Eimeria-parasites are associated with a lowered mother's and offspring's body condition in island and mainland populations of the bank vole

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SUMMARY

This study, based on correlative data, tests the hypothesis that infections with *Eimeria* spp. parasites exert a significant loss of fitness of bank voles (*Clethrionomys glareolus*) reflected in lower reproductive success and survival, declining host population densities and are associated positively with population size. The study was conducted in 20 mainland and 27 island populations in central Finland during May–September in 1999. Faecal samples showed that 28% of 767 individuals were infected with *Eimeria* spp. The presence of *Eimeria* parasites was higher in dense mainland populations than in sparsely populated islands. Eimerian infections increased during the course of the breeding season, probably as a result of the high infection rate of young individuals. Accordingly, the body masses of bank voles were negatively related to the presence of *Eimeria* spp. Reproductive output, as measured by the breeding probability of females and litter size, was not associated with the presence of eimerian infection. Interestingly, the body condition of the infected mothers appeared to be low. Moreover, mother's body condition was the single most important variable studied that showed a positive correlation to pup's body condition at birth. On small islands ($\leqslant$3·2 ha) that were comprehensively trapped, the mean number of *Eimeria* spp. in the bank vole population was negatively related to density changes of the bank vole population during the study. Our data are consistent with the idea that infection with coccidian parasites may be one of the factors responsible for declining host populations in small, isolated populations.

Key words: Protozoa, coccidia, *Eimeria* spp., host–parasite interactions, breeding success, survival, population density, bank vole, island and mainland populations.

INTRODUCTION

Parasites may inflict pathological and physiological disorders on the host resulting in impaired metabolic efficiency and absorbance of nutrients (e.g. Schall *et al*. 1982; Thompson, 1990; Chapman and George, 1991; Connors and Nickol, 1991). Because different defence mechanisms against parasites are costly, parasitic infections have been found to impair reproductive output, growth and self-maintenance of the host in various taxa (e.g. Schall, 1983; Goater *et al*. 1989; Keymer and Read, 1991; Toft, 1990). Mathematical models (Anderson and May, 1979; May and Anderson, 1979; Scott and Anderson, 1984; Scott, 1987) along with observational data (Cavanagh *et al*. 2004; Telfer *et al*. 2005) suggest that parasites and pathogens may have large-scale impacts at a population level. In accordance with this, several studies in vertebrates have documented negative associations between host survival and parasites in the wild (e.g. Boonstra *et al*. 1980; Ross *et al*. 1989; Gulland and Fox, 1992), but only a few studies have documented that parasites and their host densities may vary synchronously (e.g. Bertolino *et al*. 2003).

Coccidian parasites of the genus *Eimeria* are intestinal protozoans in the class of Coccidia. They may induce histopathological changes (Duszynski and Marquardt, 2003) and individuals generally lose body mass as a result of coccidiosis (e.g. Yun *et al*. 2000, but see Fuller and Blaustein, 1996). The infected animals may even perish (Newman *et al*. 2001), especially under adverse conditions arising in overcrowded populations of domestic and domesticated animals (Pellérdy, 1974; Catchpole *et al*. 1976; Soulsby, 1982; Tacconi *et al*. 1995). Similar results have also been found in wild animals. Some species of *Eimeria* are abundant and frequently documented in a number of rodent species (Levine and Ivens, 1990;

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Decker *et al*. 2001). They have been shown to diminish the over-winter survival of small rodents. For example, in deer mice the presence of *Eimeria* parasites was negatively related to the over-winter survival of males, as well as to the recruitment probability of females (Fuller and Blaustein, 1996). In addition, the impact of predation on voles suffering from coccidiosis was reported to be high (Vorisek *et al*. 1998). Eimerian infection may also affect the mate choice behaviour of females in terms of increasing the number of assessed males, probably in order to obtain complementary genes for the parasite resistance of offspring (Buchholz, 2004). Many studies have concentrated on the negative impacts of eimerians at the population level. Yet, there is a lack of studies performed at an individual level in free-living organisms, since most of the investigations on eimerian infections have been carried out in poultry and livestock (for a review, see e.g. Yun *et al*. 2000). To our knowledge, there exist no large-scale population studies to date exploring whether *Eimerian* infections influence the breeding success of free-living individuals. In particular, there is a lack of studies comparing mainland and island populations, since there is increasing evidence that predation, survival, reproductive output, competition, and body size of mammals may largely differ between the mainland and islands (for a review, see Palkovacs, 2003).

As model species for host-parasite interactions, we used the bank vole (*Clethrionomys glareolus*) and their coccidian parasites from the genus *Eimeria* originating from the mainland and island populations in central Finland. The bank vole is a common mammal in boreal coniferous forests of northern Europe (Stenseth, 1985). It inhabits all kinds of forested habitats and bushy fields, occupying even small and isolated islands surrounded by wide water bodies. *Eimeria* is a genera of an intestinal protozoan (coccidian), having an endogenous developmental life-cycle; they are transmitted directly, as a result of the ingestion of the contaminated faeces. The endogenous stages develop in epithelial cells of the intestinal tract in bank voles and heavy infections are referred to as coccidiosis (e.g. Lewis and Ball, 1982). Since these parasites repeatedly penetrate and burst out from the epithelial cells at different stages of their life-cycle, they have the potential to inflict severe harm to their host. Generally, symptoms including diarrhoea, dehydration and mass loss are associated with heavy infection (Yun *et al*. 2000). *Eimeria* spp. are currently known to infect bank vole populations in Finland (Laakkonen *et al*. 1998).

Our goals were to establish, whether the eimerian infection is associated with (i) breeding probability of mature females, (ii) post-partum body condition of mothers, (iii) litter size, (iv) body condition of offspring at birth, (v) survivorship, and (vi) population density.

MATERIALS AND METHODS

Study area

The study was carried out at the Konnevesi Research Station in central Finland (62°37′N, 26°20′E) in 1999. The study area consists of the islands in the Konnevesi-lake and of the surrounding mainland. The Konnevesi-lake contains a number of wooded islands varying in area. Among these, we selected 55 islands (range 0·12–70 ha), which were untouched by modern forest clear-felling and did not have permanent human habitation. The shortest neighbour-distance between study islands varied between 50 and 500 m and the mean distance from islands to the mainland was 631 m (S.D. = 553 m). Forests on islands and on the mainland are dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birches (*Betula* spp.), respectively. Bilberry (*Vaccinium myrtillus*) and red whortleberry (*V. vitis-idea*) dominate in the field layer. Eighteen out of 55 study islands were not inhabited by bank voles. In addition, only 1 individual bank vole (1 immature female and 9 males) was trapped on each of 10 islands. Therefore, the island data are based on individuals caught from 27 islands. Despite intensive live trappings, we did not observe any individuals dispersing between islands during the study. In the mainland, 20 independent quadrat areas were selected as controls. The non-overlapping areas were sufficiently far apart (mean 832 m, S.D. = 578 m, range 300–2000 m) as to prevent dispersal between different mainland populations.

Vole trappings

We used Ugglan multiple-capture live traps baited with potatoes and sunflower seeds. On the small islands ($\leqslant 3{\cdot}2$ ha, $N = 14$), trap lines were set on approximately 20 m intervals (25 traps/ha). On the large islands ($>3{\cdot}2$ ha, $N = 13$) and in the mainland areas ($N = 20$), individual voles were trapped by using the small-quadrat sampling method modified from Myllymäki *et al*. (1971); each quadrat (one side 15 m) contained 4 traps with only 1 live trap at each site (4 traps/area). There were 6 randomly placed quadrats on every larger island whereas on the mainland one quadrat per area was used. Pre-baited traps were initially left open for over 2 nights, after which they were set and checked over 3 consecutive days. This trapping method has proved effective in catching all bank vole individuals of a trappable age (Mappes and Koskela, unpublished data). Therefore, we assume that almost all bank voles were captured on small islands. Trappings started in early May and lasted until the end of the breeding season in September. Island populations were monitored in random order in respect to their location, size and vegetation characteristics. Each island was live-trapped once during the breeding season (May–August) and again

after the breeding season just before winter (late October). On the mainland, trappings were carried out 3 times during the breeding season: first of all in late May, secondly in late June and thirdly in late August. Density changes (ind/ha), breeding probabilities and survival of bank voles were studied only on the small islands which were trapped more efficiently compared to the large ones and mainland areas in which the small-quadrat sampling method was used as an estimate of vole densities (i.e. the number of voles caught per 100 trap nights). Voles were marked using toe clip-codes.

Laboratory methods

All voles trapped were brought to the laboratory where they were housed in standard mouse cages; $425 \times 266 \times 155$ mm with wooden shavings and hay as bedding. The colony was maintained under 18L : 6D photo-period and food (laboratory rodent food Labfor R36) and water were available *ad libitum*. Each individual was sexed and then weighed to the nearest 0·1 g using a Pesola-spring balance. The width of the head was measured to the nearest 0·1 mm using a digital spessimeter. After the measurements, males and non-pregnant females were immediately returned and released at the point of their original capture, whereas pregnant females ($n = 84$) were kept in the laboratory until they gave birth. Mature individuals breed from late April to September (Koivula *et al*. 2003). Pregnancy lasts for 19–20 days and pups (litter size of 2–10) are weaned until the age of 3 weeks (Mappes *et al*. 1995; Mappes and Koskela, 2004). Reproducing females are strongly territorial whereas home ranges of males and immature individuals may widely overlap (Bodrup-Nielsen and Karlsson, 1985; Jonsson *et al*. 2002). The pups were marked right after birth by using toe clip-codes and then weighed to the nearest 0·01 g using an electronic balance. We also measured the width of the head using a stereomicroscope, and sexed the individuals according to the length of the anogenital distance and other visual cues. Mothers with their pups were transported to the islands and released from the breeding cages at the very point of their capture. The cages were left open enabling mothers to carry the pups back to their nests in the field (see Mappes *et al*. 1995).

Faecal samples

Immediately after capture and transfer of voles to the laboratory, we collected faecal samples in order to quantify parasite infection by placing the animals in small plastic containers for 30 min between 12.00 and 17.00 p.m. The faecal samples from different island and mainland populations were collected in random order. The faeces (0·01–0·04 g) were stored in 2·5% aqueous potassium dichromate ($K_2Cr_2O_7$) in order to make 1 ml of suspension. The suspension was centrifuged for 3 min at 284.2 ***g*** and the pellet was re-suspended in a saturated magnesium-sulphate ($MgSO_4$) flotation solution. The intensity of the parasite infection was estimated by counting the number of oocysts in a McMaster counting chamber and the count was transformed into the number of *Eimeria* spp. oocysts per gram of the original sample (Laakkonen *et al*. 1998). Due to the lack of resources we did not incubate oocysts, as a result *Eimeria* species could not be identified.

Statistical analyses

Density estimates were compared only between large islands (>3·2 ha) and mainland areas since the small-quadrat sampling method was used there. Density differences were tested using T-test.

The model structures of 3 logistic regression analyses for the following dependent variables: (1) the presence of *Eimeria* spp. at individuals (non-infected = 0, infected = 1), (2) the breeding probability of mature females (non-breeding = 0, breeding = 1; only females weighing greater than 16·1 g were included in the analysis because that was the lowest figure of body mass observed among breeding females) and (3) the survival of individuals from summer till late autumn (disappeared = 0, re-captured = 1) are shown in Tables 1 and 3.

The model structures of 4 mixed model ANOVAs for following dependent variables: (1) mother's standardized body mass (irrespective of head width), (2) the offspring's standardized body mass (irrespective of mean head width), (3) offspring head width and (4) litter size are shown in Table 2.

In addition, we conducted a linear model with normal error using GENMOD procedure. This action was taken to investigate the population level relationship between the intensity of *Eimeria* spp. infection (independent variable) and change in the population density of bank voles from May to September (dependent variable) using the bank vole density as a covariate. This test included only small islands ($\leqslant$3·2 ha, $n = 14$) where the density estimations of populations were based on capturing almost all individual bank voles. Note, in this analysis we used the population mean for the number of *Eimeria* spp. oocysts/per gram of faeces instead of the presence, since the voles on only one of the small islands were non-infected.

In all analyses the data comprised one measurement per a vole. As individuals dwelling in the same population might not be independent of each other, the class variable 'population' (20 mainland and 27 island populations) was nested within 'origin' (mainland or island) and used as a random factor in all of the 4 mixed-model ANOVAs. In the logistic regression models (Tables 1 and 2) population nested within origin was used as a repeated subject. That is,

Table 1. The logistic regression-based likelihoods of the presence of *Eimeria* spp. in (A) all bank voles captured with time of capture (julian date), residual body mass on time of capture and sex as independent variables and (B) mature bank vole female's breeding probability (0 *vs* 1) with the presence of *Eimeria* spp. (0 *vs* 1), body size (head width mm), body mass (standardized with head width), time of capture (julian date) as independent variables

(In both logistic regressions population was nested within origin (island or mainland) and used as a repeated subject that is, the observations in a single cluster are uniquely identified by the variables population (nested within origin) and origin. Predicted probabilities and 95% confidence limits were calculated for the class variables sex and *Eimeria* spp. presence by back-transforming the logits using the formula $e^z/1+e^z$, where 'e' is the Neper's number and 'z' is the estimate for lsmeans or lower or upper 95% confidence limit. The data comprised 1 measurement per vole.)

(A) GENMOD procedure (logit link function, binomial distribution). Dependent variable: presence of *Eimeria* spp. $N=766$ individuals

Parameter	Back-transformed predicted probability for *Eimeria* spp. lsmeans/lower/upper 95% confidence limits	D.F	Estimate ± S.E.	X^2	*P*
Intercept		1	−1·95 ± 0·24	66·93	< 0·0001
Sex: female	0·26/0·21/0·31	1	−0·05 ± 0·17	0·08	0·7768
male	0·27/0·22/0·32	0	0	.	.
Residual body mass		1	−0·35 ± 0·09	13·32	0·0003
Time of capture		1	0·01 ± 0·003	9·50	0·0021

(B) GENMOD procedure (logit link function, binomial distribution). Dependent variable: breeding probability of mature bank vole females. $N=200$ mature females

Parameter	Back-transformed predicted probability for breeding lsmeans/lower/upper 95% confidence limits	D.F	Estimate ± S.E.	X^2	*P*
Intercept		1	−51·89 ± 13·82	14·09	0·0002
Eimeria spp. (0)	0·23/0·15/0·35	1	−0·49 ± 0·49	1·42	0·2341
(1)	0·32/0·17/0·54	0	0	.	.
Head width			2·56 ± 0·88	5·73	0·0167
Stand. body mass		1	0·97 ± 0·24	9·94	0·0016
Time of capture		1	−0·05 ± 0·008	17·94	< 0·0001

the observations in a single cluster are uniquely identified by population and population within origin. Responses from different subjects are assumed to be statistically independent, and responses within subjects are assumed to be correlated. In the third logistic regression model (Table 3) population was used as a repeated subject. In all of the logistic regressions the scaled deviances were near 1 (0·85–1·27) indicating that the models fit the data reasonable well. Least squares means were computed for classification variables both in mixed model ANOVAs and logistic regressions, the logit estimates of which were back-transformed using the formula $e^z/1+e^z$, where 'e' is the Neper's number and 'z' is the estimate for the lsmean or its lower or upper 95% confidence limit. All of the mixed model ANOVAs as well as other analyses were fitted by the GENMOD procedure; one linear model with normal errors and logistic regression models (binomial distribution, logit link function) were conducted with SAS 9.1.

RESULTS

Eimeria *spp. infection and breeding success*

During the breeding season the mean overall density estimate of bank vole populations in the mainland was more than two-fold compared to that of large islands (mean ± S.E. = 70 ± 6·8 *vs* 31·7 ± 6·5 ind./100 trap nights; T-test, $t_{42\cdot19}=-4\cdot09$, $P<0\cdot001$). Of all individuals ($n=767$) 28% were infected by *Eimeria* spp.; mainland populations with a higher rate (33%) than those on islands (25%: logistic regression $N=767$ individuals, $X^2=5\cdot54$, D.F. = 1, $P=0\cdot0186$). The presence of *Eimeria* spp. increased over the course of the breeding season (Table 1A). Within-season increase in the presence of *Eimeria* spp. was

Table 2. Results of the four mixed model ANOVAs for (A) mother's post-partum body mass (standardized with head width), (B) offspring's mean body mass (standardized with offspring mean head width), (C) offspring's mean head width and (D) litter size

(Population nested within origin (mainland or island) was used as a random factor in all of the analyses. Least squares means with 95% confidence limits are presented for the class variable. Numerator and denominator degrees of freedom are given as subscripts to test values, respectively. The data comprised 1 measurement per vole.)

(A) Dependent variable: mother's standardized body mass (g). $N=71$ breeding females

Parameter	Lsmeans (g)/ lower/upper 95% CL	Estimate ± S.E.	$Test_{DFs}$	P
Intercept		22·26 ± 0·55	($t_{1,37}$) 40·69	<0·0001
Eimeria spp. (0)	23·35/23·05/23·65	0·69 ± 0·25	($F_{1,30}$) 7·97	0·0084
(1)	22·66/22·16/23·16	0	.	.
Litter size		0·04 ± 0·07	($F_{1,30}$) 0·28	0·5977
Time of capture		0·004 ± 0·006	($F_{1,30}$) 0·63	0·4341

(B) Dependent variable: offspring's standardized mean body mass (g). $N=71$ litters

Parameter	Lsmeans (g)/ lower/upper 95% CL	Estimate ± S.E.	$Test_{DFs}$	P
Intercept		−13·20 ± 4·17	($t_{1,37}$) −3·17	0·0031
Eimeria spp. (0)	1·98/1·74/2·21	0·50 ± 0·26	($F_{1,29}$) 3·55	0·0695
(1)	1·48/1·00/1·96	0	.	.
Litter size		−0·18 ± 0·07	($F_{1,29}$) 7·41	0·0109
Stand. mother mass		0·31 ± 0·11	($F_{1,29}$) 8·68	0·0063
Head width of mother		0·63 ± 0·25	($F_{1,29}$) 6·37	0·0173

(C) Dependent variable: offspring's mean head width. $N=71$ litters

Parameter	Lsmeans/lower/ upper 95% CL	Estimate ± S.E.	$Test_{DFs}$	P
Intercept		49·43 ± 14·32	($t_{1,37}$) 3·45	0·0014
Eimeria spp. (0)	51·63/50·70/52·56	0·23 ± 0·81	($F_{1,29}$) 0·08	0·7769
(1)	51·40/49·77/53·02	0	.	.
Litter size		−0·79 ± 0·21	($F_{1,29}$) 13·68	0·0009
Stand. mother mass		0·32 ± 0·37	($F_{1,29}$) 0·72	0·4030
Head width of mother		−0·10 ± 0·85	($F_{1,29}$) 0·01	0·9035

(D) Dependent variable: litter size (range 1–7). $N=71$ litters

Parameter	Lsmeans (litter size)/ lower/upper 95% CL	Estimate ± S.E.	$Test_{DFs}$	P
Intercept		−3·86 ± 7·60	($t_{1,37}$) −0·51	0·6144
Eimeria spp. (0)	5·08/4·66/5·49	−0·18 ± 0·48	($F_{1,29}$) 0·14	0·7122
(1)	5·26/4·38/6·14	0	.	.
Stand. mother mass		0·08 ± 0·19	($F_{1,29}$) 0·16	0·6887
Head width of mother		0·61 ± 0·45	($F_{1,29}$) 1·83	0·1866
Time of capture		−0·02 ± 0·01	($F_{1,29}$) 4·89.	0·0351

parallel between the mainland and island populations (interaction term: origin * time, $P=0·2539$). The residual body masses of all individuals (the residuals of a regression of body mass on time) were negatively related to the presence of *Eimeria* spp. both on mainland and islands (Table 1A; time * residual body mass, $P=0·0946$). Further, the presence of eimerians did not differ between sexes (Table 1A).

Table 3. The logistic regression-based likelihoods of bank vole survival (0 *vs* 1) from summer to autumn on 14 small islands (< 3·2 ha) with the presence of *Eimeria* spp. (0 *vs* 1), body size (head width mm), body condition (irrespective of head width), time of capture (julian date) as independent variables

(Population was used as a repeated subject that is, the observations in a single cluster are uniquely identified by the variables population (nested within origin) and origin. Predicted probabilities and 95% confidence limits for survival were calculated for the class variable *Eimeria* spp. presence by back-transforming the logits using the formula $e^z/1+e^z$ where 'e' is the Neper's number and 'z' is the estimate for lsmean or lower or upper 95% confidence limit. The data comprised 1 measurement per vole.)

GENMOD procedure (logit link function, binomial distribution). Dependent variable: survival from summer to autumn. $N=285$ individuals

Parameter	Back-transformed predicted probability for survival lsmeans/lower/upper 95% CL	D.F	Estimate ± S.E.	X^2	P
Intercept		1	−3·93 ± 2·51	2·46	0·1166
Eimeria spp. (0)	0·33/0·22/0·45	1	0·05 ± 0·29	0·05	0·8248
(1)	0·32/0·20/0·47	0	0	.	.
Head width			0·21 ± 0·20	0·51	0·4734
Residual body mass		1	−0·17 ± 0·15	1·39	0·2387
Time of capture		1	0·01 ± 0·004	0·62	0·4307

In mature females, breeding probabilities decreased over time in both mainland and island populations (origin * time, $P=0·5790$) and were not related to the presence of *Eimeria* spp. (Table 1B). In contrast, a large head width and good body condition (irrespective of body size) were associated with elevated breeding probability (Table 1B). The effect of body condition was the same in mainland and island populations (origin * body condition, $P=0·0848$), but the head width was not associated with the breeding probability in island populations as indicated by the significant interaction term (origin * head, $P=0·0399$).

In breeding females, *Eimeria* spp.-infected individuals had lower post-partum body masses (irrespective of body size) as compared to that of non-infected ones both on the mainland and on islands (origin * presence of *Eimeria* spp., $P=0·9465$), whereas neither litter size nor the time of capture had any effect on the female's body condition (Table 2A). Interestingly, the mother's post-partum body condition (irrespective of size) and body size (head width) were positively and litter size negatively associated with the brood's mean body condition (irrespective of size; Table 2B). While controlling for the former variation, *Eimeria* spp.-infected mothers appeared to produce offspring characterized by lower mean body condition as compared to those of non-infected ones, but the result was marginally non-significant (Table 2B). These effects were parallel between mainland and island areas ($P>0·2164$ in all of the interactions). Likewise, the mean body size of offspring (head width) appeared to be smaller in large litters than small ones (Table 2C) both in mainland and island populations (origin * litter size, $P=0·4622$), whilst other explanatory variables were not related to body size (Table 2C). Further, litter size decreased over the course of the breeding season in both mainland and island populations (time * origin, $P=0·4510$), yet neither the presence of *Eimeria* spp. nor the mother's condition nor body size (head width) had any effect on the number of offspring produced (Table 2D).

Associations between infections, survival and population densities

On intensively trapped small islands (⩽3·2 ha), neither the presence of eimerian parasites nor body size (head width), body condition (irrespective of head width) and time of capture were associated with the survival of individuals from summer to late autumn (October; Table 3). However, the population mean of *Eimeria* spp. was related to the decline of bank vole populations dwelling on small islands (Fig. 1; GENMOD using normal distribution, $n=14$ islands, $X^2=7·37$, D.F. = 1, $P=0·0066$), when the density of bank voles was used as a covariate ($y=14·01-0·61x$: $X^2=20·32$, D.F. = 1, $P<0·0001$).

DISCUSSION

Eimeria-infections were more common in dense mainland populations than in sparsely populated islands. Moreover, the presence of infections increased from early May to August along with the rapidly increasing population density. This lends support to the idea that elevated parasite prevalences may arise in high density host populations. In addition, the restricted dispersal ability may also decrease contagiousness to parasites among individuals dwelling in isolated island populations.

One of our main findings was that mothers infected by *Eimeria* spp. appeared to experience a lower

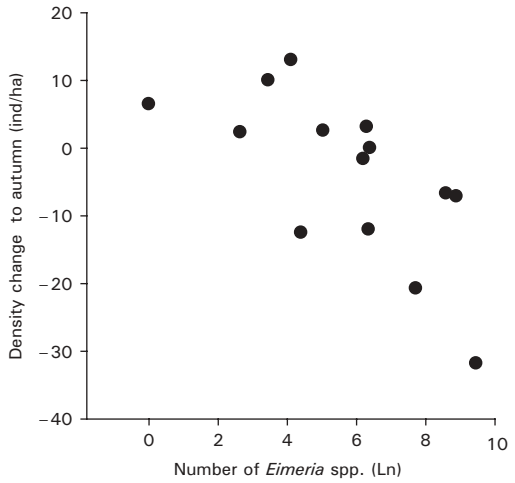

Fig. 1. The ln-transformed population mean of *Eimeria* spp. in relation to the changes in population densities of bank voles (ind/ha) on small islands ($n=14$ islands: $y=14{\cdot}01\ -1{\cdot}57x$).

post-partum body condition as compared to those of non-infected ones. Concomitantly, mothers with a good body condition produced pups characterized by a good body condition at birth. This result lends support to the idea that *Eimeria* spp. infection may impair offspring quality through the mother's condition. In the bank vole this may have serious fitness consequences, since a large body mass at birth may increase the offspring's future breeding success (Mappes and Koskela, 2004). A high energy expenditure during lactation and pregnancy in turn may expose females to adverse effects of parasites, decreasing the extent of such resources, which otherwise could be allocated to enhance the body condition of mothers and of offspring. Parasite-related mass reductions have been demonstrated, for example in adult rock doves (*Columba livia*: Booth *et al*. 1993) and snowshoe hares (*Lepus americanus*: Keith *et al*. 1986) but, as far as we know, an association between body condition at birth and mother's parasite infections has not been tested or discovered in wild mammals to date. Because the presence of *Eimeria*–parasites did not correlate with litter size or probability of reproduction, only qualitative effects of eimerians in terms of a lowered body condition of mothers and of offspring at birth were found.

The proportion of young individuals in the population increases towards the end of the breeding season. In wild populations of small rodents young individuals are suggested to have a poorer immunity against pathogens than old animals (Ball and Lewis, 1984; Stanton *et al*. 1992). Accordingly, the body mass of bank voles, which increases with age, was negatively related to the presence of eimerians. This association may also be due to acquired immunity, because older individuals are likely to have been exposed to more infections during their lives compared to that of young ones and hence more likely to express the stronger acquired immunity. In support of our results, the prevalence of *Eimeria apionodes* in the wood mice (*Apodemus sylvaticus*) varies in an annual cycle; lowest in January–May, a peak in October–November, correlating positively with both the number of animals and percentage of juveniles in the host population (Higgs and Nowell, 2000). In the badger (*Meles meles*), red squirrel (*Sciurus vulgaris*) and wild rabbits (*Oryctolagus cuniculus*) eimerians also occurred more frequently in young individuals than older ones (Newman *et al*. 2001; Bertolino *et al*. 2003; Gres *et al*. 2003). In the red squirrel infections were likewise related to host density (Bertolino *et al*. 2003).

The population density of bank voles is strongly restricted by social interactions and by the territoriality of reproducing females (Bujalska, 1970; Kruczek and Marchlewska-Koj, 1986). Hence, contagious diseases could reduce survival rates of individuals and hence population density, especially when individuals have to compete with conspecifics for limited space or other resources increasing social interactions in the population. Then more contact is made, which increases the risk of transmission. Accordingly, on our small islands ($\leqslant 3{\cdot}2$ ha), a decline in the bank vole population was associated with an increase in the abundance of *Eimeria* infections in the population. This finding is consistent with the idea that infection with coccidian parasites may be one of the factors responsible for declining host populations in small, isolated populations. Equally it could also be a secondary consequence of other population density driven changes in hosts, such as concurrent infection with other organisms and/or weakened intestinal immunity (e.g. Smith and Hayday, 2000).

Survival estimates based on capture-recapture data at an individual level were not related to eimerian infection. This result may, however, be flawed, because young and infected individuals might decease at a very early stage of their life. As a result, such individuals would not have been captured in this study, which may bias the results between the parasitic infection and survival rate. This suggests that in order to find any effects of parasitic infections on population dynamics, different life-history traits should be investigated also at a very early stage of life.

In accordance with our study, Fuller and Blaustein (1996) showed that experimentally induced eimerian infection hampered the over-winter survival of male deer mice (*Peromyscus maniculatus*) and hence had the potential to decrease population density in small field enclosure populations. In contrast, Laakkonen *et al*. (1998) concluded that eimerians do not contribute to the observed drastic declines of vole populations. In wild European rabbits (*Oryctolagus cuniculus*) in Australia, parasitism by *Eimeria* spp. did not appear to be an important mortality factor, or

to be responsible for the observed pattern of density-dependent regulation in this species (Hobbs *et al*. 1999). Impacts of eimerian infections on the population dynamics of host species may thus vary largely even among closely related and sympatric host species (e.g. Laakkonen *et al*. 1998). Hence, at this stage, the scant published data on survival and population effects appear to be inconclusive, but our data, whilst correlative in nature, are nevertheless highly suggestive that there are important underlying effects of Eimeria on host fitness. More extensive field studies in the future, building on the design and the results of the current study, to fine-tune temporal and spatial sampling, should resolve conclusively whether rodent coccidian do indeed promote declining host population densities.

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