Population biology of *Eimeria* (Protozoa: Apicomplexa) in *Apodemus sylvaticus*: a capture/recapture study

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SUMMARY

The first long-term (27 month) survey of single species of *Eimeria* occurring in a population of *Apodemus sylvaticus* in the UK showed that *Eimeria apionodes*, *E. hungaryensis* and *E. uptoni* occurred throughout the period whilst *E.* sp. E. was only found during 4 months. In first-captured animals, overall prevalence of *Eimeria* spp. was 73%: a figure higher than previously published, but possibly an underestimate. Multiple infections (2 or 3 species) occurred in 34% of first-capture infected animals, but without significant associations. There were no significant differences of prevalence rates between the sexes, nor between adults and juveniles, except for *E. uptoni* which was more common in juveniles than in adults. *E. hungaryensis* and *E. uptoni* probably occurred as near-continuous infections whilst *E. apionodes* occurred more intermittently but with no long-term total immunity. Monthly prevalence data indicated ongoing trends over the 27 months. Prevalences of *E. apionodes* indicated an annual cycle, lowest in January–May and with a peak in October–November, correlating positively with both the number of animals and the percentage of juveniles in the host population and also with the environmental relative humidity. There was no consistent pattern for *E. uptoni* and an annual cycle for *E. hungaryensis* was not apparent.

Key words: *Apodemus sylvaticus*, *Eimeria hungaryensis*, *Eimeria uptoni*, *Eimeria apionodes*, prevalence, capture/recapture.

INTRODUCTION

Parasites are believed to be important factors in the regulation and evolution of host populations (see review by Goater & Holmes, 1997) and investigation of parasite/host interactions at the population or community level is clearly important. The population biology of *Apodemus sylvaticus* L., the wood mouse, has been the focus of many published papers and there have been a number of studies of the enteric parasites (Healing & Nowell, 1985), but until recently there have been few studies going beyond isolated measurements of rates of prevalence and/or intensity of infection. However, details are now known of the interactions of the intestinal nematode *Heligmosomoides polygyrus* (Baylis) with wood mouse populations (e.g. Gregory, 1992; Gregory, Montgomery & Montgomery, 1992; Abu-Madi *et al.* 1998).

Eimeria is a frequently occurring parasite of a variety of hosts including *Apodemus* and other rodents. Species are sometimes pathogenic to their hosts (Gregory, 1990) and therefore the parasite may be a regulatory factor of host populations. There have been a few published reports on the population biology of species of *Eimeria* in wild rodents in the USA, e.g. *Spermophilus* spp. (Wilber *et al.* 1994*a*; Thomas, Stanton & Seville, 1995) and *Peromyscus* spp. (Fuller, 1996*a*, *b*), but almost nothing from rodents in the UK and elsewhere. Wood mice in the UK are known to be parasitized by at least 4 species of *Eimeria* with species prevalences of up to 40% (Lewis & Ball, 1983; Ball & Lewis, 1984; Nowell & Higgs, 1989), but there is no information on how these coccidia interact with their hosts.

In this paper we report on data from a survey, over 27 months, of a colony of wood mice. We describe prevalence levels (% of animals infected) of the individual species of *Eimeria* that they harbour and how these infection rates may be influenced by the status of the host (sex, maturity) and the presence of concurrent infections with other species of *Eimeria*. Since temperate ecosystems such as in the UK have an annual climatic cycle and wood mice have a life-cycle of about 1 year (Flowerdew, 1985), annual cycles of infection patterns may be apparent. The aim of this study was therefore to investigate: (a) how infections develop in individual animals in the field, (b) any association between host status and prevalence rates and (c) temporal variations of prevalence rates, especially annual cycles. Unlike many previous studies which have involved autopsy of trapped mice, the present work used a long-term capture-mark-recapture system which allowed an

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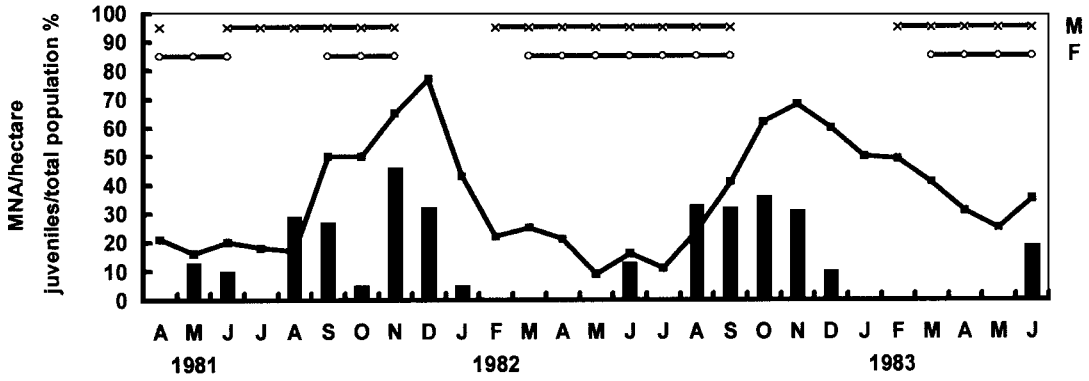

Fig. 1. Summary of the population dynamics of *Apodemus sylvaticus* at the trapping site over 27 months: monthly data for minimum number alive (MNA)/hectare; percentage of juveniles (⩽ 14 g body weight) in the population; presence of animals in breeding condition. (■——■) MNA/hectare; histogram, % juveniles; (×——×) (M) presence of males with descended testes; (○——○) (F) presence of females in breeding condition.

Table 1. Summary of first capture data for *Apodemus sylvaticus* showing numbers of animals infected with *Eimeria* spp.

(Prevalences are stated in parentheses. † Total for both sexes, includes 2 individuals of indeterminate sex.)

	Males			Females			Both sexes
	⩽ 14 g	> 14 g	T	⩽ 14 g	> 14 g	T	T†
Animals (*n*)	23	81	104	33	41	74	180
Eimeria (all spp.)	16	56	72 (69%)	24	33	57 (77%)	131 (73%)
E. apionodes	11	25	36 (35%)	15	14	29 (39%)	66 (37%)
E. hungaryensis	7	31	38 (37%)	13	19	32 (43%)	72 (40%)
E. uptoni	1	19	20 (19%)	4	18	22 (30%)	43 (24%)
E. sp. E.	0	2	2 (2%)	0	1	1 (1%)	3 (2%)

investigation of infection in individual mice throughout the time that they were trapped.

MATERIALS AND METHODS

A 7 × 7 grid of trapping stations with an interstation distance of 10 m was established in mixed woodland at New Covert, Upperwood Farm, The University of Reading (NGR SU748693). Two clean Longworth live traps, always washed and autoclaved (1·055 kg/cm² for 20 min) prior to reuse, were permanently located at each station (49 stations and 98 traps) and set for 1 night per week between April 1981 and June 1983 (127 weeks). Over each trapping night, the relative humidity and maximum and minimum air temperatures were recorded at ground level using respectively a hair hygrometer and a maximum/minimum thermometer. Mean monthly values were calculated for each parameter.

Trapped animals were examined the next morning. Animals were sexed, weighed, marked by toe-clipping (Twigg, 1975) and then released. Animals weighing 14 g or less were classified as juveniles, with heavier animals as adults. The breeding condition of adults was assessed. Changes of population density were followed using a 'minimum number alive' (MNA) index (Krebs, 1966; Gurnell & Gipps, 1989).

At least 5 faecal pellets collected directly from each animal, were soaked in distilled water for 24 h before parasite oocysts and eggs were isolated using a qualitative salt flotation technique, and *Eimeria* species were identified by oocyst morphology (Nowell & Higgs, 1989).

Two separate prevalences for the species of *Eimeria* within the host population were calculated: (a) from animals at first capture, and (b) from animals at first capture within each month. Associations between prevalences and between prevalence and host status were compared using χ^2 tests with Yates' correction on 2 × 2 contingency tables. To minimize apparent trends occurring across the whole trapping period, the monthly prevalence curve for each parasite species was replotted as the monthly deviations from the polynomial regression line (of the form $y = ax^2 + bx + c$) (Chatfield, 1989). Time series analysis autocorrelations after arcsine transformation were calculated with 95% confidence limits estimated as described by Chatfield (1989) using MINITAB 10.5 for WINDOWS (Minitab Inc.). In the Results section, these autocorrelations, where significant, are expressed as positive (+ve) or negative (−ve).

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Table 2. Summary of weekly trapping and infection data for the 4 individual wood mice which had the longest span of captures during the 27 month survey

(The number and percentage of weekly samples in which species of *Eimeria* occurred, together with the longest unbroken span of weekly samples for each species, are indicated.)

	Mouse			
	101M	103F	120F	147M
Span of capture period (weeks)	52	48	44	39
Total number of weeks in which individual sampled	38	45	38	33
Number of weeks sampled in which:				
uninfected with *Eimeria* spp.	8 (21%)	7 (16%)	5 (13%)	1 (3%)
infected with *Eimeria* spp.	30 (79%)	38 (84%)	33 (87%)	32 (97%)
infected with *E. apionodes*	5 (13%)	8 (18%)	1 (3%)	3 (9%)
infected with *E. hungaryensis*	25 (66%)	26 (58%)	22 (58%)	21 (64%)
infected with *E. uptoni*	13 (34%)	19 (42%)	28 (74%)	18 (55%)
infected with *E.* sp. E.	0	0	0	2 (6%)
Longest recorded unbroken span of infection over consecutive weeks with:				
E. apionodes	1	2	1	2
E. hungaryensis	10	5	5	4
E. uptoni	2	5	12	4
E. sp. E.				1

RESULTS

Preliminary data

Over the 27 month period, 180 wood mouse individuals were trapped a total of 1013 times, giving data for 435 monthly first captures. Data concerning the population density (MNA index), breeding seasons (as indicated by presence of reproductively active males and females) and percentage of juveniles are plotted in Fig. 1. The population was at its highest in November/December (up to 70–80 MNA/ha) and at its lowest in the period May/August (10–20 MNA/ha). Reproductively active adults were seen from February/March until late autumn and juveniles were present from May/June until December. Autocorrelation analysis of juveniles showed significance ($P < 0{\cdot}05$) at 1(+ve), 5(−ve) and 6(−ve) months. Calculated from Table 1, the sex ratio (male/female) for first-capture juveniles was 0·70 and for first-capture adults was 1·98.

Parasites isolated and identified from the faeces of wood mice included *Eimeria*, *Hymenolepis*, *Syphacia*, *Aspiculuris*, *Heligmosomoides* and trichurid nematodes. There were oocysts of 4 species of *Eimeria*: *E. apionodes* Pellérdy, *E. hungaryensis* Levine & Ivens, *E. uptoni* Lewis & Ball and the unnamed species *E.* sp. E. (Lewis, 1981; Nowell & Higgs, 1989).

Infections in individual animals

Data from the 4 most frequently weekly sampled animals (trapped over > 38 weeks) showed that the faeces were only infrequently coccidia-free (< 21% of weekly samples) (Table 2). Individuals passed oocysts of all 4 species, with *E. apionodes* being less frequent (< 20% of weekly infected samples) and with shorter periods of infection (1–2 consecutive weeks) than *E. hungaryensis* and *E. uptoni* (> 30% of weekly infected samples and periods of 2–12 consecutive weeks). The presence of *E.* sp. E. was rare, only occurring in 1 of the 4 animals.

For 21 of the most frequently sampled animals (trapped on consecutive weeks for a span of at least 12 weeks, irrespective of time of year), the times between consecutive occurrences in the faeces of each of the 3 common species of *Eimeria* were estimated (Fig. 2), the mean values for *E. apionodes*, *E. hungaryensis* and *E. uptoni* being 4·7, 1·9 and 2·0 weeks respectively. For *E. apionodes* in mice trapped between September and December, this mean value decreased to 2·3 weeks ($n = 7$). Between individual mice, there was no obvious synchrony of coccidia-free periods or of periods of passing each species.

Eimeria *and host status*

In the first-captured animals, the prevalence rate of *Eimeria* infections was 73%, and the rates for the individual species varied from 2 to 40% (Table 1). For *E.* sp. E. no analysis relating to host status was realistic since prevalence was low (3/180 animals infected). For each of the remaining 3 species of parasites, the proportions of male and female wood mice that were infected were not significantly different (χ^2 test, $P > 0{\cdot}05$). Only *E. uptoni* showed significant differences of prevalence between juveniles and adults, the rate being higher in adults when both sexes were combined (9%, 31% respectively)

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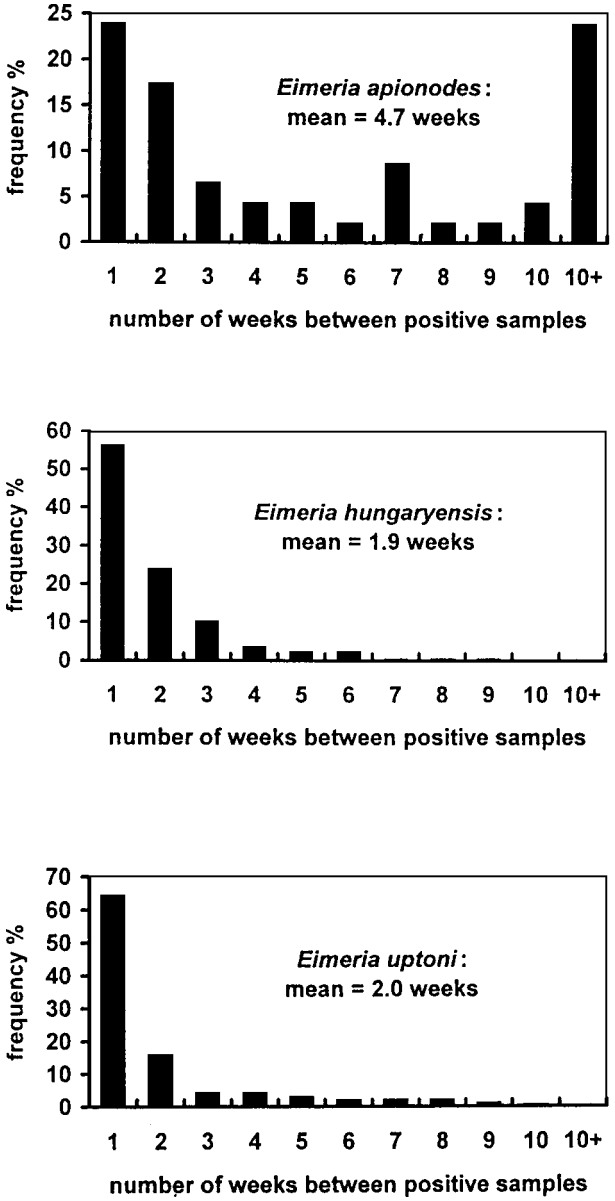

Fig. 2. *Eimeria apionodes*, *E. hungaryensis*, *E. uptoni*: frequency histograms for each species, to show the range of time-intervals (weeks) between collection of 2 consecutive positive faecal samples from individual mice for that species ($n = 21$). *E. apionodes*, 45 samples; *E. hungaryensis*, 216 samples; *E. uptoni*, 188 samples. See text for further details.

and for females (12%, 44%) (χ^2 test, $P < 0{\cdot}01$ in both cases) but not significantly so for males (4%, 23%) (χ^2 test, $P > 0{\cdot}05$). In 34% of animals infected at first capture (44/131), multiple infections with 2 or 3 (but never 4) species were present, but analysis gave no significant associations between pairs of species (χ^2 test, $P > 0{\cdot}05$).

Temporal variations in the prevalence of Eimeria *spp.*

The monthly prevalences of the 4 species in monthly first-captured animals are shown in Figs 3A, 4A and 5A, with the sample sizes indicated in Table 3. Low sample sizes may have influenced results for some months, e.g. May and July 1982. In addition, there was variation between years, for instance monthly prevalences of *E. hungaryensis* were higher in 1983 than in 1982 (comparing first 6 months of each year, Kolmogorov–Smirnov 2-sample test, $P < 0{\cdot}05$). Data transformed to remove this effect and emphasize the monthly changes are plotted in Figs 3B, 4B and 5B. Transformation was not made for *Eimeria* sp. E. which was only recorded in the spring of 1983 (Fig. 5A).

The regression line for monthly prevalences of *E. apionodes* suggest that there was a slight general decline over the 27 month period (Fig. 3). However, within each year, the monthly values were low from January to May, increased in June and July, decreased in August and were highest in October and November. The regression line for *E. hungaryensis* indicates a decline of prevalences from 1981 to 1982 with a rise in 1983 (Fig. 4). There was variation of prevalence between months but no clear annual pattern. For *E. uptoni*, the regression line indicates a slight rise in prevalences throughout the sampling period (Fig. 5). Monthly prevalences appeared to peak between March and June but no consistent pattern was seen.

Time series analysis showed no significant autocorrelation for *E. uptoni*, and only at 1(+ve) and 2(+ve) months for *E. hungaryensis* ($P < 0{\cdot}05$). However, *E. apionodes* showed significant autocorrelation ($P < 0{\cdot}05$) at 1(+ve), 6(−ve) and 7(−ve) months. There was positive, but not significant ($P > 0{\cdot}05$) autocorrelation peaking at 12 months. For *E. apionodes* alone, there was a significant positive correlation for monthly values between the prevalence of the parasite and the percentage of juveniles (Spearman's rank correlation coefficient = 0·447, $n = 27$, $P < 0{\cdot}05$) and between prevalence and the MNA index (Spearman's rank correlation coefficient = 0·911, $n = 27$, $P < 0{\cdot}01$).

There was no correlation between monthly temperatures and prevalence of any species, and mean relative humidity showed a positive correlation only with *E. apionodes* (Spearman's rank correlation coefficient = 0·533, $n = 26$, $P < 0{\cdot}01$).

DISCUSSION

We believe that this is the first time a long-term survey of defined single species of *Eimeria*, as distinct from the aggregated species within the genus, has been made in rodents in the UK. Similar studies have been made in the USA but usually only over a restricted number of months, presumably because of limited access to the hosts, e.g. due to hibernation (Wilber, Duszynski & Van Horne, 1994*b*; Fuller, 1996*b*).

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Table 3. Number of first-capture *Apodemus sylvaticus* for each month of the survey (April 1981–June 1983)

(Total monthly first captures = 435.)

	1981	1982	1983
Jan		20	23
Feb		10	22
Mar		11	17
Apr	10	10	14
May	8	3	12
Jun	10	7	10
Jul	8	4	
Aug	7	12	
Sep	23	19	
Oct	22	28	
Nov	28	30	
Dec	38	29	

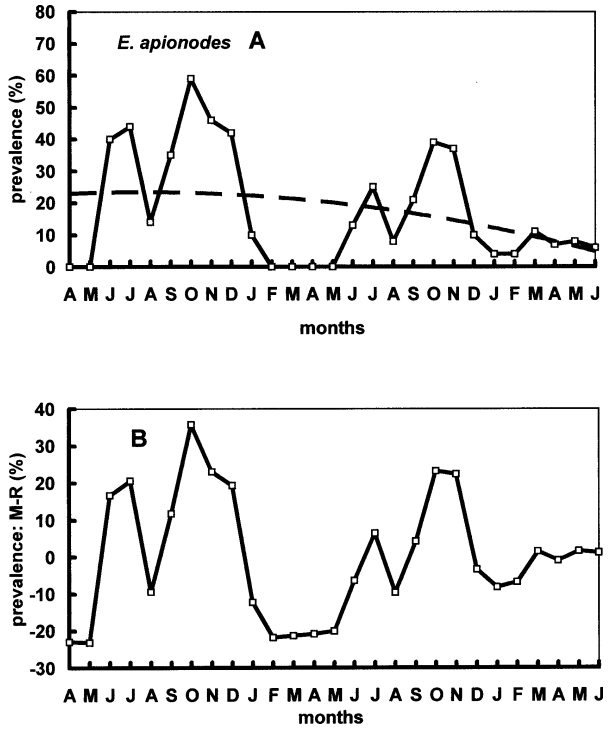

Fig. 3. *Eimeria apionodes*: monthly prevalence rates (% first-captured animals for that month showing oocysts in faecal samples). (A) Monthly prevalence rates and regression line plotted. Regression line: $R^2 = 0{\cdot}1073$, $y = -0{\cdot}0369x^2 + 0{\cdot}338x + 22{\cdot}624$. (B) Transformed monthly prevalence rates plotted as the difference between the monthly value and the value for the month estimated from the regression line plotted in (A). (□——□) Monthly prevalences.

The temporal changes of the wood mouse population are in agreement with the findings of other workers (reviewed by Flowerdew, 1985; Wilson, Montgomery & Elwood, 1993), but the use of a capture-mark-recapture technique may have reduced the numbers of surviving young in nests (Elwood, 1991; Wilson *et al*. 1993). Wilber & Patrick (1997) reviewed the use of this technique for analysis of parasites in host populations. An important advantage is that infections may be followed in individual animals, but there is the disadvantage that faecal samples are small and retrieved at a set time of day, and hence calculations of true parasite burdens may not be valid. Low levels of oocysts may have remained undetected especially if the sampling time coincided with a low point of a parasite's circadian rhythm (Fuller, Hefner & Wrosch, 1995) and prevalences may therefore be underestimates.

The prevalence of the genus *Eimeria* in *A. sylvaticus* derived from first-capture data in this study was higher than in other published accounts (Table 4). When making comparisons, this type of data set for *Eimeria* needs to be treated with caution on at least 3 counts. First, *Eimeria* infections may be of a complex of species, which has not always been recognized (e.g. Elton *et al*. 1931). Each species has its own separate gene pool and the phenotypic expression of each may be influenced uniquely by environmental factors, so prevalences may differ between species. Second, some authors have amalgamated material from several sites. Abiotic and biotic factors including host and parasite genotypes for the same species may not be identical between sites, leading to differences of infection patterns including prevalences. Third, there may be temporal cycles of host and parasite abundance that will influence estimates depending on the time of sampling. For instance, if host animals are seasonal breeders, prevalences may be influenced through changes of population age structure and differences of age-related host susceptibility. In interpreting the data from the present survey, completed over an extended time period, this third point needs to be borne in mind in relation to host breeding behaviour and to *E. apionodes* which appears to show seasonal cycles (see below).

All 4 species probably have a typical eimerian life-cycle (Levine, 1982). From laboratory studies of single infections, each species has a characteristic patent period during which oocysts are passed in the faeces. Infections are self-limiting: *E. hungaryensis* is passed from about day 3 until about day 12 after infection; *E. apionodes* from about day 8 until between days 18 and 34; and *E. uptoni* possibly from day 6 to at least day 19 (Higgs & Nowell, 1988; Nowell & Higgs, 1989). Data are not available for *E.* sp. E, but providing it is not a contaminant (see below) we would expect values similar to the other 3 species. If comparable to previous studies on other species, oocysts freed from the faeces probably become infective within a week and may survive and remain infective for several months, dependent upon abiotic environmental factors (Fernando, 1982). The precise timing would depend on the characters, e.g. temperature and humidity, of the microenvironment

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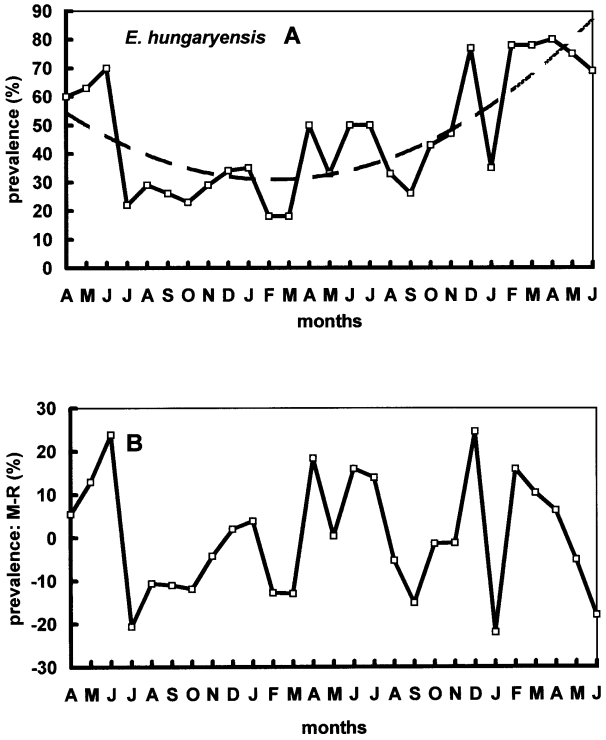

Fig. 4. *Eimeria hungaryensis*: monthly prevalence rates (% first-captured animals for that month showing oocysts in faecal samples). (A) Monthly prevalence rates and regression line plotted. Regression line: $R^2 = 0{\cdot}577$, $y = 0{\cdot}2257x^2 - 5{\cdot}0691x + 59{\cdot}373$. (B) Transformed monthly prevalence rates plotted as the difference between the monthly value and the value for the month estimated from the regression line plotted in (A). (□——□) Monthly prevalences.

in which they are deposited, for instance feeding sites, or nests, or burrows of their hosts.

Infections in individual animals

As indicated in the last paragraph, the duration of the life-cycles of the 3 most common species of *Eimeria* are shorter than the expected life-span of the wood mouse (about 1 year), and for the infections to continue in individual mice as in Table 2, reinfection derived from transmission stages must be repeatedly occurring.

E. hungaryensis and *E. uptoni* occurred frequently in more than 50% of weekly samples from individual mice, with instances of recorded infection spans of 4 or more consecutive weeks. This pattern together with the mean time between consecutive infected samples of about 2 weeks and the patent periods (3–12 days and 6–19 days post-infection respectively) suggest that the mice were sometimes becoming infected with fresh oocysts of a species before the previous infection of that species had ended. The lack of distinct breaks in infections in mice captured repeatedly over consecutive weeks suggests the lack of a complete immunity to either of these species. There may have been partial immunity, but this would not be obvious from prevalence data alone. Laboratory studies on *E. hungaryensis* support the view that total suppression of oocyst production by immunity does not occur (Higgs & Nowell, 1988), but similar work on *E. uptoni* has been done. Incomplete immunity commonly occurs for a number of other species of *Eimeria* in rodents (Stanton *et al.* 1992; Wilber *et al.* 1994*a*; Fuller, 1996*a*; Fuller & Duszynski, 1997).

E. apionodes was passed from individual mice for periods compatible with the patent period of about 10–26 days duration (see above). Overall there were longer periods between successive infected faecal samples than occurred with *E. hungaryensis* and *E. uptoni*. As expected, at times of higher prevalence of *E. apionodes* (September–December), the length of these periods decreased. The variation of infection pattern for this species may have controlled by host factors such as a more complete immunity, or environmental factors which may have altered the chances of a mouse picking up oocysts (further discussed below). Some mice, presumably for reasons of phenotypic variation of behaviour and/or susceptibility/immunity, were less likely to show infection with *E. apionodes* (120F) than others (103F). *E.* sp. E. was very infrequent, but data for mouse 147M, with 2 positive samples spaced at 12 weeks, suggest that a single infection did not always lead to permanent immunity.

Eimeria *and host status*

The finding that the sex of the host has no effect on prevalence rates is supported by laboratory experiments with the same species (Ibrahim, 1987; Higgs & Nowell, 1988) and in turn is in agreement with findings about some other *Eimeria*/rodent systems (Stanton *et al.* 1992; Fuller, 1996*b*). However, for other species of *Eimeria*, higher prevalences in males have been recorded, possibly due to higher androgen levels or to microhabitat or behavioural differences (Fuller, 1996*b*; Fuller & Duszynski, 1997). Previous reports have also indicated various conclusions concerning levels of infections in juvenile as compared with adult rodents (e.g. Stanton *et al.* 1992; Fuller, 1996 *b*). In the present study, juvenile mice (especially females) had lower prevalences of *E. uptoni* infection than adults. Since this parasite was being passed by infected animals throughout the year and adults were presumably being reinfected to maintain their infections, it seems likely that oocysts were also available to infect the juveniles. Either the juveniles were picking up less oocysts, for instance due to different behavioural patterns, or juveniles had a lower innate susceptibility perhaps due to differing immune responses or intestinal physiology, as compared with adults.

Previous studies on guilds of *Eimeria* in rodents indicate that in some cases multispecies infections of

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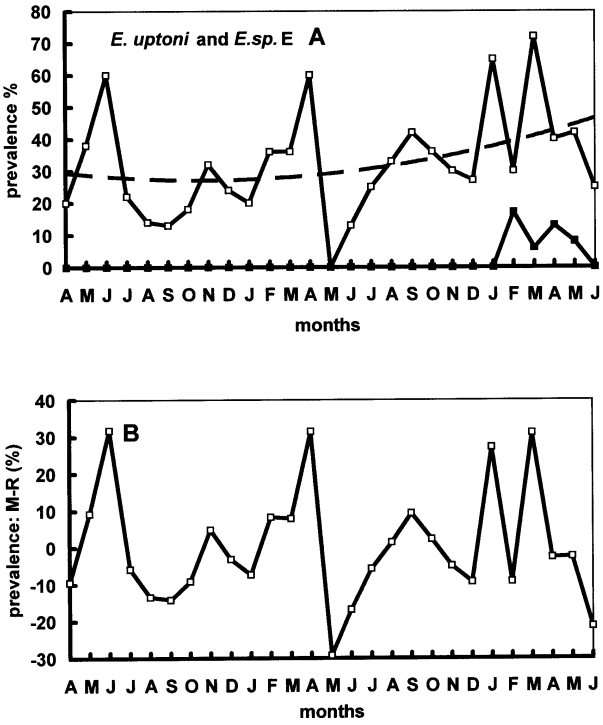

Fig. 5. *Eimeria uptoni* and *Eimeria* sp. E.: monthly prevalence rates (% first-captured animals for that month showing oocysts in faecal samples). (A) Monthly prevalence rates and regression line plotted. Regression line for *E. uptoni*: $R^2 = 0{\cdot}1228$, $y = 0{\cdot}0516x^2 - 0{\cdot}7894x + 30{\cdot}138$. Regression line not plotted for *E.* sp. E. (B) Transformed monthly prevalence rates for *E. uptoni* plotted as the difference between the monthly value and the value for the month estimated from the regression line plotted in (A). (□——□) Monthly prevalences of *E. uptoni*; (■——■) monthly prevalences of *E.* sp. E.

individual hosts occur (e.g. Stanton *et al*. 1992) whilst in others there are unexpectedly high levels of single infections (Reduker & Duszynski, 1985). Infections in wood mice fall into the former category. Whilst we have not shown any specific associations between the species of *Eimeria*, this occurs in other rodents (Stanton *et al*. 1992) and it is possible that species do interact, one species making the host either more or less susceptible to infection by others. Thus the continuing presence of *E. hungaryensis* and/or *E. uptoni* might have enhanced susceptibility to the more intermittent infections of *E. apionodes*. Some reasons for synergistic effects between species of coccidia have recently been discussed by Shehu & Nowell (1998).

Temporal variations in the prevalence of Eimeria *spp.*

The 4 species showed differing patterns of prevalence with 3 species being present over 27 months whilst *E.* sp. E was only seen during the spring of 1983. The 3 more common species were maintained in the woodland environment either as parasitic stages in *Apodemus* or as oocysts. Since *Eimeria* spp. are considered very host specific (Lindsay & Todd, 1993), it is unlikely that animals other than wood mice were involved directly in the ecology of the parasites. In laboratory experiments, Higgs (1995) failed to infect *A. sylvaticus* with viable *Eimeria* oocysts collected from bank voles *Clethrionomys glareolus*, the second most frequently trapped animal at New Covert. The appearance of *E.* sp. E. is somewhat enigmatic. It is unlikely that our technique failed to detect positive faecal samples for the first 22 months, especially as the oocysts are the largest of the four types (Nowell & Higgs, 1989). We therefore suggest that this species may have been introduced from another, geographically separate, population of hosts. From data for *E. hungaryensis* especially, there were trends in prevalences suggesting that environmental conditions may have changed over the 27 months, perhaps leading to an environment more suited to *E.* sp. E. Alternatively, as Lewis (1981) suggests, *E.* sp. E. may have been a contaminant from another host species perhaps through a food source, rather than a true infection, but it is not clear why a contaminant should have occurred for 4 consecutive months. However, to support Lewis's view, we were unable to transmit this parasite to laboratory-bred wood mice, unlike the other 3 species (Nowell & Higgs, 1989).

Prevalences of *E. hungaryensis* and *E. uptoni* showed no obvious seasonal cycle supported by autocorrelation. From first-capture data we would have expected *E. uptoni* to be more prevalent at times of year when there were more adults in the host population, but this was not supported by the monthly prevalence curve. *E. apionodes* did not show any association with weight (i.e. age) in first captured animals, but from autocorrelation and monthly data there was evidence of an annual cycle with higher prevalence in months when MNA index values were high and juveniles were present. We have no data to test directly any association with monthly levels of juveniles. However, the strong correlation of prevalence with the MNA index suggests that higher population densities may aid infection either through increased transmission or through enhancement of susceptibility/reduced immunocompetence (Behnke, 1990). There may also have been other coincident causative factors, e.g. seasonal changes of food (Watts, 1968) or of immune function (Nelson & Demas, 1996). Variations of the level of immunity may have directly influenced the numbers of oocysts passed by the animals and hence in turn the numbers of available infective oocysts in the environment. Correlation with relative humidity suggests that increased survival of oocysts occurs in damper conditions. This may not have applied equally to the other 2 species due to differences of oocyst resistance to desiccation.

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Table 4. Recorded prevalences of *Eimeria* in populations of *Apodemus sylvaticus*

Author(s)	Study site	Sample size	Prevalence (%)
Elton *et al.* (1931)	UK	380	38
Ring (1959)	UK	53	10
Musaev & Veisov (1963)	Azerbaijan (4 sites)	467	25
Mikeladze (1971)	Georgia	291	19
Glebedzin (1973)	Turkmenistan	444	13
Golemansky & Yankova (1973)	Bulgaria (2 sites)	99	25
Golemansky (1979)	Bulgaria (2 sites)	126	29
Ball & Lewis (1984)	UK (11 sites)	471	57
This study (1981–1983)	UK	180	73

In conclusion, we describe a colony of *Apodemus* parasitized by a guild of 4 species of *Eimeria*, 2 of which presented stable endemic infections probably with almost constant reinfection and no clear seasonal periodicity. The third species, *E. apionodes*, was less frequent in occurrence. However, this species did show some seasonal occurrence, being more prevalent at times of year when the wood mouse population was at its most dense and containing the highest proportion of juveniles and also when the relative humidity was highest. *E.* sp. E. may have been a contaminant or an introduction during the last months of the survey. We have attempted to relate the presence of parasites to a number of factors intrinsic and extrinsic to the host, but it is evident that more field and laboratory data are needed to elucidate the interactions between *A. sylvaticus* and its eimerian parasites.

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