisheries Research Institute; for details, see Helle & Kauhala 1991). The autumnal density index of all voles was based on regular, extensive snap-trappings in diverse habitats at Pallasjärvi (Henttonen et al. 1987, Henttonen unpubl.).

During 1987–1991, the average abundance indices of voles (18.5) and foxes (2.29) were higher than during 1970–1986 (15.8 and 1.86, respectively), and the variability of vole populations was lower than during the three earlier five-year periods (Fig. 2). Vole dynamics at Pallasjärvi, and more generally in Lapland, have changed since the mid-eighties, resulting in more stable dynamics in forest rodents (Henttonen

1987, Henttonen et al. 1987). The increase in density and stability of host populations has evidently been the key factor promoting the colonization of *T. polyacantha* at Pallasjärvi. This empirical observation supports the prediction of the theory that efficient transmission and persistence of parasites is possible only if the host populations exceed a certain threshold density (Anderson 1982).

References

- Anderson, R. M. 1982: Epidemiology. In: Cox, F. E. G (ed.), Modern parasitology: 204–251. Blackwell Scientific Publications. Oxford.
- Anderson, R. M. & Gordon, D. M. 1982: Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology 85:373–398.
- Fienberg, S. E. 1970: The analysis of multidimensional contingency tables. Ecology 51:419–433.

- Helle, E. & Kauhala, K. 1991: Distribution history and present status of the raccoon dog in Finland. — Holarctic Ecol. 14:278–286.
- Henttonen, H. 1987: The impact of spacing behavior in microtine rodents on the dynamics of least weasels Mustela nivalis — a hypothesis. — Oikos 50:366– 370.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. 1987: How much do weasels shape microtine cycles in the northern Fennoscandian taiga? — Oikos 50:353–365.
- Lester, R. J. G. 1984: A review of methods for estimating mortality due to parasites in wild fish populations. — Helgol. Meeresunters. 37:53–64.
- Rausch, R. L. 1985: Presidential address. J. Parasitol. 71:139–151.
- Verster, A. 1969: A taxonomic revision of the genus Taenia Linnaeus, 1758 s. str. — Onderst. J. Vet. Res. 36:3–58.
- Wiger, R., Lien, L. & Tenora, F. 1974: Studies of the Helminth Fauna of Norway XXXIII: Tetratirotaenia polyacantha (Leuckart, 1856) Abuladze, 1964, a parasite of Clethrionomys glareolus in Norway. Norw. J. Zool. 22:61–64.