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FACTORS INFLUENCING THE FECAL EGG AND OOCYST COUNTS OF PARASITES OF WILD EUROPEAN RABBITS *ORYCTOLAGUS CUNICULUS* (L.) IN SOUTHERN WESTERN AUSTRALIA

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ABSTRACT: Abundance of intestinal parasites was monitored by fecal egg and oocyst counts for samples of wild rabbits *Oryctolagus cuniculus* with different levels of imposed female sterility from 12 populations in southwestern Australia. Differences in egg counts of *Trichostrongylus retortaeformis* between seasons and age groups were dependent on the sex of the host. Pregnancy may have been responsible for these differences because egg counts were consistently higher in intact females than in females surgically sterilized by tubal ligation. Egg counts for *Passalurus ambiguus* were influenced by season and host age but there were no differences between sexes or between intact and sterilized female rabbits. No differences were detected in the oocyst counts of the 8 species of *Eimeria* between male and female rabbits or between intact and sterilized females. Seasonal differences were detected in oocyst counts of *Eimeria flavescens* and *Eimeria stiedai.* The overwhelming determinant of coccidian oocyst counts was host age, with 6 species being much more abundant in rabbits up to 4 mo of age. There was a suggestion that egg counts of *T. retortaeformis* and oocyst counts of several species of *Eimeria* were reduced in populations where rabbit numbers had been depressed for at least 2 yr, but there was no evidence that short-term variations in rabbit numbers had a measurable effect on parasite abundance.

Nematode and coccidian parasitism of wild European rabbits (*Oryctolagus cuniculus* (L.)) is influenced by host age and sex. In Australia, the influence of age is particularly important for species of *Eimeria* (Mykytowycz, 1962). Host age, sex and reproductive status all affect parasitism with *Trichostrongylus retortaeformis,* and pregnancy is a risk factor (Dunsmore and Dudzinski, 1968). A field study set up to determine the effects of imposing 4 levels of female sterility (0%, 40%, 60%, 80%) on rabbit populations in southwestern Australia (Twigg et al., 1998) provided an opportunity to investigate further the effects of host age and sex, pregnancy, and season on parasitism by coccidia and nematodes. The 12 discrete free-ranging populations varied considerably in rabbit numbers particularly because some of the higher sterility regimes were successful in reducing population size (Hobbs et al., 1999). This variation enabled us to investigate the relationship between host population size and parasite abundance. Although there has been a great deal of attention given to theoretical aspects of the population dynamics of infectious disease since the introduction of the mathematical models of Anderson and May (1979), there have been calls for more empirical studies on the dynamics of these diseases, particularly with respect to the density-dependent relationships between host and parasite (e.g., Dobson and Hudson, 1995; McCallum, 1995).

MATERIALS AND METHODS

The rabbit sterility trials were located in the wheat belt region of southwestern Western Australia near Wellstead (34°30′S 118°36′E). Climate is Mediterranean, with long dry summers during which time there is little breeding by rabbits. The annual average rainfall is 500 mm, concentrated in the cooler months of May to November, although some summer rainfall is normal (Twigg et al., 1998). Twelve discrete populations of rabbits were established to determine the level of female sterility that is required to cause a sustained reduction in rabbit abundance. All sites were situated on the border of narrow strips of native vegetation refuges and annual pastures. Each site was fenced in a flattened U shape such that breeding stops were confined to a strip of native vegetation 320–420 m × 60–100 m, while allowing access to adjacent pasture on the open side for food. Female rabbits were surgically sterilized by tubal ligation in the proportion of 0%, 40%, 60%, and 80%, with 3 replicates of each treatment. Sham operations were included such that 80% of females received some form of surgery.

Live-capture cage traps were set overnight (Twigg et al., 1996). Fresh fecal samples were collected from the ground under occupied traps the next morning and split into 2 subsamples: one placed in 10% formalin and the other in 2.5% potassium dichromate. Samples were not chosen randomly as they were dependent on defecation by trapped rabbits. Where possible, we collected samples from 10 kittens and subadults (<1,200 g body mass) and 10 adults at each of 6 sampling periods for each rabbit population. A total of 1,297 samples was collected, from October 1994 to March 1996, with the most intensive sampling during late winter and spring of 1995. For 1,077 of these samples, the birth date of each rabbit could be back-calculated from the body mass at time of first capture, provided that the body mass was <1,000 g at that time. The calculation was based on a birth mass of 50 g and a growth rate of 10 g per day (Twigg et al., 1998). For season and sex comparisons, age categories were based on body mass of rabbits at the time of sampling; kittens (<700 g), subadults (700–1,199 g), and adults (>1,199 g), whereas for host abundance comparisons, young rabbits were those <1,000 g.

We counted nematode eggs by a flotation technique. An aliquot of 14 ml of water was added to approximately 1 ml of formalin-fixed feces in a graduated centrifuge tube that was spun for 30 sec at 500 *g*. We determined the volume of the fecal plug to the nearest 0.1 ml. The plug was washed thoroughly with water through a 0.8-mm mesh sieve, then centrifuged at 500 *g* for 2 min. The supernatant was discarded and the plug resuspended in sufficient saturated $NaNO_3$ to form a positive meniscus. A coverslip edged with Vaseline was placed over the top of the centrifuge tube and left to stand for 15 min, and then carefully removed and placed on a microscope slide. The entire coverslip was scanned at 100× magnification, and all eggs were counted. We recorded the number of eggs per ml of feces as eggs per g (epg) for simplicity. Coccidian oocysts were counted on a single pass through the middle of the coverslip at 400× magnification. If there were <50 oocysts counted on that pass, a second pass was made close to the first. As the coverslip was 40 field-widths wide at that magnification, the number of oocysts per ml feces was estimated as: number of oocysts/ml = (40 × number counted)/[number of passes × volume of feces (ml)]. The number of oocysts/ml was recorded as oocysts/g. Repeatability of the oocyst counting technique was established by variance components according to the method of Yvore et al. (1992). We ran 10 scans on each of 2 coverslip preparations of 6 fecal samples and determined that repeatability was 0.95 for scans of the same coverslip preparation and 0.92 for preparations of the same sample. Strongyle eggs were differentiated by their

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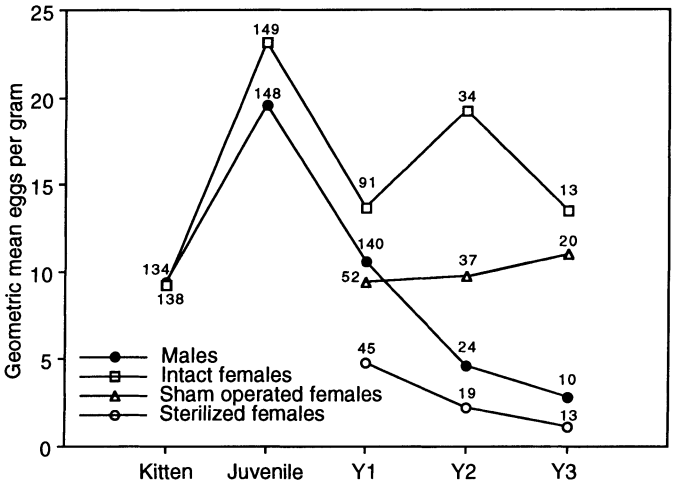

FIGURE 1. Geometric means of egg counts of *Trichostrongylus retortaeformis* in males, intact females, sham-operated females, and sterilized females. Age groups are kittens (up to 66 days), juveniles (67–114 days), Y1 (115–364 days), Y2 (365–729 days), and Y3 (730 or more days old). Sterilizations were undertaken (January–March) after rabbit recruitment had occurred each year. Sample sizes are shown above each point

length. Eggs of *Graphidium strigosum* are larger than those of *T. retortaeformis* (Bull, 1953). The other parasite eggs present in the fecal samples were easily identified as the oxyurid nematode *Passalurus ambiguus,* which occurs in the large intestine and cecum. We used the potassium dichromate subsamples to separate the species of *Eimeria* by identifying 50 sporulated oocysts for each positive sample (Hobbs and Twigg, 1998). For some samples with very low counts (10% of the total), we were unable to find 50 oocysts, and species differentiation was based on fewer oocysts. The effects of sex, sterility status, season (collecting period), and age on parasite egg and oocyst counts were determined by Mann–Whitney or Kruskal–Wallis nonparametric tests using Statview 4.0 (Abacus Concepts, Berkeley, California). The effect of host abundance on parasite egg and oocyst counts was tested by linear regression analysis of the geometric means (i.e., back-calculated means of log-transformed data) of parasite egg counts and the minimum number of rabbits known to be alive (MNKA) approximately 1 mo prior to fecal collection for those collection groups where there were at least 10 fecal samples. Each of 2 age groups based on body mass at time of capture were tested separately. Mann–Whitney tests were used to compare egg and oocyst count of the 3 lowest-density rabbit populations with those of the other 9 populations and also the 3 highest-density populations with the other 9.

RESULTS

Only 2 species of nematode parasite, *T. retortaeformis* and *P. ambiguus,* were detected in our rabbits. Postmortem examination of the intestines of 14 rabbits at the end of the sterility study confirmed the presence of these species. Oocysts of 10 species of *Eimeria* were detected, and their prevalences have been reported in Hobbs and Twigg (1998), but only the 8 most prevalent of these species are discussed here.

Log–log scatter plots of *T. retortaeformis* egg counts against host age indicated that there was no obvious decline in parasitism with age (data not shown). However, almost all the rabbits older than 1 yr with high counts of *T. retortaeformis* were intact or sham-operated females. Thus, the data were split by sex and sterility status for further analysis. Figure 1 shows geometric means for those rabbits for which the date of birth was known. The highest counts were in juveniles, and there was a decline in counts as rabbits became adult. There were further declines in subsequent year classes in male rabbits and sterilized females but not in intact or sham-operated females. Counts in juveniles were significantly higher than in kittens or adults (Table I). Among adults during breeding periods, counts were significantly higher in intact female rabbits than in males and lower in sterilized females than sham-operated females (Table I). Egg counts of *T. retortaeformis* were significantly higher during breeding periods than during nonbreeding periods for intact and sham-operated females (Table II). However there was no such difference for sterilized females, and the difference for males was very small (Table II).

There were no differences between sexes for any of the age groups for counts of *P. ambiguus* during breeding periods (Table I). Egg counts were significantly higher in adult rabbits, but prevalence was too low to test for the presence of a decline in rabbits older than 1 yr old. There was no difference in counts between intact and sterilized female rabbits (Table I). Egg counts were higher during nonbreeding periods in adult rabbits (Table III).

For the coccidia, there were highly significant differences in oocyst counts recorded from rabbits of different ages for all 8 species but no differences between sexes for any age group (Table I). Geometric mean oocyst counts and prevalences for those rabbits of known age are given in Figures 2 and 3, respectively. For all coccidian species except *Eimeria piriformis* and *Eimeria flavescens,* the highest oocyst counts were from either kitten or juvenile rabbits. Oocyst counts were higher in adult rabbits for both *E. piriformis* and *E. flavescens.*

There were seasonal differences in abundance in only 2 species of *Eimeria.* Breeding period oocyst counts were higher in *Eimeria stiedai,* whereas nonbreeding period counts were higher in *E. flavescens* (Table III).

Details of linear regressions of geometric mean egg and oocyst counts against host population size (MNKA) measured approximately 1 mo prior to fecal collection are shown in Table IV. We expected positive slopes, but none were significant at $P \leq 0.01$. Similar results were obtained using other measures of rabbit population size, and when populations were measured at the time of fecal collection or 4 mo prior. Only 2 regressions approached significance, including that of *T. retortaeformis* in young rabbits, but it was apparent from the scatterplot (Fig. 4) that variation was high. Figure 5 shows the scatterplot for *Eimeria magna* where a positive slope approached significance for adult rabbits. However, a single outlier point at high rabbit population size was responsible for the effect, and although that oocyst count was high for adult rabbits, it was lower than most means for younger rabbits. Thus, our regression analyses show that the abundance of rabbits had little effect on parasite egg and oocyst counts at the rabbit densities we encountered. However, prevalences of all species were generally quite high so it is likely that all our rabbit densities were high enough to ensure adequate transmission. We therefore compared egg and oocyst counts for the 3 sites with lowest rabbit densities to those of the other sites (Table V). The 3 low-density sites included 2 from the 80% sterility group and 1 from the 60% group, and although there were strong fluctuations in population size, these populations were consistently in the lowest third except for a single collecting period when 1 population was measured as fifth highest. There were no significant differences in parasitism

TABLE I. Sample sizes, geometric means, and statistical significance for effects of host age* and sex on fecal egg and oocyst counts during the breeding season.

	Kittens			Juveniles			Adults						
	Males	Females	*P* (sex)†	Males	Females	*P* (sex)†	Males	Intact females	*P* (sex)†	Sham-operated females	Sterilized females	*P* (sterility)‡	*P* (age)§
Sample sizes (nematodes)	122	126		143	159		147	123		82	37		
Trichostrongylus retortaeformis	9.04	8.94	0.968	22.78	21.58	0.147	9.09	20.81	<0.0001	15.96	2.45	<0.0001	<0.0001¶
Passalurus ambiguus	0.00	0.01	0.916	0.26	0.12	0.490	0.39	0.85	0.086	0.67	0.21	0.361	<0.0001
Sample sizes (coccidia)‖	113	113		128	128		129	109		78	36		
Eimeria exigua	5.03	7.43	0.369	19.90	24.46	0.368	9.54	7.42	0.342	2.88	2.61	0.956	<0.0001
E. perforans	297.07	527.46	0.095	281.19	279.50	0.452	31.41	36.21	0.534	9.13	11.58	0.596	<0.0001
E. intestinalis	14.67	11.29	0.615	2.17	2.72	0.600	0.22	0.24	0.962	0.16	0.00	0.661	<0.0001
E. piriformis	2.16	1.26	0.248	3.66	4.39	0.575	5.53	7.06	0.322	5.38	7.28	0.407	<0.0001
E. media	47.82	34.17	0.514	6.88	10.98	0.167	2.21	1.60	0.310	0.85	0.54	0.526	<0.0001
E. flavescens	11.64	6.25	0.145	11.14	19.80	0.084	5.90	7.29	0.446	2.79	3.90	0.380	0.008
E. magna	59.93	49.47	0.723	5.12	5.47	0.837	0.65	0.53	0.767	0.15	0.25	0.468	<0.0001
E. stiedai	8.65	6.60	0.593	10.46	8.25	0.546	0.91	1.12	0.829	0.50	0.34	0.966	<0.0001

* Age groups are based on body mass at time of capture: kittens (<700 g), juveniles (700–1,199 g), adults (>1,199 g).
† Significance (Mann–Whitney) between males and intact females within age group.
‡ Significance (Mann–Whitney) between sham-operated and sterilized adult females.
§ Significance (Kruskal-Wallis) between age groups (sexes combined). For adults, only males and intact females are included.
‖ Sample sizes are smaller for coccidia because many samples did not sporulate so that species could not be differentiated.
¶ Also tested separately within sex: males ($P < 0.0001$), intact females ($P < 0.0001$).

TABLE II. Geometric means (and sample sizes) of *Trichostrongylus retortaeformis* egg counts (epg) in adult rabbits.

	Breeding period*	Non-breeding period†	Significance Mann–Whitney (*P*)
Males	9.09 (147)	6.46 (155)	0.035
Intact females	20.81 (123)	5.24 (42)	<0.0001
Significance Mann–Whitney (sex) (*P*)	<0.0001	0.5787	
Sham-operated females	15.96 (82)	4.75 (55)	<0.0001
Sterilized females	2.45 (37)	3.13 (82)	0.364
Significance Mann–Whitney (sterilization) (*P*)	<0.0001	0.1555	

* Samples include October–December 1994, August–September 1995, October 1995, and November–December 1995.
† Samples include March 1995 and March 1996.

TABLE III. Geometric means (and sample sizes) of *Passalurus ambiguus* egg counts and *Eimeria* spp. oocyst counts (opg) in adult rabbits.

Parasite species	Breeding period* (352)	Nonbreeding period† (334)	Significance (*P*) Mann–Whitney
Passalurus ambiguus	0.56‡	1.41	<0.0001
Eimeria exigua	6.06	6.50	0.78
E. perforans	22.73	29.81	0.11
E. intestinalis	0.19	0.29	0.82
E. piriformis	6.10	8.38	0.09
E. media	1.47	2.55	0.06
E. flavescens	5.18	11.63	<0.0001
E. magna	0.45	1.17	0.08
E. stiedai	0.80	0.28	0.005

* Samples include October–December 1994, August–September 1995, October 1995, and November–December 1995.
† Samples include March 1995 and March 1996.
‡ Sample size larger (n = 389) for *Passalurus*.

in young rabbits, but sample sizes were low. In adult rabbits, 3 parasite species had significantly ($P \leq 0.01$) lower egg or oocyst counts in the low-density sites than in the other sites. When young and adult rabbits were combined, 4 of the 8 species of *Eimeria* showed a similar effect. Conversely, when egg counts from rabbits in the 3 highest density populations were compared to the others, the only case where high-density populations had higher egg counts was for *T. retortaeformis* in young rabbits. There were 3 cases where high-density rabbit populations had lower oocyst counts.

DISCUSSION

Egg counts of *T. retortaeformis* were affected by age, sex, and season. There was a clear rise in fecal egg output from kittens to juveniles, followed by a decline in the first year for both sexes. There was a subsequent decline for male rabbits and sterilized females but not for intact or sham-operated females. It is unclear whether the decline in egg counts was due

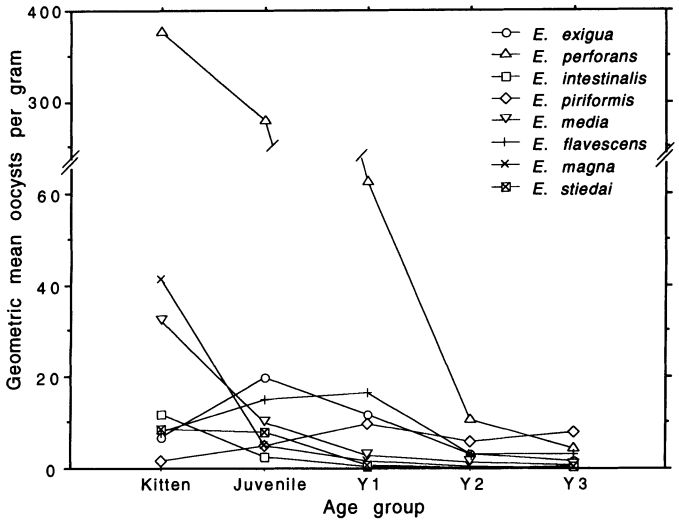

FIGURE 2. Geometric means of oocyst counts of species of *Eimeria* in rabbits of different age. Age groups are kittens (up to 66 days), juveniles (67–114 days), Y1 (115–364 days), Y2 (365–729 days), and Y3 (730 or more days old).

to an actual decline in worm numbers or an effect on fecundity of the worms. Dunsmore (1966a) and Dunsmore and Dudzinski (1968) reported a difference in worm counts between sexes, particularly late in the breeding season. Dunsmore (1966a) reported that female rabbits that had been sterilized by the removal of their Fallopian tubes and that underwent pseudopregnancies had *T. retortaeformis* burdens almost as high as intact females. Females sterilized by ovariectomy, however, harbored much lower worm burdens, similar to those in males. Dunsmore (1966a) concluded that reproductive hormones were responsible for these differences, and this was supported by a later study in which estrogen implants resulted in increased burdens of naturally acquired *T retortaeformis* in both males and females (Dunsmore, 1971). There has been much interest in the effect of reproductive hormones on immunity to nematode parasitism in domestic ruminants. Although prolactin levels have been associated with a periparturient rise in egg counts, it is now becoming clear that prolactin is not the cause of this phenomenon (Jeffcoate et al., 1990; Barger, 1993). In our study the sterilized females had lower egg counts. These rabbits were already adult when sterilized, and both ovaries and Fallopian tubes remained intact because the method of sterilization was tubal ligation. They also often underwent pseudopregnancy, and in contrast to Dunsmore's (1966a) rabbits, they would have been hormonally intact. Thus, our results conflict with Dunsmore's (1966a) high worm burdens in those rabbits that had their Fallopian tubes removed, but it should be pointed out that his sample size was only 10 rabbits per group. The differences that we found between sterilized and entire female rabbits appear to be due to factors associated with pregnancy other than reproductive hormones. Further study is needed to confirm these findings.

The abundance of *P. ambiguus* was seasonal and age related but did not appear to be affected by host sex. Egg counts were highest in the late summer samples when there were no kittens. In Wales (U.K.), where the breeding season is in late spring, *P. ambiguus* were found to have higher prevalences and intensities in winter, outside the breeding season (Evans, 1940). This was attributed to a greater proportion of young, uninfected rabbits in the breeding season samples. However, this was not a factor in our study because kittens and juveniles <1,000 g were excluded from the analysis. It is also surprising that the highest egg counts occurred in summer in our study, because the area is subject to quite hot and relatively dry summers. There was above average rain prior to the March 1996 sample (Twigg et al., 1998), but the count was similar to the March 1995 sample

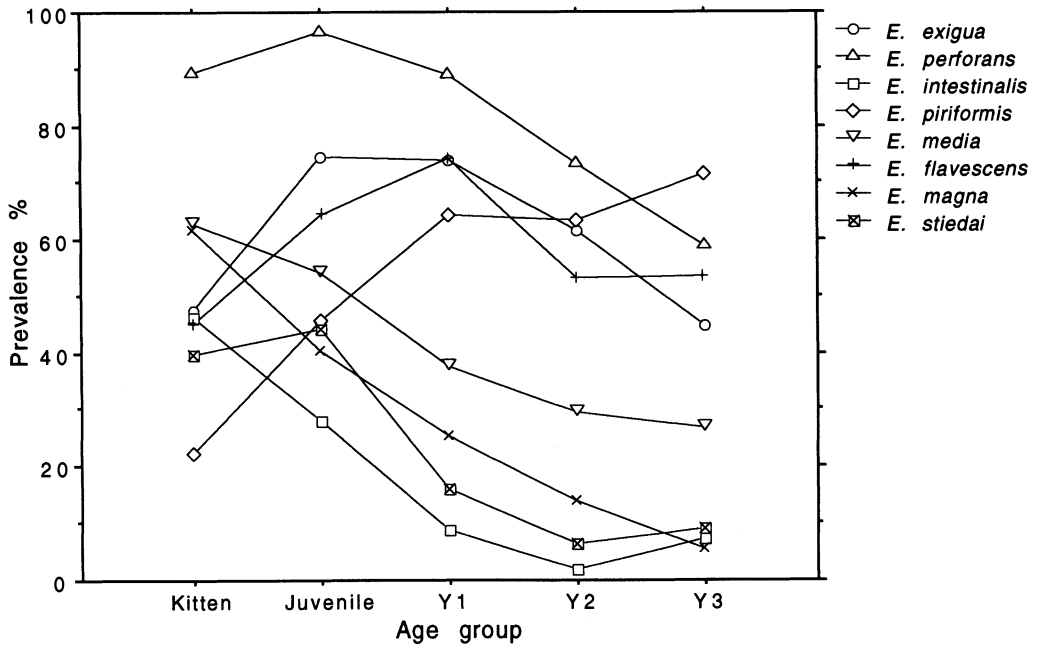

FIGURE 3. Prevalence (%) of species of *Eimeria* in rabbits of different age. Age groups are kittens (up to 66 days), juveniles (67–114 days), Y1 (115–364 days), Y2 (365–729 days), and Y3 (730 or more days old).

TABLE IV. Analysis of variance for regression of geometric means of egg and oocyst counts against host abundance.*

	Young rabbits†				Adult rabbits			
	n	Slope	*F*	*P*	n	Slope	*F*	*P*
Trichostrongylus retortaeformis	26	+0.304	6.532	0.017	28‡	+0.030	0.241	0.628
Passalurus ambiguus					19§	0.000	0.000	0.996
Eimeria exigua	25	+0.099	0.525	0.476	42	−0.023	0.172	0.680
E. perforans	25	+1.210	0.073	0.789	42	+0.305	0.722	0.400
E. intestinalis	25	−0.070	0.299	0.590	42	+0.006	4.074	0.050
E. piriformis	25	+0.027	0.610	0.443	42	+0.033	0.626	0.434
E. media	25	−1.566	1.616	0.216	42	+0.037	1.091	0.303
E. flavescens	25	−0.115	0.607	0.444	42	+0.080	0.630	0.432
E. magna	25	−0.837	2.507	0.127	42	+0.032	5.849	0.020
E. stiedai	25	+0.917	1.531	0.228	42	+0.013	0.837	0.366

* Geometric means are based on groups of collection period and site. Only those groups for which there were 10 or more fecal samples per age group were included.
† Young rabbits are those with body mass <1,000 g.
‡ Samples from March each year (summer nonbreeding period) were excluded because egg counts were low.
§ Samples other than March each year were excluded because egg counts were low.

that followed average rain. Dunsmore (1966b) found *P. ambiguus* to be relatively rare at his most arid site. The prepatent period for this species is about 2 mo, and the delay before egg production may be the cause of the shift of the peak from early to late summer. Also, it is likely that the eggs of *P. ambiguus* are relatively resistant to desiccation. In summer, rabbits are eating closer to the ground and therefore come into closer contact with the infective eggs. This is in contrast to *T. retortaeformis* for which the infective stage is a motile larva that can climb off the ground and onto food plants.

The effect of host age on the abundance of coccidia is well recognized (Bull, 1958; Mykytowycz, 1962) and has been shown to be due to host immunity rather than physiology (Stodart, 1968a). Although the prevalence of *E. piriformis* continued to increase with host age in our study, oocyst counts reached a peak at about 1 yr of age. This suggests that host immunity acts to limit an existing infection rather than by preventing a new infection at least in this species. We were unable to find seasonal patterns in coccidian oocyst counts except for *E. flavescens* and *E. stiedai*. This may be explained partly by the lack of seasonality in rainfall patterns during our study period due to lower winter rainfall and unusually high rainfall in December 1995 (Twigg et al., 1998). Coccidian oocysts on pasture require mild temperatures and a relatively moist environment for sporulation and survival. Stodart (1968b) found peaks in abundance after good rains at her semiarid sites and considered rainfall to be a major factor determining seasonality.

The abundance of parasites that utilize the oral route of infection and that have direct life cycles is assumed to increase in higher density host populations by increased transmission rate due to increased contact frequency between hosts (May and Anderson, 1979). In addition, individuals in higher density populations may undergo higher stress resulting in lower immunity that could enhance establishment and reproduction of parasites (Lloyd, 1995). Our study has demonstrated the difficulty of detecting the effect of host density on parasitism in the wild. We expected density-dependent effects to show up clearly in the regression analyses, yet none were detected. One explanation is that our fecal egg and oocyst counts might not have related to real parasite abundance. However, we have shown that pre-

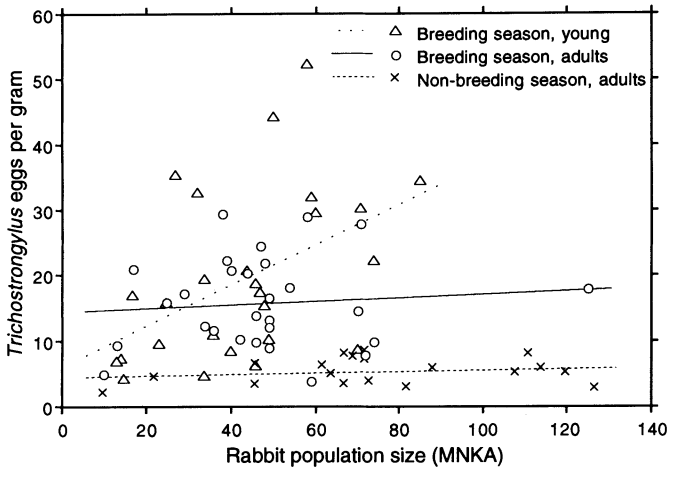

FIGURE 4. Regression of geometric mean egg counts of *Trichostrongylus retortaeformis* at different collection sites, against rabbit population size measured approximately 1 mo prior to fecal collection. Young rabbits are those with body mass <1,000 g.

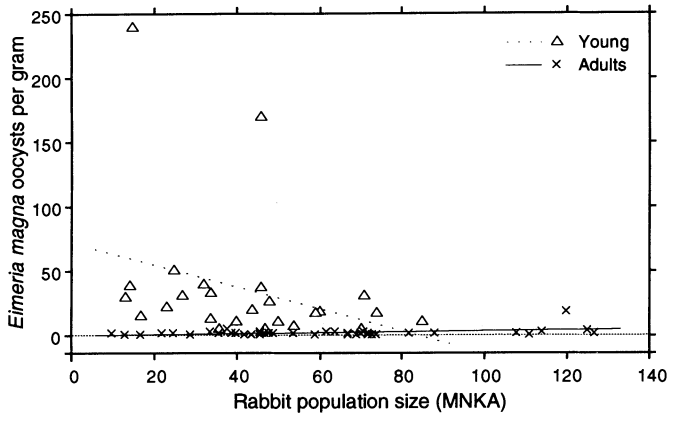

FIGURE 5. Regression of geometric mean egg counts of *Eimeria magna* at different collection sites, against rabbit population size measured approximately 1 mo prior to fecal collection. Young rabbits are those with body mass <1,000 g.

TABLE V. Nonparametric Mann–Whitney significance levels (P) for comparisons between sites of different rabbit density.

	Low density vs. others *			High density vs. others†		
	Young‡	Adults	Combined	Young	Adults	Combined
Trichostrongylus retortaeformis	0.1671	0.0016§	0.0950	0.0003§	0.5089	0.0482
Passalurus ambiguus		0.1170			0.1486	
Eimeria exigua	0.7672	0.0017§	0.0068§	0.0244	0.0441	0.0018‖
E. perforans	0.3757	0.1775	0.0007§	0.1764	0.0027‖	0.0745
E. intestinalis	0.2873	0.8067	0.1333	0.4208	0.6349	0.6770
E. piriformis	0.4930	0.0011§	0.1251	0.6604	0.0098‖	0.0510
E. media	0.1187	0.0116	0.0001§	0.6508	0.8660	0.3703
E. flavescens	0.7068	0.1915	0.1636	0.6650	0.0567	0.2047
E. magna	0.5249	0.2331	0.0066§	0.8437	0.7995	0.7152
E. stiedai	0.0885	0.0350	0.0509	0.9185	0.1391	0.5413

* The low-density group contains rabbits from the 3 sites with the lowest rabbit densities over the period of the study. These rabbits are compared to rabbits from the other 9 sites.
† The high-density group contains rabbits from the 3 sites with the highest rabbit densities over the period of the study. These rabbits are compared to rabbits from the other 9 sites.
‡ Young rabbits are those with body mass <1,000 g.
§ Significant and expected effect ($P < 0.01$) where the rabbits from higher density sites have higher egg or oocyst counts.
‖ Significant but unexpected effect ($P < 0.01$) where the rabbits from lower density sites have higher egg or oocyst counts.

viously known patterns of nematode population distributions in rabbits according to season, host age, and sex were detectable using fecal egg counts, so we can be reasonably confident that our egg counts do reflect worm numbers. In other intensively studied hosts, egg counts do correlate with worm burdens (e.g., Cabaret et al., 1998). Coccidian oocyst counts may not reflect abundance of the organisms in an individual, but the mean count from a population of rabbits should reflect the abundance and transmission rate in that population (Yvore and Esnault, 1987). A second explanation for the lack of significant regressions is that there were in fact no density-dependent relationships. However, our contrasts between sites with long-term low-density rabbit populations and the other sites did provide some evidence for density dependence. Thus, it appears that the short-term fluctuations in both host and parasite abundance may have obscured the long-term trend. A New Zealand study where rabbit numbers underwent a gradual decline over a period of 5 yr showed that the abundance of the nematodes *T. retortaeformis* and *G. strigosum,* and 2 spp. of *Eimeria* also declined (Bull, 1957). It is interesting that although we detected declines at low densities for several parasite species, we detected only 1 case of enhancement at high densities. This suggests that contact with infective stages is normally high, and only at low host densities is it low enough to result in lower abundance. As a corollary to this, if the density-dependent effect is due to stress (Lloyd, 1995), then we must conclude that at Wellstead, stress is the normal state. Parasites are thought to contribute to the regulation of natural populations of their hosts by reducing their fecundity and survival. If this is density dependent, then there must be a relationship between host density and parasitism, irrespective of the mechanism of the regulatory effect (Holmes, 1995). At the host densities and parasite abundances observed in our study, evidence for such a relationship was equivocal.

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