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BIOTIC AND ABIOTIC EFFECTS ON ENDOPARASITES INFECTING *DIPDOMYS* AND *PEROGNATHUS* SPECIES

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ABSTRACT: Between 1989 and 1998, 3,504 rodents of the genera *Dipodomys* and *Perognathus* were collected from 4 permanent collecting sites on the University of New Mexico's Long Term Ecological Research station, located on the Sevilleta National Wildlife Refuge (SNWR), Socorro County, New Mexico. All animals were killed and examined for endoparasites (acanthocephalans, cestodes, coccidia, and nematodes). The present report focuses on 3 endoparasite groups, cestodes, coccidia, and nematodes. Specific analyses address how prevalence changes were related to abiotic factors such as habitat, season, or precipitation, and how prevalence of each parasite species in each host species differed in relation to host age, host sex, host reproductive status, host body mass, host density, parasite–parasite interactions, and host specificity. A logistic regression was used to determine which host characters and which abiotic factors are correlated with a parasite infection. Significant variables for at least half of the parasites include season, site, and winter precipitation. However, no parasite prevalences were correlated, and significant variables were not identical between parasites, indicating that each parasite species varied independently and that no generalizations can be drawn. The parasite prevalences in these rodents on the SNWR vary in independent and complex ways.

Patterns of distribution and prevalence of rodent parasites in xeric environments have yet to be defined conclusively (May and Anderson, 1979; Dobson, 1989; Patrick, 1994). However, studies have shown that rodent hosts in mesic habitats have higher prevalences of infection and species richness with eimeriid coccidia than hosts in xeric environments (Ford et al., 1990; Stanton et al., 1992).

Many short-term studies, e.g., 1–4 yr, on rodents and their parasites have described new parasite species, prevalence of infection, seasonality and host differences to parasite infection (Garner et al., 1976; Betterton, 1979; Ball and Lewis, 1984; Keymer and Dobson, 1987; Stanton et al., 1992; Wilber and Patrick, 1997); however, long-term field studies of parasites are rare (Esch et al., 1996). Long-term studies are needed for assessing parasite prevalence through many host generations over time and climatic variability. This study is unique among mammal parasite surveys in that it spans 10 yr of data on the endoparasites, i.e., coccidians and helminths (acanthocephalans, cestodes, nematodes) in 5 common rodent hosts (*Dipodomys merriami*, *D. ordii*, *D. spectabilis*, *Perognathus flavus*, and *P. flavescens*) from 4 sites on the Sevilleta National Wildlife Refuge (SNWR), Socorro County, New Mexico.

In the present analysis, the following questions are addressed: (1) What is the prevalence of parasite species in these heteromyid rodents at these SNWR sites? (2) How many parasite species infect individual rodents? (3) Are host sex, host age, host reproductive status, host body mass, host density, host species, precipitation, site, or season important factors influencing parasite prevalence?

MATERIALS AND METHODS

Study site and host collection

The SNWR is located in Socorro County, New Mexico, approximately 88 km south of Albuquerque, and is approximately 100,000 ha in size (Fig. 1). There were 3 collecting seasons: May–June 1989–1998 (season 1), July–August 1989–1993 (season 2), and September–October 1994–1998 (season 3). Four trap sites were chosen to include 2 of the

predominant habitat types found on the SNWR (grassland, creosote) with a site on each side (east, west) of the Rio Grande. The vegetation on the 2 western sites (Rio Salado) are a mixed grassland–shrubland (grassland west) and Chihuahuan desert shrubland (creosote west) with sandy soils. The 2 eastern sites (Five Points) are Great Plains grassland (grassland east) and Chihuahuan desert shrubland (creosote east) with a mix of clay and sandy soils (Wilson et al., 1997, for site photos; Kieft et al., 1998).

Each site had 5 permanent collecting webs. Each web had 148 traps, Sherman® live traps (model XLF15 and SFAL, H. B. Sherman Traps, Tallahassee, Florida) arranged in a radial pattern from a central point (Anderson et al., 1983; Parmenter et al., 1989; Buckland et al., 1993). Of the 5 webs at each site, 3 webs were for capture–mark–release and 2 webs were for removal. Each site was trapped for 3 consecutive nights, 2 seasons a year.

The parasite data were derived from rodents taken from the removal webs. A list of each web and associated global positioning satellite coordinates for each site are in Wilson et al. (1997). All post-1993 field and laboratory procedures followed Mills et al. (1995) to ensure personnel safety and protection from zoonotic disease transmission.

Host and parasite selection

Host and parasite species were used in this study only when sufficiently large sample sizes of both existed for statistical analysis; otherwise, parasites were grouped by genus when species identifications could not be made. Parasite prevalence (no. infected/no. caught) may be overestimated when host sample sizes are very small (Gregory and Blackburn, 1991). Prevalence is reported for all parasites in host groups. The number given as the total number caught may vary between prevalence for coccidia and prevalence for helminths because sometimes a different number of fecal samples was collected than necropsies performed, or some samples were lost, or both.

Host processing and collection of parasites

Small rodents were brought back to the Sevilleta Field Research Station alive, where they were killed, weighed, measured, sexed, aged, and identified to species; trap location was noted and each was given a unique New Mexico karyotype (NK) number.

The gastrointestinal (GI) tract was cut from above the stomach to the anus and placed into a petri dish with tap water and marked with its corresponding NK number. Fecal material (when present) was removed from the colon and placed into Wheaton vials (20 ml) containing 2.5% (w/v) potassium dichromate ($K_2Cr_2O_7$). Later, feces were screened for oocysts and, if found, these were measured, photographed, and identified, as described elsewhere (Duszynski and Wilber, 1997). Each GI section was slit lengthwise and examined with a dissecting microscope. Nematodes were fixed in glacial acetic acid (3–4 min), then stored in 10% (v/v) buffered formalin. Cestodes and acanthocephalans were placed into distilled water (30–45 min) to help them expel their eggs

Received 6 April 2000; revised 16 August 2000; accepted 18 September 2000.

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† Deceased.

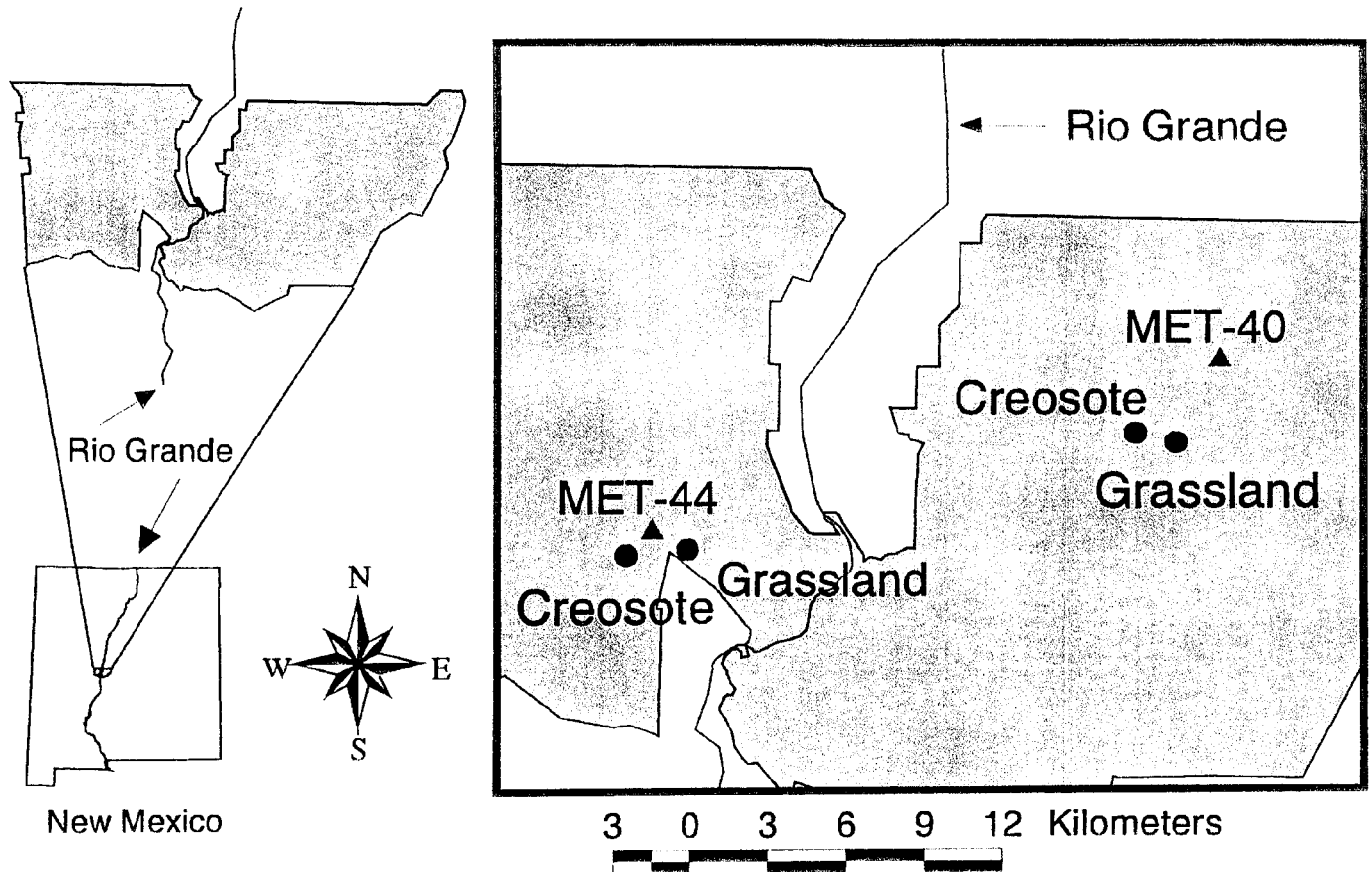


FIGURE 1. Location of web sites at the Sevilleta National Wildlife Refuge, Socorro County, New Mexico. ▲, MET stations; ●, Web sites.

and to force the acanthocephalans to extrude their probosci. Both were stored in 10% buffered formalin.

Reference collection and deposition of specimens

Host skeletons, skins, and frozen tissues were deposited in the Division of Mammals, Museum of Southwestern Biology (MSB), University of New Mexico (UNM). Host symbiotypes for new parasite species (Frey et al., 1992; Brooks, 1993) were deposited in the separate symbiotype collection of the MSB. Phototypes of new coccidians (Bandoni and Duszynski, 1988) and helminth-type specimens were deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland.

Data analysis

Population densities (no./ha) on all webs were calculated with density theory (Buckland et al., 1993) using the DISTANCE program (Laake et al., 1993).

Logistic regression (PROC LOGISTIC SAS, 1985) was used on categorical and continuous data to determine which independent variables affected the prevalence of each parasite species. Results are given as the odds ratio $p/(1 - p)$ where p is the probability that the rodent will be infected with this parasite. If the odds ratio was greater than 1 for variables in the logistic regression, then the prevalence of that parasite was positively correlated with that variable. If the odds ratio was less than 1 for variables in the logistic regression, then the prevalence of that parasite was negatively correlated with that variable. We used a 95% confidence level to determine significance for variables. Host body mass was converted to a Z-score, $(M - m)/SE$ where M is the mass of the individual rodent, m is the mean mass for that rodent species, and SE is the standard error, so that each species was comparable. Reproductive animals included females that were pregnant, lactating, or exhibited vaginal bleeding and males that exhibited scrotal testes. Season

1 was split into 2 5-yr lengths (= seasons 2 and 3). If a parasite species infected fewer than 30 individuals over the 10 yr, the host species was not included in the analysis for that parasite.

A correlation analysis (PROC CANCORR SAS, 1985) was performed on the presence or absence of each parasite species against each other.

Meteorological (MET) stations

Precipitation data were collected by a tipping-bucket rain gauge connected to a Campbell Scientific CR 10 data logger. The MET stations used were no. 40, 3.5 and 5.5 km from the east sites, and no. 44, 1 and 2 km from the west sites (Fig. 1). Winter precipitation was summed for the October–May months preceding the collection of rodents for each year except 1989. For the 1989 winter precipitation, we used data from Socorro County MET records. Precipitation, used in the regression for the *Eimeria* species, was summed for 21 days before the first day of each trapping period (3-wk precipitation) because these coccidians have direct life cycles that are completed in approximately 21 days.

RESULTS

Hosts and prevalences of parasite species

3,504 *Dipodomys* spp. and *Perognathus* spp. were collected from 1989–1998 (Table I, Fig. 2). Coccidia and helminths were extracted and identified from the intestines of these rodent genera. The prevalences for every parasite collected in each rodent species by site, season, and year are in Appendix A (<http://sevilleta.unm.edu/data/species/parasite/>).

TABLE I. Selected biological parameters and results from this study on the heteromyid species from the University of New Mexico Long Term Ecological Research Program on the Sevilleta National Wildlife Refuge, Socorro County, New Mexico, 1989–1998.

Heteromyid species	Total feces*	Total necropsies*	Mean body mass† (g)	Mean body mass* (g)	Max. age‡ (yr)	Eats insects†	Exhibits territoriality†
<i>Dipodomys merriami</i>	1,337	1,342	40	41	2	yes	yes
<i>D. ordii</i>	710	718	52	48	—‡	yes	no
<i>D. spectabilis</i>	234	234	123	117	6	yes	yes
<i>Perognathus flavescens</i>	304	305	10	12	—	—	no
<i>P. flavus</i>	897	905	8	7	2.5	—	no
Total	3,482	3,504					

* This study.

† References used to compile Table I: Britt, 1972; Alcoze and Zimmerman, 1973; Flake, 1973; Bienek and Klikoff, 1974; Reed, 1987; Schroder, 1987; Jones, 1993; Nagy and Gruchacz, 1994.

‡ — indicates no information.

Parasite species

Analysis of the fecal samples from all *Dipodomys* spp. and *Perognathus* spp. revealed sparse infections of *Eimeria* spp. (10 spp.), *Adelina* sp. (1 sp.), and *Isospora* sp. (1 sp.), all of which have a direct life cycle (Appendix A).

The helminths found over the 10 yr in these 2 host genera were nematodes, cestodes, and, rarely, acanthocephalans. Nematode species exhibit 2 life-cycle strategies, direct (monoxenic) and indirect (heteroxenic). The monoxenic nematodes found in this study include *Heligmosomoides polygyrus* (USNPC 88079, NK 46578), *Heteromyoxyuris deserti* (USNPC 88080, NK 46537), *Nematodirus neotoma*, *Oxyuris* sp., *Syphacia* sp., and *Trichuris* sp. (USNPC 88086, NK 46834). The heteroxenic nematodes are *Mastophorus dipodomis* (USNPC 88081, NK 46659), *Physaloptera massino* (USNPC 88082, NK 46557), *Protospirura ascaroidea* (USNPC 88083, NK 46562), and *Pterygodermatites dipodomis* (USNPC 88084, NK 44038). The heteroxenic cestodes include *Catenotaenia* sp., *Hymenolepis* sp. (USNPC 88090, NK 44171), *Mathevotaenia* sp., *Oochoristica* sp. (USNPC 88093, NK 45030), *Paranoplocephala* sp., and *Railletina* sp. (USNPC 88091, NK 44073; USNPC 88092, NK 46735). The acanthocephalan *Moniliformis clarki* (USNPC 88087, NK 45193) is heteroxenic and rare in these host species.

Of the 29 endoparasite species identified, 4 of the 12 *Eimeria* species, *Eimeria balphae*, *E. chobotari*, *E. dipodomys*, and *E. reedi*, 5 of the 10 nematode species, *H. deserti*, *M. dipodomis*, *P. ascaroidea*, *P. dipodomis*, and *Trichuris* sp., and 3 of the 6 cestode species, *Hymenolepis* sp., *Oochoristica* sp., and *Railletina* sp., are sufficiently abundant in these host populations to examine their patterns statistically (Table II).

Logistic regression

The results from the logistic regression analysis show which variables are significant in determining how likely it is for a parasite species to infect the host population (Table III). Host sex, host age, host reproduction, host body mass, host density, host species, and 3-wk precipitation are significant in fewer than half of the parasites. For further results and discussion see Decker (1999). Site, season, and winter precipitation are significant in at least half of the parasites; therefore these will be the variables discussed in this paper.

Winter precipitation exhibited substantial temporal variation (Fig. 2), and was significantly correlated with *E. chobotari*, *E. dipodomys*, *H. deserti*, *M. dipodomis*, *Oochoristica* sp., and *P. dipodomis* (Table III). Parasite prevalence decreased with increasing winter precipitation for all of these parasites (Table III). When precipitation values over 150 mm were removed, *M. dipodomis* and *Oochoristica* sp. were marginally nonsignificant with $P = 0.0520$ and 0.0577 , respectively. All other parasites were negatively correlated with regard to precipitation. Figure 3 illustrates the dynamic temporal variation of these 6 parasites.

The variables site, season, and host species represent 3 or 4 values. In the logistic regression, if there was a difference in a parasite prevalence among the values, then the variable was significant and the raw data needed to be consulted. For instance, in the variable site, each parasite was either more prevalent at 1 site or had a similar prevalence at several sites (Decker, 1999), except *Oochoristica* sp., for which site was not significant (Table III). Of the parasites where season was signifi-

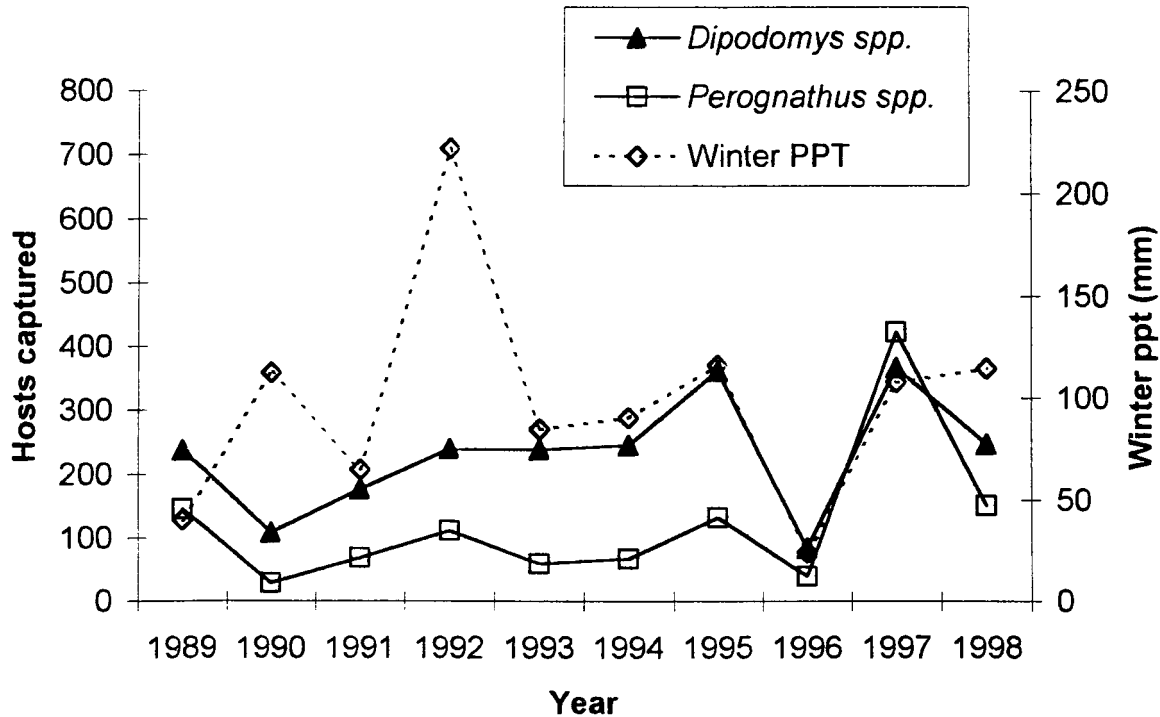


FIGURE 2. Numbers of *Dipodomys* and *Perognathus* species captured each year, from 1989–1998, and winter precipitation (see *Methods*).

cant (8 of 12), *E. chobotari* and *M. dipodomis* were more prevalent in seasons 2 and 3 (Decker, 1999). *H. deserti* prevalence was the highest in season 2. Host species was a significant variable for only 4 helminth species (Table III). *D. spectabilis* had the highest prevalence for *H. deserti*, *Trichuris* sp., and

TABLE II. Total parasite prevalence: no. infected/no. caught (%) for the dominant parasite species from 1989–1998 in 5 dominant host species at the University of New Mexico Long Term Ecological Research Program on the Sevilleta National Wildlife Refuge, Socorro County, New Mexico.

Parasite species	Prevalence (%)
Coccidia	
<i>Eimeria balphae</i> *†	53/944 (6)
<i>E. chobotari</i> ‡	445/1,275 (35)
<i>E. dipodomys</i> *‡	128/2,047 (6)
<i>E. reedi</i> §	93/897 (10)
Cestodes	
<i>Hymenolepis</i> sp.†‡	107/1,576 (7)
<i>Oochoristica</i> sp.‡	41/1,342 (3)
<i>Raillietina</i> sp.*‡	49/2,047 (2)
Nematodes	
<i>Heteromyoxuris deserti</i> *†‡§	509/3,199 (16)
<i>Mastophorus dipodomis</i> *†	444/2,365 (19)
<i>Protospirura ascaroidea</i> †	89/1,647 (5)
<i>Pterygodermatites dipodomis</i> ‡	357/1,342 (27)
<i>Trichuris</i> sp.*†‡	195/2,294 (9)

* *Dipodomys ordii* included.

† *D. spectabilis* included.

‡ *D. merriami* included.

§ *Perognathus flavus* included.

|| *P. flavescens* included.

Hymenolepis species. *M. dipodomis* were most dominant in *D. merriami*.

Multiple infection and correlation

Over 10 yr, 80% of *D. spectabilis*, 71% of *D. merriami*, 55% of *D. ordii*, 16% of *P. flavus*, and 15% of *P. flavescens* individuals were infected with 1 or more parasite species (Table IV).

D. merriami had the largest prevalence of single and double *Eimeria* infections, 39 and 2%, respectively (data not shown). Other single infections of *Eimeria* included *D. spectabilis* (17%), *D. ordii* (13%), *P. flavus* (11%), and *P. flavescens* (2%); 1% of *D. ordii* and *D. spectabilis*, and 0.1% of *P. flavus* had double infections. Only 0.1% of *D. ordii* had a triple eimerian infection.

The correlation analyses revealed that presence or absence of 1 parasite species does not indicate, or contraindicate, the presence or absence of another parasite.

DISCUSSION

Historically, hosts have been collected in 1 or 2 capture episodes, and their parasites have been extracted, preserved, identified, and recorded according to the host. However, on the SNWR, this process was extended. Instead of examining each host and its parasites, we have chosen to study the parasite community of the dominant heteromyid host species at these 4 sites during the 3 collecting seasons over the entire decade that collections were made. Rather than examine abundance, we chose to document the prevalence of the parasites found because the coccidia infections cannot be quantified. Prevalence is a common way to describe parasite populations because host sample sizes usually vary. Because dominant hosts and para-

TABLE III. Logistic regression results for 12 parasites and 10 independent variables from 1989–1998 at the University of New Mexico Long Term Ecological Research Program at the Sevilleta National Wildlife Refuge, Socorro County, New Mexico: *Eimeria balpae* (EBAL), *E. chobotari* (ECHO), *E. dipodomys* (EDIP), *E. reedi* (EREE), *Heteromyoxuris deserti* (HEDE), *Trichuris* sp. (TRsp), *Mastophorus dipodomis* (MADI), *Protospirura ascaroidea* (PRAS), *Pterygodermatites dipodomis* (PTDI), *Hymenolepis* sp. (HYsp), *Oochoristica* sp. (Oosp), *Railletina* sp. (RAsp), significance level $P < 0.05$, . = not significant, + = significant and >1 odds ratio, - = significant and <1 odds ratio, n = significant result, variable not included in analysis, x = variable not included in analysis.

	Parasite species											
	EBAL	ECHO	EDIP	EREE	HEDE	TRsp	MADI	PRAS	PTDI	HYsp	Oosp	RAsp
Hosts included												
<i>Dipodomys ordii</i>	*		*		*	*	*					*
<i>D. spectabilis</i>	*				*	*				*		
<i>D. merriami</i>		*	*		*	*	*	*	*	*	*	*
<i>Perognathus flavus</i>				*	*							
<i>P. flavescens</i>							*	*				
Variables												
Host sex	+	.
Host age	.	-	.	.	.	n	-	.	-	+	n	n
Host reproduction	.	.	-	.	.	+
Host body mass	.	.	.	+	+	.	.	.
Host density	+	.	+	.	.	-	.	.	.	-	.	-
Winter precipitation	.	-	-	.	-	.	-	.	-	.	-	.
3-week precipitation	+	-	.	.	x	x	x	x	x	x	x	x
Habitat/site	s	s	s	s	s	s	s	s	s	s	.	s
Season	.	s	s	.	s	s	s	s	s	.	.	s
Host species	.	x	.	x	s	s	s	.	x	s	x	.

* indicates that the host is in the analysis of that parasite. For habitat/site, season, and host species s = significant, see Results.

sites were selected for statistical analysis, and the results combined for the full 10 yr, the effect of sample size is not a problem in most comparisons here (Gregory and Blackburn, 1991). However, prevalence measures can be misleading when sample sizes vary greatly, and the raw data must be consulted to discern the sample sizes of the host populations and the number of individuals infected by a parasite (Appendix A).

Our study showed a conservative estimate of 29 parasite species in 5 host species, which supports the hypothesis that there are more parasite species than free-living species (Windsor, 1998). *E. chobotari*, *H. deserti*, *M. dipodomis*, and *P. dipodomis* are the most prevalent parasites (Table II, Appendix A).

There is a dramatic difference in the percentage of species of *Dipodomys* infected with any parasite versus species of *Perognathus* (Table IV). *Perognathus* individuals are less likely to be parasitized by any parasite than *Dipodomys* individuals (Table IV).

Insectivory has been recorded in a few studies for *Dipodomys* species mainly from stomach content (Table I). These 10-yr data confirm that all of these heteromyid species consume intermediate host species because there were 10 heteroxenic helminth species infecting *D. ordii*, 9 infecting *D. merriami*, 5 species infecting *P. flavescens* and *D. spectabilis*, and 4 species infecting *P. flavus* at the SNWR (Appendix A). Unfortunately, not much is known about the life cycles of these particular parasite species.

In the logistic regression, we are interested in which independent variables predict the prevalence of a parasite (Table III). If the variable is significant, then the raw data can be examined for meaning. Of these 12 parasites, none share an identical set of significant variables, which illustrates the uniqueness

of each parasite regardless of life cycle and taxonomic grouping (Table III). For this reason, the grouping of these parasites by life cycle or taxonomic level above genus was avoided because the group result masked the variation among the individual parasites. This illustrates that parasites are living independently of each other and that there may be more influential variables at work that were not considered here.

Precipitation in the southwestern United States is unpredictable and generally scarce. Most of the 10 yr in this study were a mixture of dry and wet summer and winter seasons with 1 extremely wet year, 1992, and 2 extremely dry years, 1989 and 1996 (Fig. 2). Winter precipitation reflected how wet or dry the previous winter was at the SNWR and is a better reflection of yearly precipitation than summer or monsoonal rainfall. As winter precipitation increases, 6 parasite prevalences decrease (Table III). Further analysis of these data during each year did not show that a particularly dry or wet year influenced all parasite prevalences. Ernest et al. (2000) examined all rodents at the SNWR and found that the rodent densities at these sites were correlated with precipitation from various periods of the previous year; however, these correlations were not significant, suggesting that other factors, such as predation and competition, may have more influence on densities. Perhaps more moisture in the area gives the rodents more vegetative food choice, reducing their intake of insects that are intermediate hosts to some of these parasites. However, monoxenic parasites also decrease in prevalence with higher winter precipitation, which seems counterintuitive. We would expect that with higher precipitation, more of the propagules from the monoxenic parasites would be viable in the environment and infect more individuals.

We noticed that as winter precipitation increases, host num-

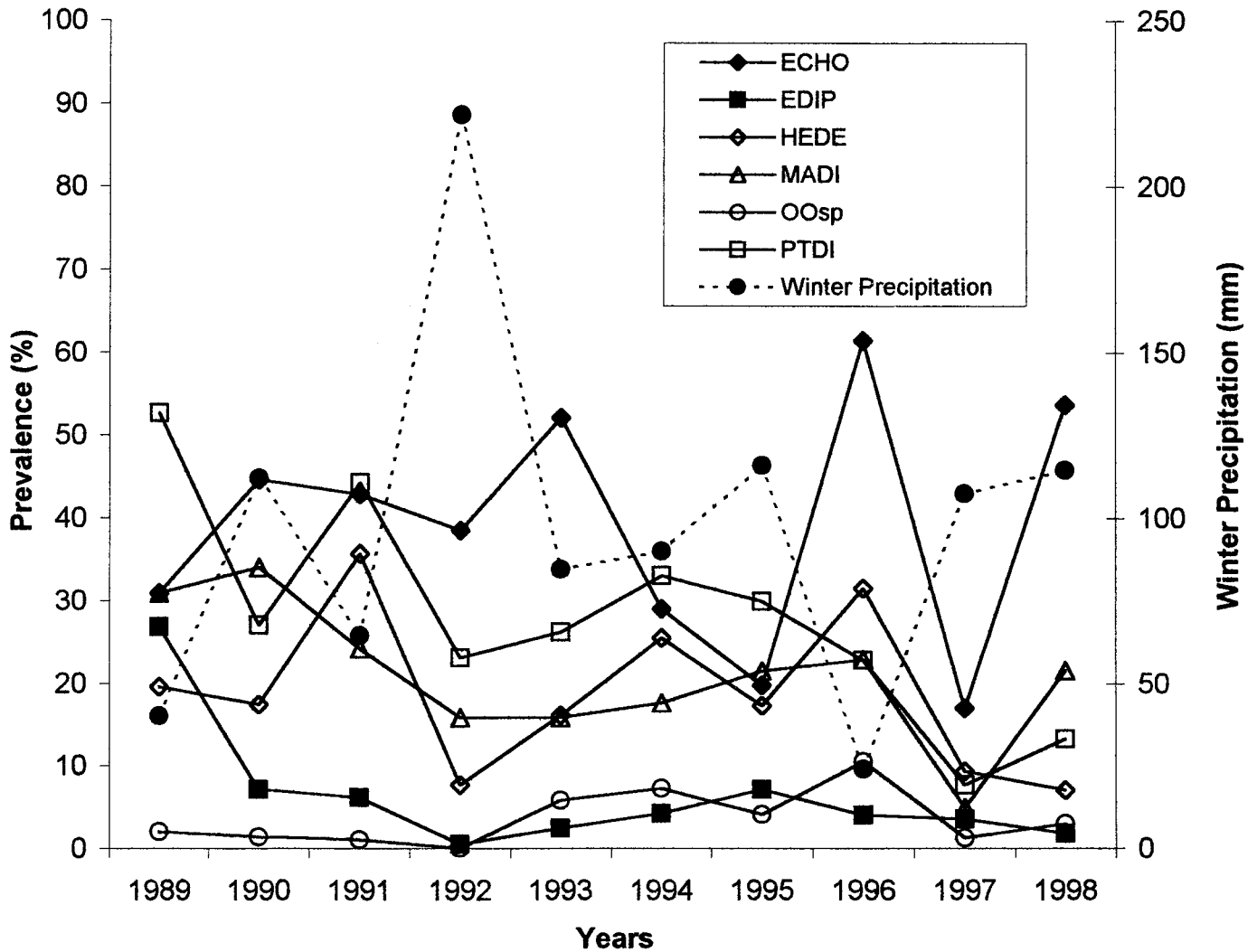


FIGURE 3. *Eimeria chobotari* (ECHO), *E. dipodomys* (EDIP), *Heteromyoxuris deserti* (HEDE), *Mastophorus dipodomis* (MADI), *Oochoristica* sp. (OOSp), and *Pterygodermatites dipodomis* (PTDI) prevalences from 1989–1998 and winter precipitation (see Methods).

bers increase and parasite prevalence decreases (Figs. 2, 3). This may just be a reflection of the effect of host sample size on prevalence, especially if parasite infections remain fairly constant (Gregory and Blackburn, 1991). This is why it is important to look at the raw data. For instance, in 1996 there was a drought and very few rodents (Fig. 2). However, some were infected, which produced high prevalences (Fig. 3). In 1997,

there was more precipitation and rodent populations rebounded, yet all of the parasite prevalences decreased even though more animals were infected in 1997 than 1996 (Appendix A).

Site and season are significant variables for a majority of the parasites (Table III). Site encompasses a plethora of factors that are potentially difficult to control and more difficult to evaluate. It is difficult to speculate about the differences in parasite prev-

TABLE IV. Percentage of each heteromyid species infected with 1 to 6 parasite species at the University of New Mexico Long Term Ecological Research Program on the Sevilleta National Wildlife Refuge, Socorro County, New Mexico, 1989–1998.

Heteromyid species	No. parasite species						Total percentage (infected/collected*)
	1	2	3	4	5	6	
<i>Dipodomys merriami</i>	30	25	13	3.0	0.3	0.1	71 (949/1,337)
<i>D. ordii</i>	40	11	3.0	0.4	0.1	0	55 (388/705)
<i>D. spectabilis</i>	47	27	6.0	0.4	0	0	80 (187/234)
<i>Perognathus flavescens</i>	14	1.0	0	0.3	0	0	15 (45/300)
<i>P. flavus</i>	15	1.0	0.1	0	0	0	16 (142/890)

* Only individuals with fecal and necropsy samples were used.

alence between seasons with only 2 sampling times in a year. Sampling every month in a year would give a more complete picture of seasonal prevalence variation among parasites in these hosts.

There were no strong correlations between parasites. This suggests host specificity or parasite competition, or both, within individuals.

Although we only looked at intestinal parasites in these 5 host species combining 10 yr, sites, and seasons, the monoxenic and heteroxenic debate can be examined. There are 11 heteroxenic helminth species and 6 monoxenic helminth species infecting these 5 rodent species. This does not follow Dobson's (1989) hypothesis that xeric hosts will have more monoxenic helminths. Yet neither does it support May and Anderson's (1979) hypothesis that heteroxenic helminths will dominate host populations at low densities; when we examined the number of monoxenic versus heteroxenic helminth species in a year with different densities, the heteroxenic helminths outnumbered or equaled the monoxenic helminths in almost every host species (data not shown). Information on intermediate hosts and their densities may help to explain why heteroxenic helminth species are more numerous in these rodents (Patrick, 1994).

Host densities fluctuate and parasites persist. Dobson's hypothesis (1989) provides an explanation for how macroparasites exist in xeric environments. Although it seems plausible for animals that span mesic and xeric habitats, most of these rodent species have evolved and proliferate in this extreme habitat. Parasites are complex, and to generalize about life cycles only using helminths disregards many other parasites. If the coccidia are added, then monoxenic parasite species outnumber or equal heteroxenic parasites in almost every host species in both low- and high-density years. These data suggest that within helminth species, heteroxenic species are more numerous than monoxenic species. However, among all intestinal parasites that we surveyed, monoxenic parasite species are more numerous than heteroxenic parasite species.

Overall, the most significant variables predicting parasite prevalences are site, season, and winter precipitation. Some parasite prevalences exhibit a negative relation to winter precipitation, which may be a secondary effect of host density changes. The parasite prevalences in these rodents at the SNWR vary in independent and complex ways. Grouping of parasites should be avoided above the generic level. Future work is needed to examine each parasite species more thoroughly.

ACKNOWLEDGMENTS

This work is dedicated to the memory of M. J. Patrick, who worked for 5 yr in UNM's Long Term Ecological Research (LTER) station and who identified many of the helminths. Thank you to all of the mammal and parasite crew workers led by S. K. M. Ernest, W. D. Wilson, and M. Friggens. M. D. Dailey and J. E. Ubelaker helped with identification of the helminths, and the Duszynski Lab community identified the coccidia, especially L. Couch. J. M. Roberts and J. Craig provided invaluable assistance with the statistics and SAS. My deepest gratitude to E. H. Decker for his editing and unending support. We also thank 2 anonymous referees for their comments. This project was supported by the UNM Sevilleta LTER program, publication no. 174, (NSF, BSR-88-11906; DEB 95-9411976)

and by a Survey and Inventory grant (NSF, DEB-95-05025) to D.W.D.

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