EVALUATION OF THE ASSOCIATION OF PARASITISM WITH MORTALITY OF WILD EUROPEAN RABBITS *ORYCTOLAGUS CUNICULUS* (L.) IN SOUTHWESTERN AUSTRALIA

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ABSTRACT: Abundances of the parasitic nematodes *Trichostrongylus retortaeformis* and *Passalurus ambiguus,* and 8 *Eimeria* species were estimated by fecal egg and oocyst output in 12 discrete free-ranging populations of wild rabbits (*Oryctolagus cuniculus*) in southwestern Australia. Comparisons of parasite egg and oocyst counts were made between those rabbits known to have survived at least 2 mo after fecal samples were collected and those rabbits that did not survive. There were significant negative relationships between parasite egg and oocyst counts and survival when all age groups and collection periods were pooled for several species of coccidia and for *T. retortaeformis.* However, when the same comparisons were made within rabbit age groups and within collection periods, there were very few significant differences even where sample sizes were quite large. The differences indicated by the pooled analysis for coccidia were most likely due to an uneven host age distribution with respect to survival, combined with an uneven distribution of the oocyst counts with rabbit age. The result for *T. retortaeformis* was similarly affected but by a seasonal pattern. Parasitism by nematodes and coccidia did not appear to be an important mortality factor in these rabbit populations, at least at the range of host densities we examined. This suggests that other factors must have been responsible for the observed pattern of density-dependent regulation in these rabbits.

There is increasing interest in the role of infectious diseases in regulating their host populations. In order to regulate host populations, parasites must cause a decrease in survival, or fecundity, or both, and their abundance should increase with increasing host density at least over most of the range in abundance of their hosts (Scott and Dobson, 1989). Current population models for macroparasites contain assumptions that disease agents such as parasites increase host mortality (Anderson and May, 1979; Roberts et al., 1995), but there have been very few field studies that have tested this assumption (for discussion see Gulland [1995]).

In 1992, a field experiment was established to measure the effect of reducing the fertility of female rabbits *Oryctolagus cuniculus* (L.) on rabbit abundance. The experiment was carried out in the southwest of Western Australia (Twigg et al., 1998). Twelve discrete rabbit populations were created by a combination of rabbit-proof fences and maintenance of buffer zones. Breeding stops (warrens) were confined to areas of native shrub habitat adjacent to the pasture where rabbits fed. Thus, the experimental rabbits were living under essentially natural conditions. All rabbits were live-trapped at 4–6 weekly intervals that allowed for repeated nondestructive sampling of parasite abundance by fecal egg counts. In contrast, most parasitological studies of wild mammal populations involve the destructive sampling of hosts for the determination of actual parasite numbers by postmortem (e.g., Dunsmore and Dudzinski, 1968; Gulland, 1992). Fecal egg counts are effective in detecting patterns in parasite abundance related to the age and sex of the host and seasonal differences for *Trichostrongylus retortaeformis* and *Passalurus ambiguus* in European rabbits (Hobbs et al., 1999). The abundance of coccidia (*Eimeria* spp.) in rabbit populations can also be estimated by fecal oocyst output (Hobbs et al., 1999). These techniques allowed the relationship of parasite abundance with host survival to be examined for the nematodes *T. retortaeformis,* which is suspected of regulating rabbit populations (Bull, 1964; Dunsmore, 1981), and *P. ambiguus,* which

is considered nonpathogenic (Soulsby, 1982). The relationship was also examined for the 8 most prevalent species of coccidia (*Eimeria* spp.) in these rabbits (Hobbs and Twigg, 1998), some of which are known to cause mortality in laboratory studies (Coudert et al., 1995).

MATERIALS AND METHODS

Details of the study area, experimental design, and parasitological methods are given in Twigg et al. (1998) and Hobbs et al. (1999), respectively. Rabbit numbers were determined by live-trapping and represent the minimum number of animals known to be alive (MNKA) at the site for each collection period. Although host populations were monitored every month, fecal samples were collected only 6 times during 1994–1996. All rabbits were individually tagged. For each collection period, rabbits were deemed to be survivors if they were known to be alive for at least 2 mo after the mean collection time (Table I). In the sterility trial, 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.

We tested the density dependence of survival by regression analysis of the proportion of rabbits that survived, against rabbit abundance (MNKA). Each data point corresponds to a single site (rabbit population) at 1 collection period. Data points based on less than 10 rabbits were excluded. Two methods were used to explore the relationship between parasite abundance and host mortality. The first method used regression analysis of survival against site means of log-transformed fecal egg and oocyst counts. The second was based on individual rabbits and simply compared fecal egg and oocyst counts of survivors to that of nonsurvivors, regardless of site. Comparisons were made using nonparametric Mann–Whitney U-tests. Because egg counts of the nematodes were found to be influenced by season (Hobbs et al., 1999), and both coccidian oocyst counts and host mortality were strongly influenced by the age of the host (Twigg et al., 1998; Hobbs et al., 1999), samples were split by sampling period (time) and rabbit age for further statistical analysis. Significance levels were set at $P \leq 0.01$.

RESULTS

Survival of rabbits

The estimated survival of rabbits for each age group over the 6 collection periods is shown in Table II. These estimates were based only on the rabbits included in the parasitological study from which fecal samples were obtained. Trends in the changes in rabbit abundance were similar between sterility levels (Fig. 1). Rabbit numbers increased at the end of 1994, declined over

TABLE I. Collection dates and the dates used to determine the survival of rabbits for each of the 6 fecal collection periods.*

Collection period	Collection dates	Mean collection date	Date for survival
A	11 Oct–7 Dec 1994	24 Oct 94	1 Jan 95
B	28 Feb–5 Apr 1995	10 Mar 95	1 Jun 95
C	1 Aug–13 Sep 1995	20 Aug 95	1 Nov 95
D	27 Sep–10 Nov 1995	9 Oct 95	1 Jan 96
E	22 Nov–7 Dec 1995	28 Nov 95	1 Feb 96
F	27 Feb–11 Apr 1996	9 Mar 96	20 May 96

* Rabbits were scored as survivors for the collection period if they were known to be alive at the subsequent survival date.
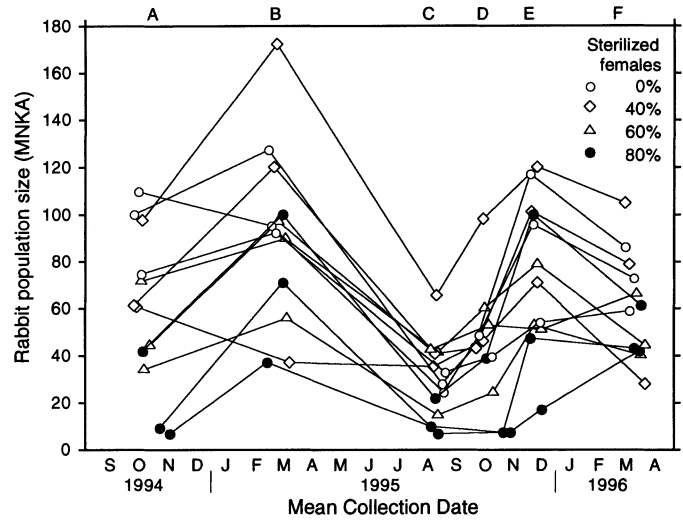

FIGURE 1. Population sizes for each of the samples of rabbits estimated from trapping data (minimum number known alive at that plot for that collecting period), plotted against mean date of collection. Plots are labeled according to sterilization regime.

the first half of 1995, then increased late in 1995 before declining over the summer/autumn of 1996. Survival was generally highest in adults and lowest in kittens (Table II). Survival in subadults was slightly higher on average than for kittens. Survival was highest for all age groups in early spring (August) 1995. For the kittens, there was very poor survival from early summer (November–December) 1995 into late summer 1996, a time when survival for the other age groups was quite high. Sites with high rabbit numbers generally had relatively low survival (Fig. 2), suggesting density-dependent regulation of the host populations.

Nematode parasites

There was a negative regression of rabbit survival against *T. retortaeformis* egg counts ($P = 0.002$), but for the nonpathogenic *P. ambiguus,* the slope was positive ($P = 0.004$) (Fig. 3). The negative slope found for *T. retortaeformis* is indicative of a relationship between infection and mortality. However, closer

scrutiny of the regression suggests that the relationship may be due to the seasonality of both infection and rabbit mortality, rather than a direct effect of parasite abundance on mortality. Solid points on the graph are late summer samples (March 1995, 1996) where survival of adult rabbits was high and fecal egg output low, and if these are considered separately, the regression slopes are not significantly different from 0 (summer, $P = 0.661$; other, $P = 0.055$). Conversely, with *P. ambiguus* the only samples that had high mean egg counts were the summer samples, and if summer and other samples are considered

TABLE II. Comparisons of *Trichostrongylus retortaeformis* egg counts between rabbit survivors and nonsurvivors.*

Age group	Sampling period	Survival (%)	Sample sizes		Geometric mean epg		Mann–Whitney U significance
			Nonsurvivors	Survivors	Nonsurvivors	Survivors	
Kittens 50–699 g	A	56	23	29	13.77	6.08	0.093
	C	71	26	63	7.06	9.19	0.659
	D	37	38	22	7.42	12.78	0.313
	E	20	40	10	7.77	13.85	0.427
	A–F	49	131	125	7.83	8.99	0.564
Subadults 700–1,199 g	A	47	43	38	22.55	20.15	0.639
	C	74	8	23	23.93	29.37	0.416
	D	62	40	64	22.60	25.92	0.588
	E	49	36	34	27.00	25.62	0.893
	A–F	56	139	177	19.14	20.42	0.591
Adults >1,199 g	A	79	17	63	18.86	13.45	0.378
	B	69	35	78	6.61	3.12	0.010
	C	90	11	96	19.21	8.73	0.162
	D	82	15	69	11.70	13.65	0.559
	E	64	43	75	13.63	11.22	0.931
	F	83	38	183	8.01	5.26	0.110
	A–F	78	159	564	10.76	7.48	0.016
All ages	A–F	67	429	866	11.83	9.49	0.020

* Rabbits were scored as survivors for the sampling period if they were known to be alive at the date for survival (see Table I). Age groups were determined by body mass. Summer samples in kittens and subadults were not tested due to low sample sizes.
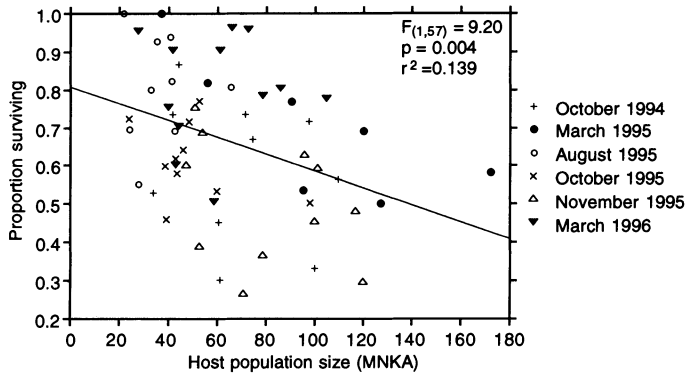
FIGURE 2.   Scatterplot and regression line of the proportion of rabbits that survived versus rabbit abundance (minimum number known alive) for site and collecting period where there was at least 10 fecal samples. Dates used in calculating the proportion of rabbits surviving are shown in Table I.

separately, slopes were not significantly different from 0 (summer, $P = 0.264$; other, $P = 0.322$).

Egg counts of *T. retortaeformis* for surviving rabbits were compared with counts of nonsurvivors using nonparametric Mann–Whitney U-tests. There were insufficient kittens or subadults from the late summer (March 1995, 1996) collections, but of the remaining 14 comparisons, only 1 produced a significant difference (Table II), and that was the case with the lowest egg counts. There were no significant differences for *P. ambiguus* (data not shown).

Coccidian parasites

Regressions of rabbit survival against logarithms of the means of oocyst counts had significantly negative slopes in 5 species and a positive slope for 1 species (Table III). Significant regression slopes may have been due to the fact that oocyst counts differed between age groups (Hobbs et al., 1999). For all of the coccidia species with negative slopes, abundance was lowest in adult rabbits. For example, *Eimeria intestinalis* was found in very few rabbits older than 4 mo (Hobbs et al., 1999). Late summer samples (March) had very few young rabbits and, therefore, low mean abundance of *E. intestinalis*. Rabbit survival was also relatively high in late summer. In contrast, *Eimeria piriformis* was more abundant in adult rabbits (Hobbs et al., 1999), and this could account for the positive slope.

With the more direct approach of comparing oocyst counts of rabbit survivors and nonsurvivors (Table IV), rabbit mortality for 5 of the 8 species of coccidia was associated with higher oocyst counts, when all age groups and sampling periods were pooled. However, because rabbit survival is lowest in kittens (Twigg et al., 1998), and most species of coccidia are more abundant in kittens (Hobbs et al., 1999), significant associations were inevitable and can neither imply nor exclude causality. Therefore samples were split by age group. Only 1 species (*Eimeria media*) was associated with mortality in subadult rabbits, and 1 different species (*Eimeria perforans*) in adults, when sampling periods were pooled. There were no such associations in kittens. After samples were further split by collecting period, because survival differed between collecting periods, very few associations remained (Table IV), even though sample sizes re-
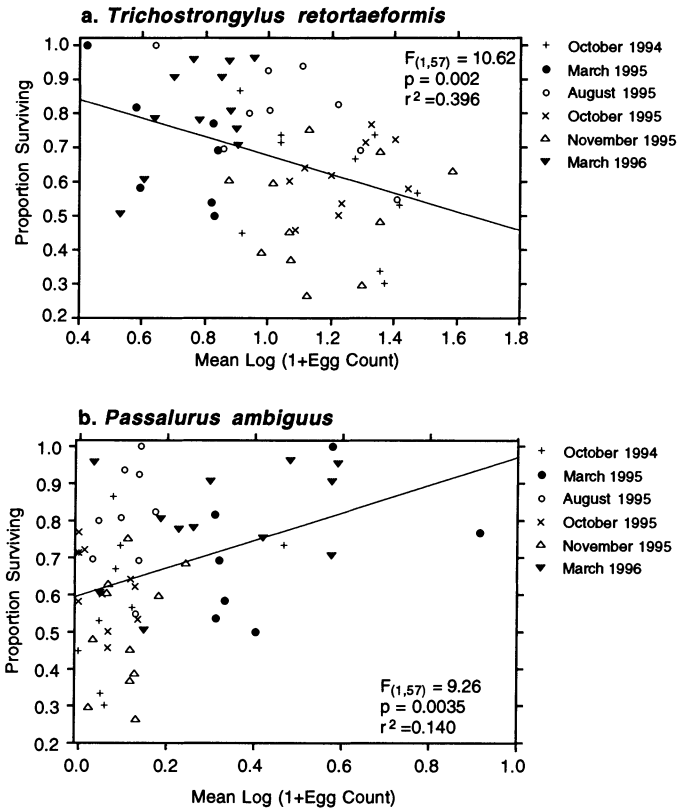

FIGURE 3.   Scatterplot and regression line of the proportion of rabbits that survived versus mean of the logarithm of number of (a) *Trichostrongylus retortaeformis* and (b) *Passalurus ambiguus* eggs per g feces (epg), for each of the collection periods where fecal samples were collected from at least 10 rabbits per site. Survival dates used in calculating the proportion of rabbits that survived are given in Table I. The F-value, significance of the regression slope (P), and r^2 values are shown for each graph.

mained quite high. Particularly noteworthy is the similarity of oocyst counts between surviving and nonsurviving kittens, because kittens are subject to the greatest mortality. In subadult rabbits, high counts of *E. intestinalis* and *E. media* were associated with mortality. In adult rabbits, high counts of *E. perforans* were associated with mortality in late summer (March)

TABLE III.   Slopes, F-values, significance of slope, and r^2 for the regression of the proportion of rabbits that survived on the logarithm of means of fecal oocyst counts, for sites and collection periods with sample sizes of at least 10 rabbits.*

Species	Slope	F	P†	r^2
Eimeria exigua	−0.101	1.69	ns	0.032
Eimeria perforans	−0.124	6.77	0.012	0.115
Eimeria intestinalis	−0.279	10.98	0.002	0.174
Eimeria piriformis	0.213	9.80	0.003	0.159
Eimeria media	−0.200	9.38	0.004	0.153
Eimeria flavescens	0.047	0.39	ns	0.007
Eimeria magna	−0.144	4.20	0.046	0.075
Eimeria stiedai	−0.147	8.32	0.006	0.138

* Sample size for each of the regressions is 54 cases. Survival dates used in estimating the proportion of rabbits that survived are given in Table I.
† ns = Not significant.

TABLE IV. Comparisons of *Eimeria* spp. oocyst counts between survivors and nonsurvivors.*

Age group	Collection period	Survival (%)	Sample size	E. exigua	E. perforans	E. intestinalis	E. piriformis	E. media	E. flaves-cens	E. magna	E. stiedai
Kittens											
50–699 g	A	56	52	ns	ns	ns	ns	ns	ns	ns	ns
	C	71	89	ns	ns	ns	ns	ns	ns	ns	ns
	D	37	60	ns	ns	ns	ns	ns	ns	ns	ns
	All periods	51	233	ns	ns	ns	ns	ns	ns	ns	ns
Subadults											
700–1,199 g	A	47	81	ns	ns	ns	ns	0.006	ns	ns	ns
	D	62	104	ns	ns	ns	ns	ns	ns	ns	ns
	E	49	38	ns	ns	0.010	ns	ns	ns	ns	ns
	All periods	56	284	ns	ns	ns	ns	0.005	ns	ns	ns
Adults											
>1,199 g	A	79	80	ns	ns	ns	ns	ns	ns	ns	ns
	B	69	113	ns	0.002	ns	ns	ns	ns	ns	ns
	C	90	107	ns	ns	ns	ns	ns	ns	ns	ns
	D	82	84	ns	ns	ns	ns	ns	ns	ns	ns
	E	64	81	ns	ns	ns	ns	ns	ns	ns	0.005
	F	83	221	ns	ns	ns	ns	ns	ns	ns	ns
	All periods	79	686	ns	0.0003	ns	ns	ns	ns	ns	ns
All age groups	All periods	68	1,203	ns	<0.0001	<0.0001	<0.0001†	<0.0001	ns	<0.0001	<0.0001

* Rabbits were scored as survivors for the collecting period if they were known to be alive at the date for survival. Rabbit age groups were determined by body mass. Summer samples (collections B and F) for kittens and subadults were not tested due to low sample sizes. Kitten samples in period E and subadult samples in period C were not tested due to low sample sizes within survival group. Statistical significance of Mann–Whitney *U*-tests are given for each case where *P* was less than or equal to 0.01, otherwise it is marked ns. Unless otherwise indicated, significant values indicate that survivors had lower oocyst counts than nonsurvivors.

† Survivors with higher oocyst count.

1995. Although high counts of *Eimeria stiedai* were also associated with higher mortality in early summer 1995, only 7 adult rabbits were infected at this period, so the association must be regarded with some suspicion.

DISCUSSION

Although the abundance of *P. ambiguus* was not expected to be associated with rabbit mortality, *T. retortaeformis* is a known pathogen of European rabbits (Barker and Ford, 1975). Other species of *Trichostrongylus* have also been associated with mortality, for example in domestic sheep (Gordon, 1950) and wild red grouse (Hudson et al., 1992). Although Bull (1964) and Dunsmore (1981) have shown that *T. retortaeformis* can reduce fecundity and weight gain in rabbits, there have been no field studies that indicate that this species affects survival of European rabbits. Furthermore Iason and Boag (1988) found no evidence that *T. retortaeformis* had any effect on mortality, fecundity, or weight gain in mountain hares (*Lepus timidus*) in Scotland. In our study, rabbit mortality did not appear to be associated with high egg counts of *T. retortaeformis*.

In experimental infections, several species of coccidia are known to cause mortality in European rabbits (Bull, 1958; Coudert et al., 1995). There have also been claims that coccidia, particularly *E. stiedai,* are associated with rabbit mortality in the wild (Tyndale-Biscoe and Williams, 1955; Bull, 1958; Dunsmore, 1971). However, these studies were based on destructive sampling, so rabbit survival was only able to be inferred. Furthermore, conclusions in these field studies were based on observations that coccidia were most abundant at the time of high mortality, particularly in the age group experiencing that mortality. Thus, Bull (1958) and Dunsmore (1971) suggested that *E. stiedai* would be particularly important in kittens from litters born late in the breeding season. In our study situation, Twigg et al. (1998) have shown that late-born kittens suffered increased mortality also. However, we could find no evidence that oocyst counts were higher in late-born kittens (Kruskal–Wallis tests, data not shown) or that coccidia were associated with this reduced survival, with the possible exception of *E. media* and *E. intestinalis* (Table IV). The results shown in Table IV do indicate that higher oocyst counts of some species of coccidia are associated with reduced survival at those times when survival was lower than normal. Thus, it is possible that *E. media* caused mortality in subadult rabbits in late spring 1994, and *E. intestinalis* in late spring 1995. Similarly, *E. perforans* may have increased mortality of adults in late summer 1995. We found no evidence that other species were associated with mortality, and it appears that other factors may have caused most of the mortality in our study.

The protocol used in the present study that allowed a direct measure of the association of parasitism with survival was similar to that used by Mykytowycz (1962) on an enclosed population near Canberra. He was unable to show any differences in oocyst output between survivors and nonsurvivors on a within-litter basis. For many of his analyses, all species of coccidia were pooled; however, *E. stiedai* was the most common species in his young rabbits. Mykytowycz (1962) did find that the rabbits that were disappearing from his site were those at that age when *E. stiedai* was most prevalent, but he was able to show that other factors such as predation and myxomatosis were more

important causes of mortality. We suggest that other factors may have caused the mortality patterns in the studies of Tyndale-Biscoe and Williams (1955), Bull (1958), and Dunsmore (1971).

Parer (1977) found that the highest mortality rate for rabbits at a site with a drier climate in south-central New South Wales was in kittens aged 21–30 days old, before the onset of coccidiosis, so in that area also, other factors must have been more important causes of mortality. Other studies in semiarid areas of Australia have either discounted or ignored parasitism as a significant cause of mortality (Wood, 1980; Richardson and Wood, 1982; Wheeler and King, 1985). In a survey of rabbit population dynamics in Australia and New Zealand, Gilbert et al. (1987) concluded that while diseases and predators may exert a large influence on population size in some circumstances, there was no common pattern across sites.

Coudert et al. (1995) have warned that in rabbits there is no correlation between oocyst excretion and severity of disease and have recommended that oocyst counts only be used when other methods are not available, such as in field studies like ours. It is quite possible therefore that coccidiosis was a major mortality factor in our rabbits, but that it was not possible to detect this using our methods. However, in our study, we could not demonstrate a clear relationship between parasitism and host density (Hobbs et al., 1999). We were able to find little evidence for a relationship between mortality and nematode egg counts or coccidian oocyst counts. We therefore consider that factors other than parasitism caused most of the observed mortality.

ACKNOWLEDGMENTS

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