

Seasonality of the ectoparasite community of woodland rodents in a Mazurian forest, Poland[1]

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ABSTRACT. *Myodes glareolus* and *Apodemus flavicollis* support a large and diverse community of arthropod ectoparasites. This study of rodents in a Mazurian woodland sampled at monthly intervals between 2007 and 2009 revealed an ectoparasite community composed of 2 species of tick, 1 louse, 9 flea species, 7 species of gamasid mites, 4 fur mites and one trombiculid mite. A strong seasonality was noted in the dynamics of the ectoparasite community, with the fur mite *Listrophorus* sp. and the hypopus larva of a glycyphagid mite especially common in winter. Several of the ectoparasites have the potential to be pathogenic; the impact of these organisms on the population dynamics of their hosts remains to be investigated.

Key words: ectoparasites, rodents, parasite community, Poland

Introduction

A great deal of recent theoretical, experimental and field research has been devoted to the topic of endoparasite communities in rodents [1], and the extent to which different parasites exploiting the same host interact [2]. The same attention has not, however, been devoted to the assemblage of ectoparasites found on these rodents, although this represents a rich and complex research resource for the experimental field parasitologist. This paper sets out to describe the ectoparasite community of the two common rodent species found in Polish forest, the red backed vole *Myodes glareolus* and the yellow-necked field mouse *Apodemus flavicollis*. There are a number of reasons why such a paper is needed. In the first place, *M. glareolus* and *A. flavicollis* are central in the transmission of sylvatic zoonoses such as borreliosis (Lyme disease) and tick borne encephalitis (TBE) to humans. As the first intermediate host of the ticks responsible for transmitting these diseases to humans, rodents play a fundamental part in regulating tick populations. Secondly, these rodents support a range of ectoparasite species, and are therefore at the interface of genetic interchange between micro-organisms using different ectoparasites as vectors; this could potentially also be important for emerging zoonotic disease in forest environments. Thirdly, rodents represent a major food source for environmentally valuable top predators such as owls, eagles and mustelids, and their populations undergo wide fluctuations in abundance [3]. Despite 70 years of theoretical and field study, the reasons for these fluctuations are poorly understood [4,5], but the role of ectoparasites in causing morbidity and mortality represents an understudied area of rodent population ecology. Ectoparasites may interact with other parasites within the hosts via the immune system; thus Jackson et al. [6] found that lice were, with *Heligmosomoides polygyrus*, the best predictors of

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immune status in wild-caught wood mice (*A. sylvaticus*) in England. Finally, but by no means the least important, ectoparasites on rodents represent an excellent teaching resource and research opportunity. We are not clear why studies of this community have been so neglected in the past, but suspect it is because the literature on identification of ectoparasites, although detailed, is scattered through both English and Russian language journals. We hope therefore that this paper, by establishing a baseline for seasonal patterns and taxonomy of the ectoparasite community of *M. glareolus* and *A. flavicollis* in a Polish forest, will make future studies of this fauna more accessible to interested researchers.

Materials and methods

Methods for analysing ectoparasite communities. The details presented here are based on experience with *M. glareolus* and *A. flavicollis* in the Urwitałt forest, Mazuria, between 2007 and 2009. Methodologies for this work as related to collection of rodents and processing of ticks have been described elsewhere [7]. Rodents were live-trapped in the forest and returned to the laboratory, where they were anaesthetised and screened for all ectoparasites. A small number of animals were also killed using an overdose of ether and screened for all ectoparasites.

Specific collection methods. Fleas were collected into 70% ethanol and examined at 25× using a binocular microscope, which allowed identification of all except *Megabothris* females. Lice on the other hand could only be reliably found by detailed combing of the fur with fine forceps using a binocular microscope at 10× magnification. The presence of egg cases was a useful (but by no means absolute) indicator of the presence of lice. All lice found were removed to 70% ethanol. Ticks were removed with forceps to absolute methanol as described [7], while the ears were checked for the presence of trombiculid mites. As with lice, removal of all ticks required searching the fur while looking through a binocular microscope. However, the majority of larvae and nymphs could be found using the naked eye.

Fur mites could only be found using a binocular microscope. A range of examination methods were evolved for these parasites. For recently dead rodents, the body was weighed and sexed and then placed in a small plastic bag at room temperature for 8–24 hours. At the end of this period many of the ectoparasites had migrated into the bag, which was filled with 5–10 ml of 70% ethanol, swirled to suspend the ectoparasites, and the corner cut off over a Petri dish. Any ectoparasites remaining attached to the bag were washed through with ethanol. The Petri dish could then be screened using a binocular microscope and parasites individually removed to vials. This method was particularly useful with mite hypopid larvae, and always recorded more of these than were seen by direct observation. The body of the rodent was then also screened using a binocular microscope, with direct combing of fur using forceps.

When animals could not be analysed immediately, the body minus the intestine was frozen individually in a plastic bag at –20°C. Hypopid larvae of mites survived this treatment for several months, but freezing killed all other ectoparasites. When ready for examination, the body was thawed at room temperature and allowed to air dry for 12 hours to ensure that no condensation remained in the fur. Fur mites, lice, fleas and ticks could all then be found in the pelage of the dead thawed rodent.

A method was also evolved for screening of living *M. glareolus*. Animals were lightly anaesthetised with ether, then restrained on the stage of a binocular microscope by holding the scruff. The animal was then screened on the sides of the face and top of the head for *Radfordia*, and down the fur of the back for lice, louse eggs, *Listrophorus* and hypopid larvae. Trombiculids were counted directly in the ears of the living rodent. The fur and ear condition of the animal was recorded, and with data on reproductive status and recapture history, used to establish probable age. The animal was tagged with an ear ring (World Precision Instruments, Inc., Sarasota, FL, USA) and fed on apple and corn prior to subsequent release at the capture site.

Preparation of specimens for identification. All male fleas and lice could be identified using a binocular microscope, but permanent preparation was essential for distinguishing between the females of *Megabothris turbidus* and *M. walkeri*. Fleas were first rehydrated in water and placed in a potassium hydroxide solution [8,9] for a few days to hydrolyse internal proteins. The best method for doing this was found to be addition of a single grain of potassium hydroxide to 2 ml water in a vial, and leaving at room temperature until hydrolysis was complete. The rate of reaction could be increased in

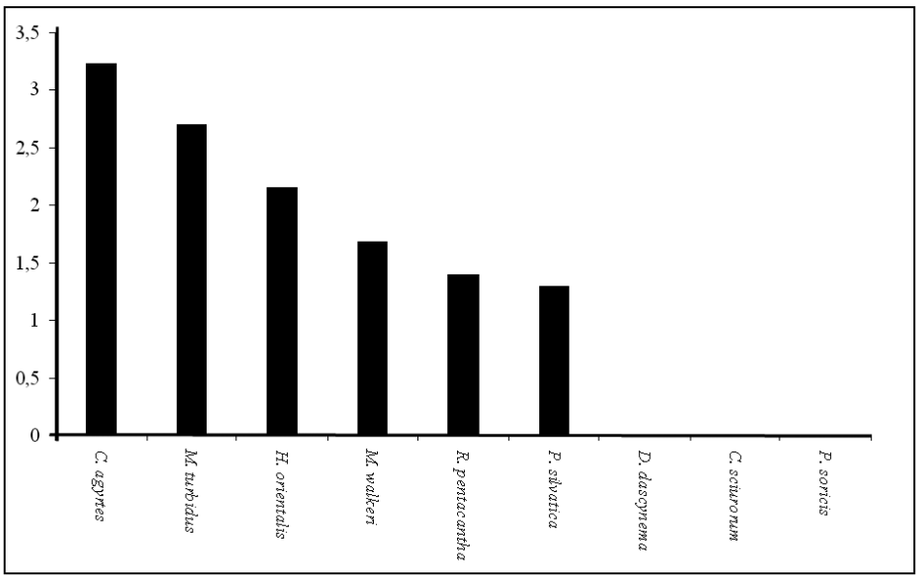

Fig. 1. Log_{10} abundance curve of flea species on *Myodes glareolus* and *Apodemus flavicollis* at Urwitałt forest, ordered from the most abundant to the least abundant

the field by placing the vial on a radiator. Where the flea was also needed for PCR (e.g., to establish micro-organism prevalence), only the female genitalia were hydrolysed, by slicing through the body with a razor just anterior to the terminalia. When hydrolysis was judged adequate (the body colour had lightened to a pale brown), the flea was washed in water and 10% acetic acid (to remove hydroxide deposits) and dehydrated in ethanol. Following clearing in xylene, the flea was mounted on its right side in Canada Balsam. Further details of these methods are given in Skuratowicz [9] and George [8]. Lice were prepared in a similar manner, and mounted with the ventral surface uppermost in Canada balsam.

Mites were prepared using glycerin jelly. Heavily sclerotised or blood-filled mites were also hydrolysed in potassium hydroxide for several days, this time individually in watch glasses. The mite was then rinsed in water and placed in lactic acid. A slide was prepared with a drop of glycerin jelly at 60°C on a hot plate. The mite was placed on its back in the drop of jelly using heated needles and left to sink onto the slide. Bubbles could be removed using a heated loop passed over the surface of the jelly. A heated cover slip was then lowered into position and the preparation allowed to cool. When cold, excess jelly was trimmed from the mount with a razor blade, and the cover slip ringed with enamel paint (Humbrol).

Results

The ectoparasite community

Fleas (Siphonaptera). Nine species of flea were recorded from *M. glareolus* and *A. flavicollis* from within Urwitałt forest. These were the ctenophthalmids *Hystrichopsylla orientalis*, *Ctenophtalmus agyrtes*, *Rhadinopsylla pentacantha*, *Doratopsylla dasycnema* and *Palaeopsylla soricis*, the leptopsyllid *Peromyscopsylla sylvaticus*, and the ceratophyllids *Megabothris turbidus*, *M. walkeri* and *Ceratophyllus sciurorum*. These fleas varied in abundance by three orders of magnitude; over one thousand *C. agyrtes* were collected, but only one individual of each of *P. soricis* and *C. sciurorum* (Fig. 1). The latter two species can be regarded as accidental infections. *P. soricis* is normally a shrew flea, while *C. sciurorum* is a moderately strict specialist infecting *Sciurus vulgaris*. *Megabothris walkeri* is also regarded as a shrew specialist [8,9], but nevertheless more than 20 were collected from rodents over the two years field study. An important feature of the present study was the continuation of sampling into the early winter (November 2007 and December 2008). This revealed increasing populations of some flea species (*R. pentacantha* and *D. dascynema*) which are clearly winter specialists, and would presumably have been encountered in greater numbers if rodents could be trapped between January and March. The fleas showed clear seasonal patterns which influenced the diversity of the ectoparasite

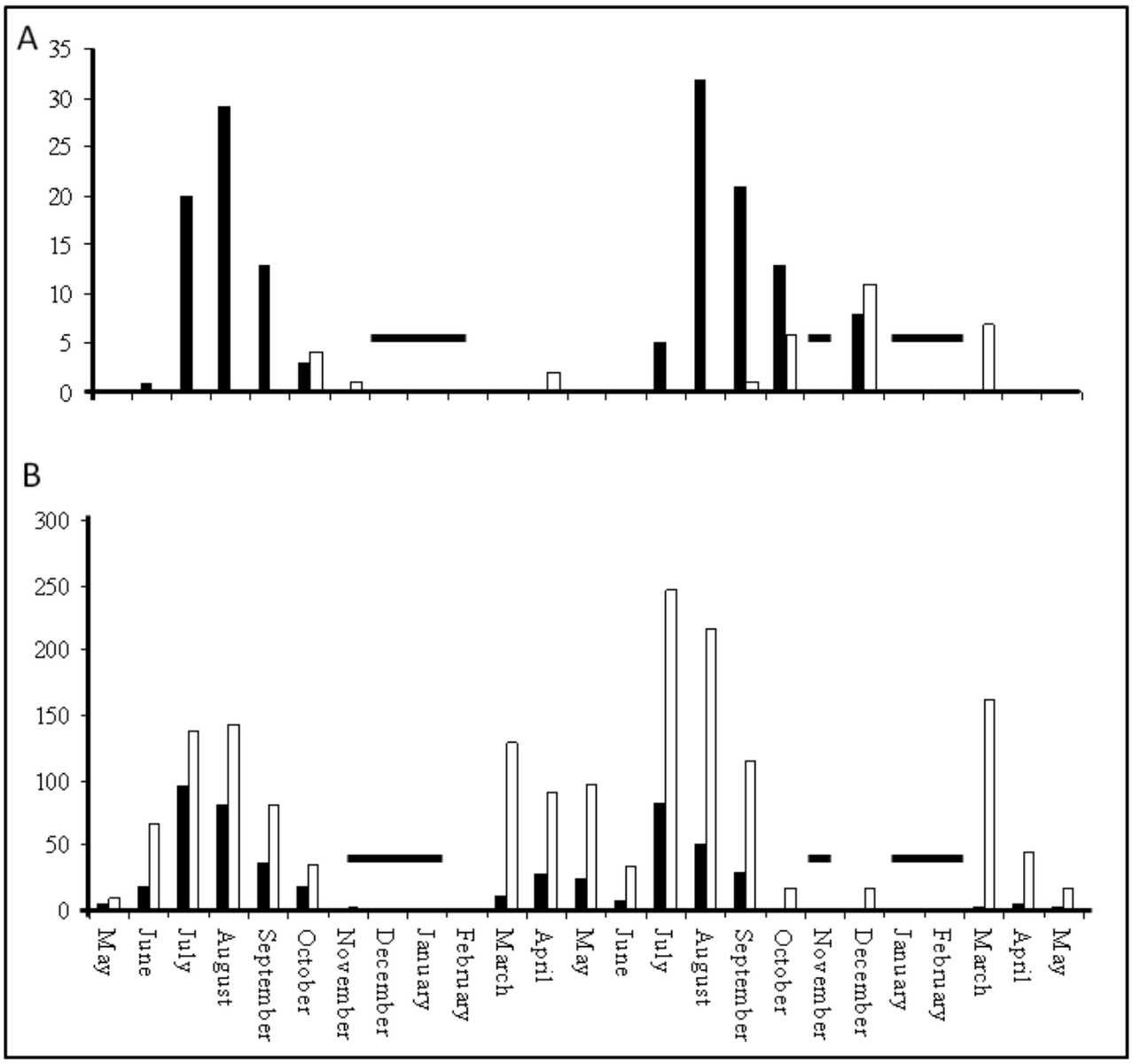

Fig. 2. Seasonality of flea species from small rodents at Urwitałt. **A.** Total counts of collected *Hystrichopsylla orientalis* (solid bars) and *Rhadinopsylla pentacantha* (unfilled bars). **B.** Total counts of collected *Ctenophthalmus agyrtes* (unfilled bars) and *Megabothris turbidus* (solid bars). Horizontal bars, periods when no sampling was undertaken.

community. *Hystrichopsylla orientalis* is a univoltine species, appearing in the late summer with emergence in July and August. The population then declines slowly with the last individuals being collected in October (Fig. 2A). *R. pentacantha* (Fig. 2A) is also univoltine, adults appearing in October–December with the last individuals collected in April. The commoner species, *C. agyrtes* and *M. turbidus* (Fig. 2B), were both bimodal, with an early peak between March and May, and a subsequent late summer emergence in August and September. This pattern was more obvious in *C. agyrtes*.

Lice (Mallophaga). At Urwitałt, only a single louse species, *Hoplopleura edentula* has been collected from *M. glareolus*. The lice were identified using Wegner [10]. At the start of the study, lice were very rare, and were not encountered until August 2007. From August until November 2007, however, the number of lice increased exponentially (Fig. 3A,B), a total of 172 (mean 2.4 per vole) being collected in November. The populations of lice were again small in March 2008, but then increased exponentially until August 2008. There was a significant reduction of abundance in September 2008, and they then remained more or less constant in abundance (both total numbers and means) until the end

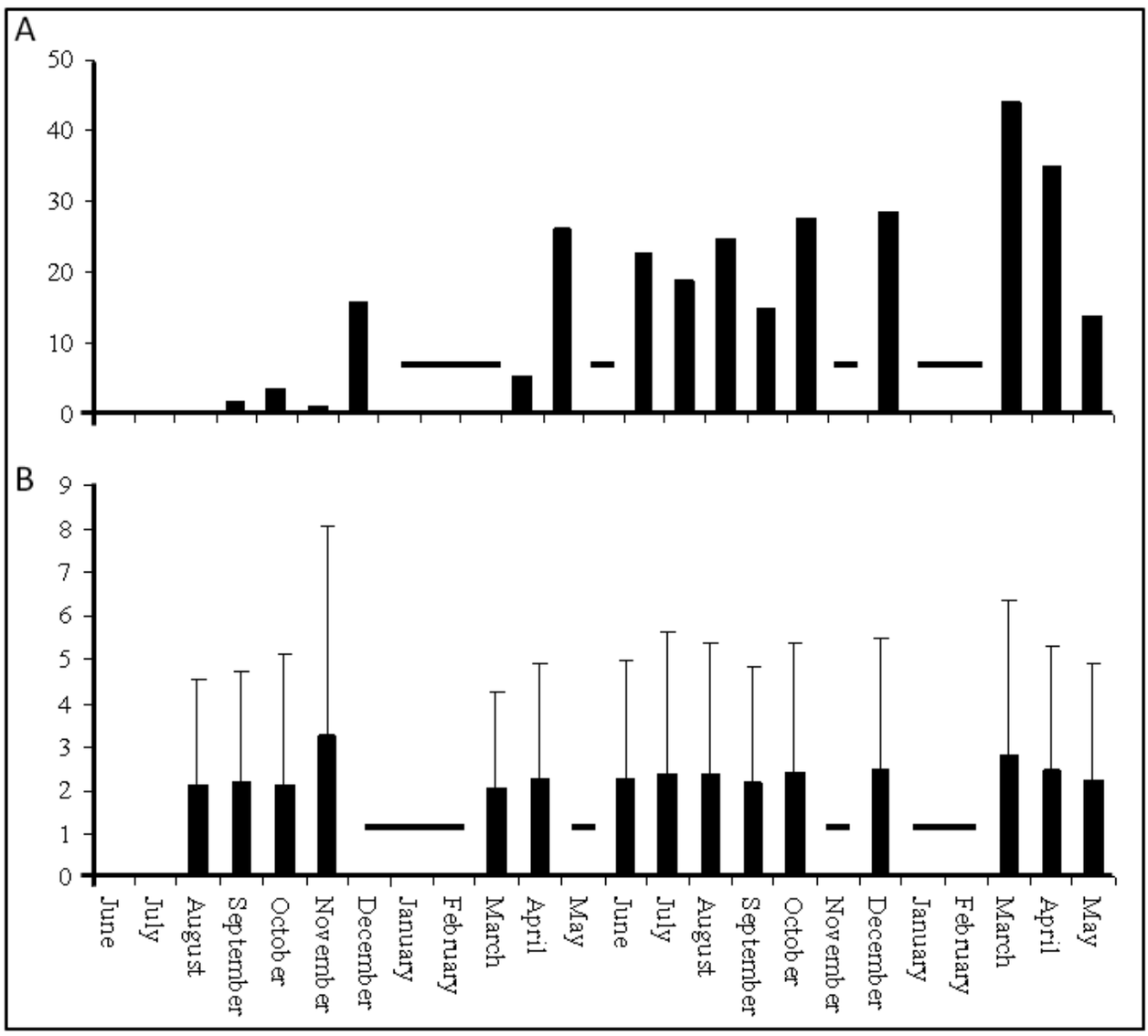

Fig. 3. **A.** Prevalence (%) and **B.** Mean intensity based upon $\log_{10}$+1 transformed counts for the louse *Hoplopleura edentula*, infecting *M. glareolus* at Urwitałt (error bars – SD). Horizontal bar, period with no sampling.

of 2008. Contrary to 2008, March 2009 saw a substantial rise in mean and total abundance, followed by a decline in April and May (Fig. 3A,B).

Mites and ticks (Acari). The ticks present on the rodents have been dealt with elsewhere [7]. Two tick species, *Ixodes ricinus* and *Dermacentor reticulatus* were recorded on the rodents. *I. ricinus* showed a bimodal peak of attachment, with the highest densities in May and September, although individual larvae could be found throughout the year. *D. reticulatus* showed a single peak for larvae in July.

Trombiculid mites. An unidentified trombiculid mite larva was found in the ears of *M. glareolus* at high density. These larvae were absent from the ears during midsummer (June and July), increased in abundance and prevalence during August, and were then present at almost 100% prevalence and up to 100 per ear throughout the autumn, winter and spring.

Gamasid mites. Gamasid mites were identified from March 2008 until the end of the study using the keys presented by Bregetova [11]. The most common gamasid mite encountered was *Laelaps agilis*, which as shown in previous studies, is found predominantly on *A. flavicollis* and was most abundant in the summer months (Fig. 4A). Although found predominantly on *A. flavicollis*, the proportion found on *M. glareolus* early in the summer was much greater than that found on this host in the autumn (Fig. 5B,D). The almost complete absence of this species from collections in 2009 was due to the collapse of the *A. flavicollis*

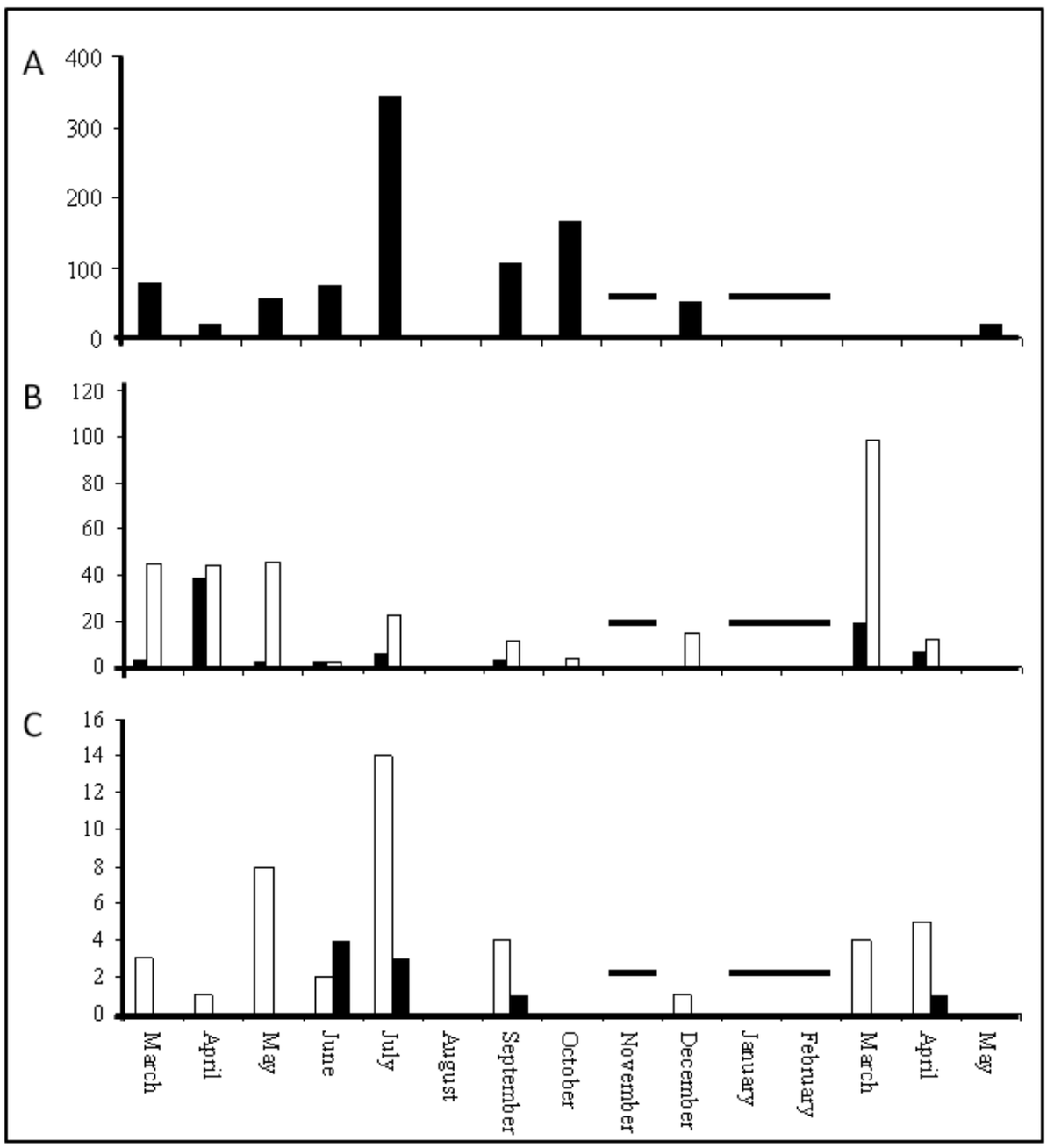

Fig. 4. Total number of **A.** *Laelaps agilis*; **B.** *Haemogamasus serdjukovae* (unfilled bars) and *H. nidiformis* (solid bars); **C.** *Eulaelaps stabularis* (unfilled bars) and *Hirstionyssus isabellinus* (solid bars) at Urwitałt, March 2008–May 2009. Note different vertical scales (total number of mites). Horizontal bar, period with no sampling.

population at this time. On *M. glareolus*, the most abundant species was *Haemogamasus serdjukovae*, present at an intensity of 2–3 per animal in the early spring. This, and the rarer *H. nidiformis*, were winter/spring species, becoming much less common in late summer (Fig. 4B). Other mite species were relatively scarce. *Eulaelaps stabularis* was found in small numbers (never more than 2 per rodent), and was most abundant in the early – midsummer period (Fig. 4C). This species was collected twice as frequently from *M. glareolus* as from *A. flavicollis*. *Hirstionyssus isabellinus* was present at low densities (up to 4 per month), mainly occurring in midsummer (Fig. 4C). Five specimens of a *Myonyssus* species were collected, all from *A. flavicollis*, and 4 specimens of *Euryparasitus*, all from *M. glareolus*. Log_{10} distribution curves (Fig. 5) for gamasid mites on the two rodent species show the relative abundance of each in spring (March and April) and autumn (October and

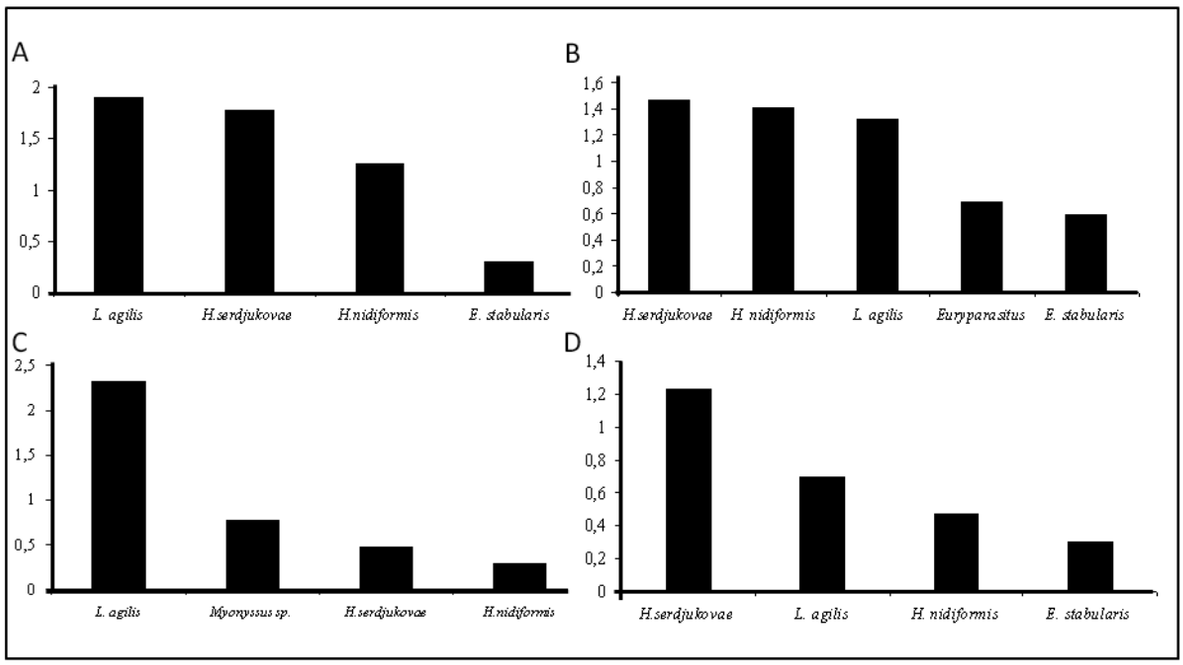

Fig. 5. Relative abundance of mite species on rodents in Urwitałt forest during spring and autumn 2009. Note differences in logarithmic abundance scale. **A.** *A. flavicollis*, spring (March and April); **B.** *M. glareolus*, spring; **C.** *A. flavicollis*, autumn (October, November); **D.** *M. glareolus*, autumn.

November); the total number of species of mite infecting each rodent is more or less the same in both seasons, and the species composition is similar. The biggest change is the great increase in abundance of *L. agilis* on *A. flavicollis* during the late summer and autumn.

Fur mites. Fur mites present a different problem to the gamasid mites, because they are generally non-mobile, obligate inhabitants of the fur environment. These are delicate, easily overlooked organisms, and the status of some as parasites is unclear.

Only *M. glareolus* was systematically examined for fur mites, because of the difficulties of examining *A. flavicollis* under light anaesthesia. Four fur mite species were collected. *Radfordia clethrionomydis* (Fig. 6A) showed a predilection for the head, especially the sides of the face and the dorsal surface of the muzzle, and was not normally found posterior to the ears. Eggs and larvae were found permanently attached at the base of hairs, where the latter feed on tissue fluid. Adults were more mobile, and could be found moving through the fur in heavy infections. Prevalence of *R. clethrionomydis* reached 80% or more in autumn 2007, but was generally lower, around 50%. Infections were found all year round, ranging in size from 1–500 mites.

The hypopus larvae of glycyphagid mites were also very common in the fur of *M. glareolus*. These larvae were found attached to the fur, and in some cases were phoretic on fleas. The nutritional status of these larvae is not clear. They represent a resistant larva of mites which live in the nests, and therefore are not strictly parasitic. However, they represent a considerable burden in terms of grooming for the rodent, and are the intermediate hosts for *Catenotaenia*, the commonest tapeworm. The number of hypopi was considerably increased in animals which had been dead for some time, suggesting a reservoir in the superficial layers of the skin, from which the larvae appeared as the animal cooled. Hypopi rose in abundance towards the end of the autumn, and then declined in both prevalence and abundance during the spring, achieving their lowest abundance during midsummer (Fig. 6B).

The other abundant fur mite was a species of the genus *Listrophorus*, found attached to the hairs predominantly on the back and hind quarters of the animal. The egg strings were also found, glued to hairs on the back. The more abundant the mite became, the further forward it, and the egg strings were found in the fur on the back of the animal. This mite was not observed until September 2007, after which prevalence increased substantially, reaching 40% by the late autumn of 2007. Prevalence declined in midsummer 2008, but then increased again to c. 60% during autumn and winter 2008/9. The abundance in 2007 was relatively low (mean of up to 9 mites per rodent), but was much higher than this in

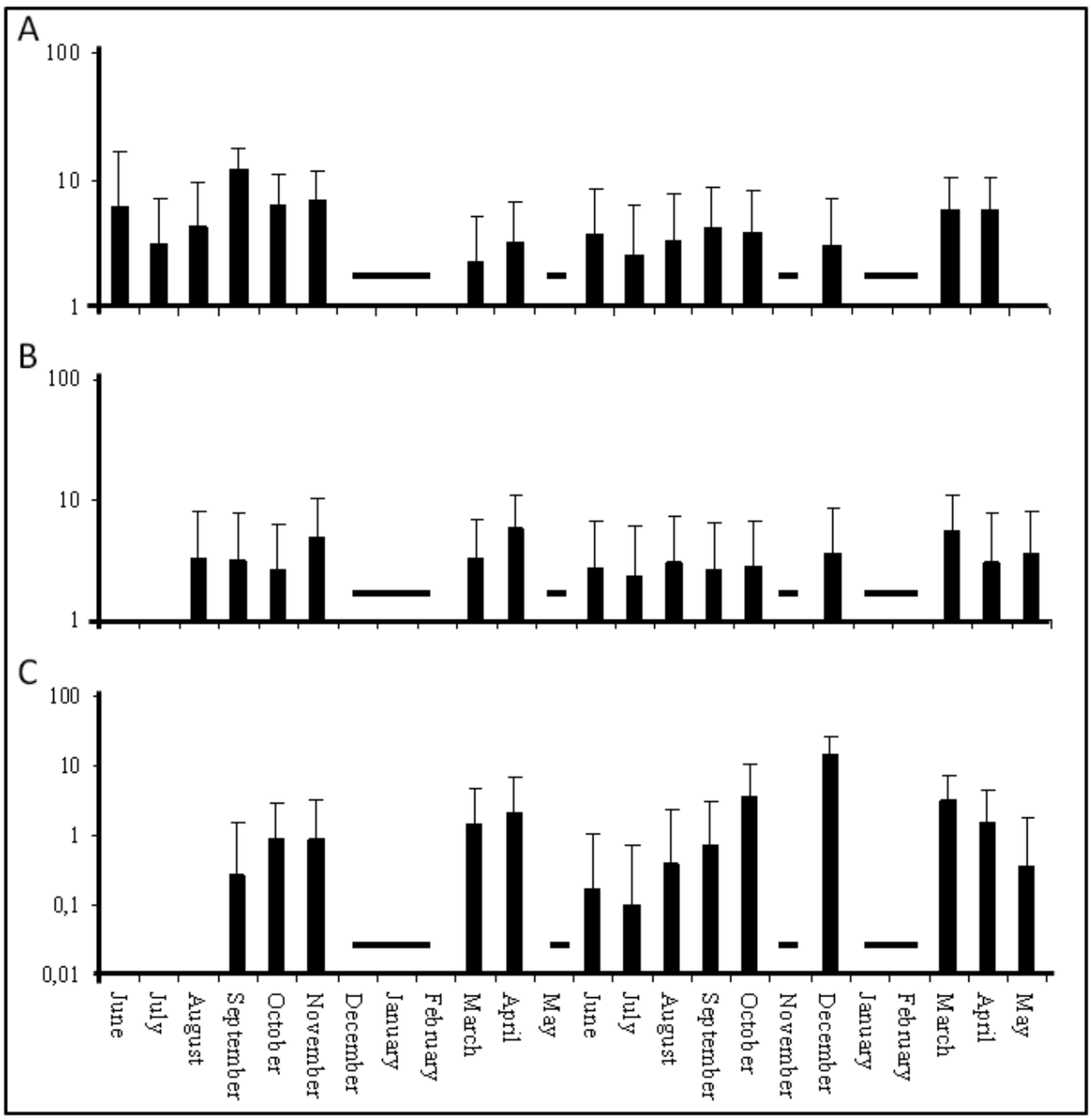

Fig. 6. Abundance of fur mites on *M. glareolus* in Urwitałt forest. **A.** *Radfordia clethrionomydis*; **B.** Hypopus larvae of a glycyphagid mite; **C.** *Listrophorus* sp. Y axis – mean intensity based upon $\log_{10}$+1 transformed counts for mites infecting *M. glareolus* at Urwitałt – logarithmic scale (error bars – SD). Note difference in Y scale between each. Horizontal bar, period withon sampling.

winter 2008/9, achieving means in excess of 100 per rodent in December 2008. Remarkably, this species was much rarer in spring 2009, when the rodents were themselves much rarer, and had almost disappeared again by May 2009 (Fig. 6C).

A *Myocoptes* species was also seen occasionally in the fur of rodents. Never more than one or two individuals of this species were collected, and no seasonal pattern could be discerned.

Discussion

This work has revealed a rich and complex ectoparasite fauna of *Apodemus flavicollis* and *Myodes glareolus*. The latter, for example, has proved to be infected by a total of 22 ectoparasites (9 fleas, 1 louse, 2 ticks, 1 trombiculid mite, 5 gamasids and 4 fur mites), ranging in abundance from species collected in thousands (*Ctenophthalmus agyrtes*, *Ixodes ricinus*, *Laelaps agilis*, *Listrophorus* sp.) down

to those for which only one or a few specimens were collected (*Doratopsylla dascynema*, *Ceratophyllus sciurorum*, *Euryparasitus* sp., *Myocoptes* sp.). This is in stark contrast to the relatively impoverished endoparasite fauna of *M. glareolus* at this site, which is dominated by three species (*Heligmosomum mixtum*, *Catenotaenia hentonneni*, *Paranoplocephala omphalodes*) with a further 9 species encountered less commonly [12,13].

Although some aspects of the ectoparasite community of woodland rodents (especially fleas and ticks) have been studied exhaustively, others, the lice and especially the prostigmatid fur mites, have been much less thoroughly studied, and we know of only one study, that of Balashov et al. [14] on the bank vole from central Russia, which is comparable. This study was however only over 18 months, and worked entirely from autopsied rodents. The current study, making use of living, recaptured rodents, was able to greatly increase sample size, such that some months included samples from over 100 rodents. There are substantial difficulties in quantifying burdens of ectoparasites of rodents; mites and lice remain hidden in fur, fleas and gamasids can escape before capture and censussing, and in the case of the latter, collections on the rodent may not reflect the numbers remaining in the nest or burrow (but see Krasnov et al. [15]). We would argue that, although questions about the completeness of censussing of individual animals are an issue, the large sample sizes used in this work more than compensate for possible inaccuracies in the counts of individual animals. The range of ectoparasites obtained in this work was comparable to that seen by Balashov et al. [14], although the abundances of some was quite different; in particular they recorded *Myocoptes japonensis* and *Trichoecius clethrionomydis* commonly from voles, whereas only a very small number of specimens of the former genus, and none of the latter, were collected in the present work. The species composition of gamasid mites also differed in detail with Balashov et al. [14] recording substantial numbers of *Laelaps clethrionomydis*. This species is easily distinguished from *L. agilis* by the length of the spines on the anal plate, and has not been found at Urwitałt.

The question arises, do these ectoparasites have any negative impacts on host survival, reproduction and fitness? The ectoparasites of rodents are generally ignored as potential pathogens, despite clear indications from other groups that these organisms might be pathogenic. Thus, although regular population fluctuations are well known in many rodent populations, and although these form an important paradigm of animal ecology, as far as we know there are no studies considering the role of ectoparasites in causing such fluctuations. And yet there is considerable evidence from other systems that pathogenic effects of ectoparasites on wild rodents are likely. *Radfordia clethrionomydis*, for example, is a close relative of *Myobia musculi*, a mite with similar ecology from the mouse *Mus musculus*, which is known to be responsible for mange and other health problems in laboratory colonies. *M. musculi* has also been found, in mice, to have significant impacts upon IgE [16] and upon levels of inflammatory cytokines [17], and so an immunomodulatory effect on the hosts cannot be ruled out for *R. clethrionomydis*. The ticks are self-evidently pathogenic, and *I. ricinus* causes severe pathology in wild rodents, in particular causing erosion of the ear margin. There was also evidence in spring (June) of crusted weeping scabs on hairless skin, particularly on the chin of *M. glareolus*, within which could be found large numbers of *I. ricinus* larvae. The role of *I. ricinus* and of *Radfordia* in generating this mange syndrome has not been fully investigated. Likewise, lice have recently been shown [6] to be correlated with reduced sensitivity of toll-like receptor mediated immune responses in *Apodemus sylvaticus*; the levels of louse infection defined as 'heavy' in that paper, and causing the greatest effect on receptor sensitivity were frequently exceeded by *H. edentula* infestations in the present work. An impact of ectoparasites on the health status of woodland rodents is therefore likely. The impact of ectoparasite abundance on the endoparasite community present in the same animal has not been considered, but may be worthy of attention. The discovery of an impact of an ectoparasite (lice) on overall immune function [6] suggests this might be the case, but it is normally argued that the immune responses to ectoparasites and endoparasites are quite different in character. However, the observation that the mites also induce a strong IgE response [16], so strong that inadvertant fur mite infection can induce dermatitis-like syndromes in some mouse strains [18], suggests that immunological linkages between endoparasites and ectoparasites may occur, and may have a role in determining the overall parasite fauna of individual animals.

It is also the case that infestations collected from rodents represent a small part of the challenge which these animals face, as the majority of fleas and gamasid mites probably remain in the nest. It is curious that fleas and blood-sucking hippoboscid flies are widely recognised as pathogens of bird nestlings (e.g., [19]), and yet, as far as we are aware, no comparable data are available for the survival of rodent nestlings, and the possibility of ectoparasites impacting upon survival and growth of young rodents has rarely been discussed [20]. Although the study of gamasid mites and fleas within rodent nests is technically challenging, nevertheless it is surprising that the ecological significance of rodent nest parasitism has not been considered theoretically.

The ectoparasite community studied here showed a strong seasonality, which in some species was straightforward to explain. The clearest example, the flea *Hystrichopsylla orientalis*, is univoltine at Urwitałt, emerging between June and August and then undergoing a slow decline due to mortality and not being present in samples after October. This pattern of emergence presumably coincides with the availability for the larvae of large numbers of rodent nests during the late summer and autumn. *Ctenophthalmus agyrtes* is bivoltine, with emergence of adult fleas in March in both 2008 and 2009, from larvae or pupae which had overwintered, followed by a second generation of emerged adults in July and August. *Megabothris turbidus* probably shows the same pattern, but in this case the emergence in spring 2009 almost failed, with only 7 fleas of this species altogether being recorded. This bivoltine strategy probably takes advantage of the vole breeding cycle at Urwitałt, with the summer (July/August) generation feeding as larvae on breeding rodents of the spring (April–June) generation, while the spring (March/April) generation feed as larvae in the nests of late-summer rodents which will overwinter and breed in the following year. *Rhadinopsylla pentacantha* appears to be univoltine, with adults found only between the months of October and April, but in this case the pattern was complicated because of the lack of sampling between November and March. This highlights a problem with studies of rodent ectoparasites in boreal forests, that sampling is normally suspended during winter, at a time when ectoparasite diversity may be considerable. The pattern of other species was more complicated. Of the gamasid mites, the *Haemogamasus* species were both most abundant in the early spring, in March and April of both years, suggesting a single maturational peak for these mites, with other stages at other times of year in rodent nests. However, individual adults of these species could be found in any month until September, suggesting that a clear pattern of emergence does not exist. The fur mites are clearly multivoltine and are thought to mature all year around on the rodents. The life cycle of *Myobia musculus* is c. 16 days [21], and that of *Radfordia clethrionomydis* is probably similar. This species was most abundant in summer, although with a distinct decline in abundance in July, while the *Listrophorus* sp. and glycyphagid hypopus larvae were both most abundant in winter. The increased abundance of *Listrophorus* and glycyphagids in late autumn and winter is probably related to the increased length of the fur of *M. glareolus* at this time, making grooming more difficult. This might also account for the rise in abundance of lice during the autumn of 2007, but these insects then remained common throughout 2008, irrespective of vole coat length.

The decline in abundance of several ectoparasites in midsummer is an artefact caused by reproduction of the voles outstripping the availability of ectoparasites to infect them. The vole population in Urwitałt is nearly bivoltine. Animals born in the autumn mature in the following spring and give birth to the first litters in March and April. These young-of-the-year are then mature and sexually active by June and July, and between July and August occurs the greatest recruitment of young animals into the *M. glareolus* population. This July/August cohort do not become sexually mature in the season of their birth, but instead overwinter and become reproductively active in the next spring. This reproductive pattern is typical of *M. glareolus* throughout much of its range [22]. The rapid recruitment of young animals into the population in July and August dilutes the number of ectoparasites available to infect them, and so an apparent dip in prevalence and mean abundance takes place at this time of year. This was most apparent for *Listrophorus*, hypopus larvae and *Radfordia*, the three mite species with the closest, most intimate relationship with *M. glareolus*. Interestingly it was not noted in 2008 for lice, which therefore must have a sufficiently high transmission rate to maintain their prevalence and abundance, despite the rapidly increasing rodent population.

An interesting point concerns the difference in

exposure of rodents of the two generations (summer and overwintering) to ectoparasites, and the possible evolutionary implications of this. Because of the seasonality of the ectoparasite populations, each rodent generation is exposed to a distinct community of ectoparasites. Thus, only the overwintering population is exposed to *Rhadinopsylla pentacantha*, and to the *Haemogamasus* species; *Listrophorus* sp. also, and perhaps the hypopus larvae, have a much greater impact on this generation of rodents. Since this generation lives longer before breeding, and is exposed to higher risk of mortality than the spring generation of rodents, it is likely to be upon this generation that selective impacts of ectoparasites can most clearly be discerned.

These seasonal patterns were nevertheless complicated by the superimposition of a longer-term trend in numbers. *Hoplopleura edentula*, the louse, was not found in any numbers at Urwitałt prior to August 2007, when only 3 individuals were found. Similar results had been found in previous visits to Urwitałt in August 1999, 2002 and 2006, that lice on voles were very rare (Behnke et al., unpublished). From August 2007, however, *H. edentula* populations increased exponentially, and remained relatively high throughout the study, with over 300 collected in August 2008. Similarly, *Listrophorus* sp. was not encountered prior to August 2007, but subsequently increased in abundance to become one of the commonest ectoparasites infecting *M. glareolus*. This long-term change in abundance of certain ectoparasite species is probably related to the abundance of voles on the study site. When the study began, vole and mouse populations within the study area was estimated using mark-recapture methods at ca. 150–200 individuals of each species [7], but after a particularly good overwinter survival in 2007/8, by summer 2008, the *M. glareolus* populations had increased substantially from this level. A sharp, catastrophic decline in abundance then took place between September 2008 and May 2009, such that, by the end of the study, only 36 *M. glareolus* and 6 *A. flavicollis* could be captured during a week-long trapping session. The relationship between ectoparasite abundance and long-term rodent dynamics is not clear, but certainly there is a linkage. In particular, the increase in louse populations, known from the work of Jackson et al. [6] to be immunomodulatory, during the growth phase of the rodent population, and their continuing abundance while the rodents underwent a population contraction, suggests a role for these ectoparasites in host population cycling. Further, long-term studies are needed to confirm this, and to consider the relevance of the observed dynamics of ectoparasites to the forest-wide population cycles of their rodent hosts.

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