Intestinal helminths of spiny mice (*Acomys cahirinus dimidiatus*) from St Katherine's Protectorate in the Sinai, Egypt

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Abstract

Spiny mice, *Acomys cahirinus dimidiatus*, inhabiting the wadis close to St Katherine in the mountains of the Sinai peninsula, were trapped and their helminth parasites were studied. Sixty one mice provided faeces for analysis and 27 were killed and autopsied. Six species of helminths were recorded (the spirurid nematodes, *Protospirura muricola* (74.1%) and *Mastophorus muris* (11.1%), the oxyuroid nematodes, *Dentostomella kuntzi* (59.3%), *Aspiculuris africana* (3.7%), and *Syphacia minuta* (3.7%) and the hymenolepidid cestode *Rodentolepis negevi* (18.5%)). The spirurids were the dominant species present, accounting for up to 0.87% of total host body weight. Analysis of worm weights and lengths suggested that transmission had been taking place in the months preceding our study. No sex difference in the prevalence or abundance of spirurids was detected. Significant differences were identified in the abundance of total nematode burdens and the mean helminth species richness between the three wadis which provided multiple captures of mice. There was also a marked effect of host age on both parameters. A highly significant positive correlation between spirurid egg counts and total worm biomass indicated that non-invasive techniques based on egg counts could be used to quantify worm burdens and when this technique was applied to a larger sample size ($n = 61$), a significant difference between sites but no host sex or age effects were detected for spirurid faecal egg counts. The data suggest that there are differences between helminth component communities infecting spiny mice in different neighbouring wadis, a hypothesis which will be explored further through our continuing studies in the Sinai.

Introduction

The ecology, and particularly the component community structure, of helminth parasites in small rodent populations has been well documented in temperate regions of Europe (Kisielewska, 1970; Haukisalmi *et al*., 1988; Montgomery & Montgomery, 1990; Abu-Madi *et al*., 1998) and northern America (Murphy, 1952; Grundman, 1957; Boggs *et al*., 1991). In contrast, and despite the wealth of information on species lists and taxonomy (Myers *et al*., 1962), there is little comparable data for rodents living in the tropics (Ow-Yang, 1971). In particular, ecological studies on the parasites of rodents inhabiting hostile, arid regions in the Middle East and Africa are scarce (Greenberg, 1969; Erhardova-Kotrla & Daniel, 1970; Wertheim & Greenberg, 1970) and little is known about the relative importance of factors responsible for variation in the helminth infracommunity structures of small rodents inhabiting these regions.

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The recently established St Katherine's Protectorate in the Sinai Mountains of Egypt is a unique habitat, comprising an extensive and complex system of dry valleys (wadis) (Hobbs, 1995). It is known to be the most biologically diverse region of all Egypt, with a very high proportion of Egypt's fauna and flora (e.g. 2/3 of all the butterflies), including many endemics (44% of Egypt's endemic flora). The Park is currently being documented and studied at a variety of levels, with an ultimate goal of formulating specific management plans to preserve this habitat (Zalat & Gilbert, 1998). Projects include basic biodiversity studies to establish population and community structures within the wadi system (Willmer *et al*., 1994; Gilbert *et al*., 1996) and the impact on these of encroaching human settlement and pastoral activities. Studies have focused particularly on the effects of grazing on coevolved plant and insect pollination communities and, more recently, on the effects of increasing commensalism of rodent communities and rodent-borne parasites.

Little is known about the diseases of wild animals in the region, but, as part of the documentation of the wild life in the Park, rodents were trapped and identified, creating an opportunity for the assessment of their parasite burdens. We report here the results of our preliminary investigations into the diversity of parasitic helminths of the most common desert rodent in the region, the Egyptian spiny mouse *Acomys cahirinus dimidiatus*. Our second objective was to assess whether the helminth component community structures of small rodent populations living in five disparate wadis differed, particularly with respect to the dominant parasite species. Because of the fragile nature of the local habitats and in order to enable long-term studies to be initiated, it was important to establish for the future whether helminth burdens could be monitored reliably by non-invasive methods. If successful, this would enable subsequent projects to minimize the numbers of animals killed for research purposes. Our third objective was therefore to evaluate faecal analysis as a method for quantifying infections of the dominant helminths, the spirurid nematodes *Protospirura muricola* and *Mastophorus muris*.

Materials and methods

The study sites

The study was conducted during a two week period in May–June 1997 and was based at the Environmental Research Centre of Suez Canal University, located on the periphery of the town of St Katherine, Central Sinai, Egypt. All trapping was carried out close to St Katherine, in the surrounding wadis. The environment has been described by Hobbs (1995) and Zalat & Gilbert (1998). Wadi El Arbain (called Wadi El Lega until 1979) and Wadi Tofaha radiate from the town of St Katherine, and are fully described in Willmer *et al*. (1994) and Gilbert *et al*. (1996). Wadi Abu Seylah is part of the Plain of El Raha and is currently the site of the town's refuse dump. Wadi Gebal is a system of wadis separated from St Katherine by a ridge of mountains, and is well known as a popular destination for trekkers (fully described in Zalat & Gilbert, 1998). A feature of the wadis of the high mountains is the many walled Bedouin gardens, built around sources of water, and acting as foci for the fauna and flora (Hobbs, 1995). Trapping usually took place in or near such gardens, which can be considered as semi-isolated vegetated patches in the landscape. Wadi Sheikh is a wide flat wadi running towards the Oasis of Feiran from St Katherine, bearing the road to Feiran and the Suez Gulf.

Rodents

Rodents were caught in Sherman traps placed among the rocks and boulders in the wadi bases and partially up the lower slopes. Traps were set out at dusk and inspected in the early morning soon after sunrise when captured animals were removed. The traps were then closed and reset in the evening. All animals were inspected in the field. Each was identified, sexed, weighed, measured, scrutinized for any evident lesions, then fur-marked to enable identification on recapture and either released near to the point of capture or brought back to the centre for autopsy. Animals were trapped on several nights in three of the sites but in the case of Wadi Gebal and Wadi Sheikh for no more than a single night because of the distance from the field centre. Faecal samples were taken from the traps and placed immediately into modified SAF fluid (9 g anhydrous sodium acetate, 20 ml glacial acetic acid, 100 ml 40% formaldehyde and distilled water to 1l, with pH = 4.15) in 1.5 ml plastic tubes, for subsequent transport to Nottingham.

Worm recovery

Animals for autopsy were brought back to the field centre, and killed usually within 24 h of capture. Each was again carefully inspected for ectoparasites and any evident lesions. The entire intestinal tract was removed, the stomach was examined immediately after its removal and worms were counted, collected into labelled, air-tight tubes and preserved in 70% ethanol for subsequent examination. Some of the small intestines were also examined on the same day, but in most cases the whole of the remaining intestinal tract (small intestine, caecum and colon) was placed into 10% formalin and conveyed to Nottingham for subsequent examination. All of these preserved intestines were carefully examined in February–March 1998, 9–10 months after the expedition. Worms were removed and transferred to 70% ethanol.

Identification of worms

Nematodes were removed from 70% ethanol and cleared in lactoglycerol on glass slides immediately before examination by light microscopy. Relevant measurements were recorded through a calibrated eyepiece graticule and the data were compared with published species descriptions. In some cases, scanning electron microscopy was used to differentiate between species, particularly in the case of *Protospirura muricola* and *Mastophorus muris*. Specimens for scanning electron microscopy were dehydrated stepwise to 100% ethanol, critical point dried, mounted with the anterior end facing upwards on metal stubs with silver adhesive, sputter coated with gold (Polaron E5100), and examined with a Joel 840 scanning electron microscope at 15 kV.

Worm biomass and length

Each intact worm was individually weighed on an electronic top-pan balance reading to the nearest 0.1 mg. The worms were removed from 70% ethanol, blotted with tissue paper to absorb surface alcohol and then placed on the balance. Readings were taken exactly 20 s after removal from the tube. All nematodes were drawn to scale under appropriate magnification using a camera lucida. Line drawings were then converted into units of length by using a digitizer pad and an IBM computer with a programme for conversion of lengths traced into metric units. Each drawing was measured three times and the mean value used. All intact worms were measured.

Egg counts

It was not possible to analyse faecal samples at the field centre, so all specimens were carefully examined in the period November 1997 to February 1998 in Nottingham. The material in each tube was broken down by careful stirring with a sharp seeker, until no large clumps remained. Each tube was then centrifuged at 1000 rpm for 10 min. The height of the deposit was measured and converted to volume by comparison with calibrated tubes. The total volume was adjusted to no more than 1 ml. In turn, the contents of each tube were resuspended with the aid of a standard laboratory bench rotamixer and a 10 μl aliquot was removed, transferred to a glass slide, covered with a cover slip and examined under the microscope. All eggs observed in each specimen were identified by morphology, measured, photographed and each type was counted separately. Four samples were examined from each tube, and all specimens which failed to show any eggs were re-examined four more times. Egg counts were then expressed as eggs per ml of faecal deposit.

Statistical analysis

Summary statistics are presented as mean abundance (including all uninfected animals) ± standard error of the mean (S.E.M.). However, following multifactorial ANOVA, we also present fitted (least squares) means for factors showing significant effects.

Prevalence is given as the percentage of animals carrying a specific parasite taxon or taxa and was analysed by maximum likelihood techniques based on log linear analysis of contingency tables, implemented by the software package, Statgraphics Version 7. Beginning with the most complex model, involving all possible main effects and interactions, those combinations which did not contribute significantly to explaining variation in the data were eliminated stepwise beginning with the least significant. A minimum sufficient model was then obtained, for which the likelihood ratio of χ^2 squared was not significant, indicating that the model was sufficient in explaining the data.

Parametric statistics (multifactorial ANOVA, Statgraphics Version 7) were used for analysis of worm burdens, where data (sometimes suitably transformed) met the required assumptions, otherwise non-parametric tests were employed. The negative binomial exponent k was estimated using the maximum likelihood procedure of Elliott (1977). The goodness of fit to the negative binomial distribution was tested by χ^2.

Results

Numbers of mice examined

The number of *A. cahirinus dimidiatus* caught at each site and examined by faecal analysis and by autopsy is shown in table 1. In total, 61 mice (28 males and 33 females) were caught and provided faeces for analysis. Of these, 27 (15 males and 12 females) were killed and autopsied.

Helminth species

Six species of helminths were recovered from the autopsied animals (table 2) and 96.3% harboured at least one species. The majority of mice carried two helminth species, (fig. 1) and the mean species richness (no. of helminth species per mouse) was 1.7 ± 0.1, with a slightly,

Table 1. Number of *Acomys cahirinus dimidiatus* examined by faecal analysis and by autopsy in relation to host sex, age and site of capture.

Site	Sex	Age	Autopsy	Faecal analysis
Wadi El-Arbain	Male	Adult	5	14
	Female	Adult	5	13
Wadi Tofaha	Male	Juvenile	3	4
	Male	Adult	2	5
	Female	Juvenile	0	3
	Female	Adult	2	12
Wadi Abu Seylah	Male	Juvenile	1	1
	Male	Adult	3	3
	Female	Adult	4	4
Wadi Sheikh	Male	Adult	1	1
Wadi Gebal	Female	Adult	1	1
Total			27	61

Table 2. The prevalence and abundance of intestinal helminths in *Acomys cahirinus dimidiatus*, from St Katherine's Protectorate in the Sinai, Egypt.

Species of parasites	Sex of host	Prevalence	Abundance			
			Mean ± S.E.M.		Median	Range
Protospirura muricola	Male mice	66.7	4.7	1.3	3	0–15
	Female mice	83.3	7.3	2.4	4	0–27
	Sexes combined	74.1	5.9	1.3	3	0–27
Mastophorus muris	Male mice	6.7	0.2	0.2	0	0–3
	Female mice	16.7	1.8	1.4	0	0–17
	Sexes combined	11.1	0.9	0.6	0	0–17
Dentostomella kuntzi	Male mice	53.3	2.8	1.1	1	0–12
	Female mice	66.7	3.1	0.8	2	0–7
	Sexes combined	59.3	2.9	0.7	1	0–12
Aspiculuris africana	Male mice	6.7	1.5	1.5	0	0–22
	Female mice	0	0	0	0	0
	Sexes combined	3.7	0.8	0.8	0	0–22
Syphacia minuta	Male mice	0	0	0	0	0
	Female mice	8.3	6.4	6.4	0	0–77
	Sexes combined	3.7	2.9	2.9	0	0–77
Rodentolepis negevi	Male mice	20.0	0.7	0.5	0	0–8
	Female mice	16.7	1.0	0.7	0	0–7
	Sexes combined	18.5	0.8	0.4	0	0–8
Nematoda combined	Male mice	86.7	9.2	2.7	6	0–38
	Female mice	100.0	18.5	6.2	13	2–81
	Sexes combined	92.6	13.4	3.2	10	0–81

although not significantly, higher mean among female compared with male mice (females = 1.92 ± 0.15, males = 1.53 ± 0.19; Kruskal-Wallis test $H = 2.265$, P = NS).

Spirurid nematodes were common in the stomachs of the mice. *Protospirura muricola* Geodelst, 1916 was the dominant species occurring at four of the five sites studied, but *Mastophorus muris* (Gmelin, 1790 = *Protospirura muris*) was also present in three of the autopsied animals, one from each of Wadi Gebal, El Arbain and Tofaha (table 3). The two species could not be reliably distinguished on morphological grounds when the head of the worm had been damaged during processing, and no attempt was made to differentiate spirurid larvae. Hence, in some of the analyses which follow, the two species are treated as part of a single taxon. Collectively, the spirurids were present in 85.2% of the mice (73.3% of males and 100% of females).

Three species of oxyuroids were identified but only one, *Dentostomella kuntzi* Myers, 1961 (Heteroxynematidae) was widespread infecting 59.3% of the animals, although this species was relatively rare in Wadi El Arbain in comparison with other sites. *Syphacia minuta* Greenberg, 1969 (Oxyuridae) was found in one animal from Wadi Gebal, while *Aspiculuris africana* Quentin, 1966 (Heteroxynematidae) was found in a single mouse from Wadi Abu Seylah.

Four mice carried hymenolepidid tapeworms. Two individuals contained only scoleces, but the remaining two mice were infected with gravid worms which conformed to the description of *Rodentolepis negevi* Greenberg, 1969

Table 3. Mean parasite abundance by site of capture.

Site	Mean worm burden of parasite taxon[1] (± S.E.M.)				Mean no. of species[1] (± S.E.M.)	
	Spirurids	*D. kuntzi*	All Nematoda	Cestoda	Nematoda	Helminths
Wadi El-Arbain	6.4 ± 1.84	0.9 ± 0.71	7.3 ± 1.86	1.7 ± 0.98	1.1 ± 0.18	1.5 ± 0.17
Wadi Tofaha	4.1 ± 2.25	3.3 ± 1.44	7.4 ± 3.08	0.7 ± 0.7	1.4 ± 0.30	1.6 ± 0.37
Wadi Abu Seylah	9.3 ± 3.09	5.8 ± 1.46	17.8 ± 4.67	0	2.0 ± 0.19	2.0 ± 0.19
Wadi Sheikh	12	1	13	0	2	2
Wadi Gebal	4	0	81	0	2	2

[1] Arthimetic means of parasite abundance based on all the animals autopsied (including the uninfected mice) at each site.

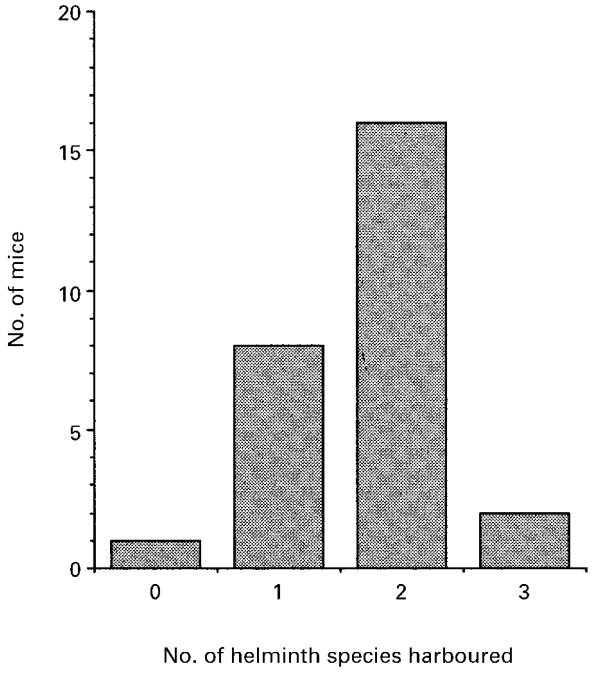

Fig. 1. Frequency distribution of number of helminth species harboured by the mice which were autopsied ($n=27$).

(Hymenolepididae Ariola, 1899). This species was found only in Wadi El Arbain and Wadi Tofaha.

Frequency distribution of the spirurid nematodes and D. kuntzi

The distribution of both of the spirurid nematodes and *D. kuntzi*, in the host population, conformed to the negative binomial distribution as illustrated in fig. 2.

Effect of site of capture on nematode abundance and helminth species richness

Statistical analysis was limited to the three sites which yielded multiple captures: Wadi El Arbain, Wadi Tofaha and Wadi Abu Seylah. Multifactorial analysis of variance for these three sites, taking age, sex and body weight into account, showed a significant main effect of site on total nematode burden ($F_{2,19}=4.075$, $P=0.034$), with abundance of nematodes increasing from Wadi El Arbain, through Wadi Tofaha to Wadi Abu Seylah (fig. 3A). A similar result was found for the effect of site on mean species richness (fig. 3C; $F_{2,19}=5.373$, $P=0.014$). No significant effect of site emerged for any other overall measure of parasite burden. Therefore, mice from Wadi Abu Seylah showed a higher abundance of nematodes and had more species of helminths per individual than those from Wadi El Arbain, with Wadi Tofaha showing similar species richness to the former and an intermediate level for abundance of nematodes.

Dentostomella kuntzi was relatively rare in Wadi El Arbain compared with the other sites (table 3) and multifactorial analysis of variance for the three sites yielding multiple captures, taking age, sex and body weight into account, confirmed that there was a significant main

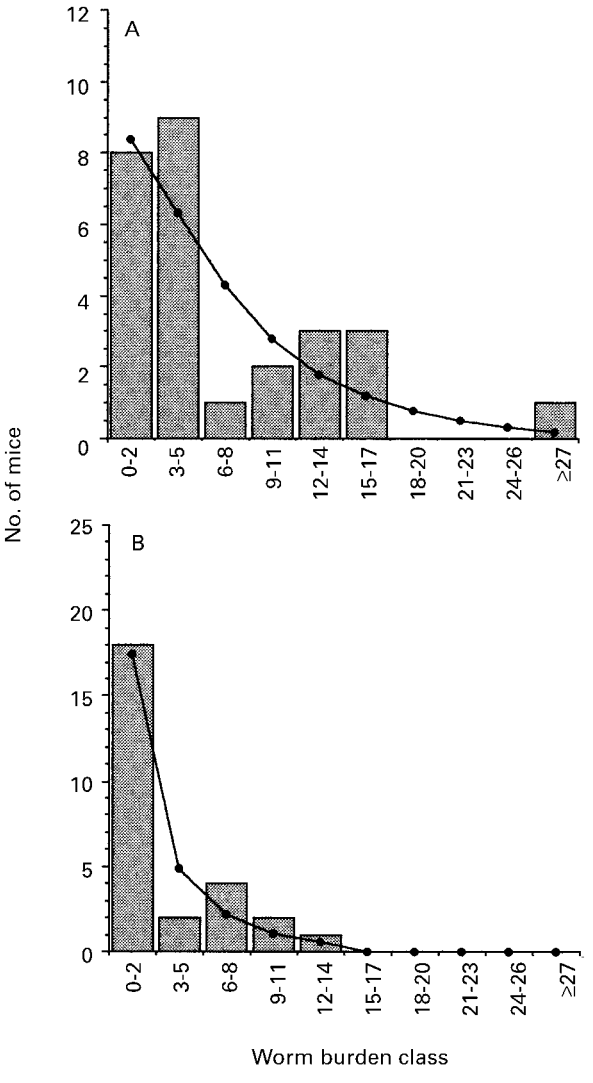

Fig. 2. Frequency distribution of spirurid nematodes (A) and *Dentostomella kuntzi* (B) in *Acomys cahirinus dimidiatus* ($n=27$). Columns illustrate the observed data and the line graph shows the fitted negative binomial distribution. For A, $k=1.197\pm0.620$ ($\chi^2=1.51$, dof = 2, $P=0.216$); for B, $k=0.456\pm0.304$ ($\chi^2=0.02$, dof = 1, $P=0.870$).

effect of site on *D. kuntzi* worm burdens ($\log_{10}(x+1)$ transformed) worm burdens, $F_{2,19}=12.976$, $P=0.0003$): worm burdens increased from El Arbain, through Wadi Tofaha to Wadi Abu Seylah. No difference emerged from analysis of the spirurid nematodes by site of capture.

Effect of host age on nematode abundance and helminth species richness

Multifactorial analysis of variance for the two age categories (mature versus juvenile) across the three wadis yielding multiple captures, taking site of capture, sex and body weight into account, revealed a significant main effect of age on abundance of nematodes ($F_{1,19}=4.823$, $P=0.041$; abundance of nematodes increased with age, fig. 3B). A similar, but considerably more marked effect was found

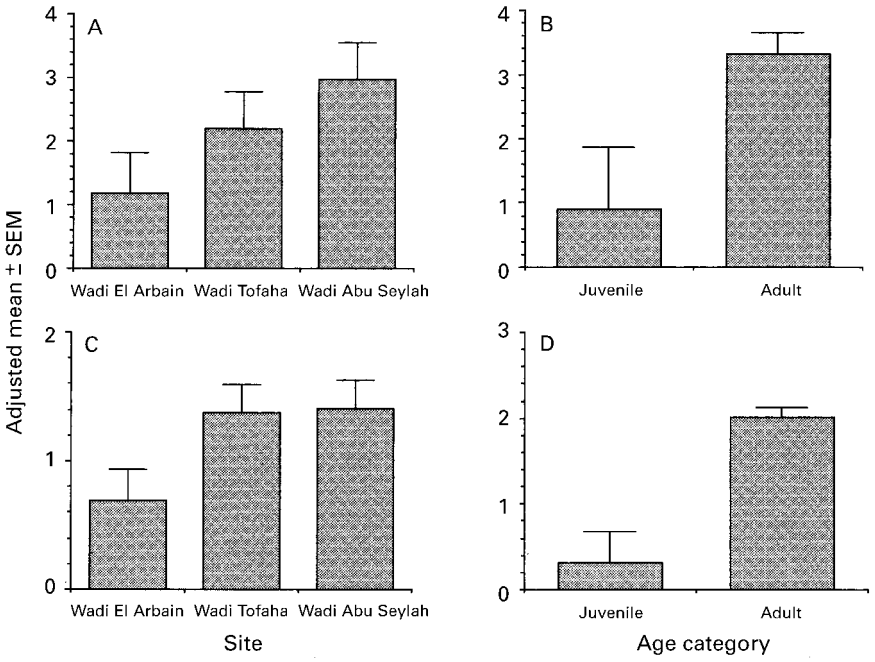

Fig. 3. Variation in abundance of nematode infections (A and B) and helminth species richness (C and D) between sites of capture (A and C) and in relation to host age (B and D). The figure shows adjusted means as fitted by a 3-way ANOVA (site + sex + age) with weight as a covariate on (A and B) total nematode burdens (square root transformed data) and (C and D) number of helminth species per mouse (not transformed data). For full statistical analysis see text.

for the effect of age on mean species richness (fig. 3D; $F_{1,19} = 16.537$, $P = 0.0007$). There was no significant effect of host age on any other measure of parasite burden.

The effect of other host factors on helminth abundance and species richness

No effect of host sex was detected on any of the measures of parasite abundance nor on helminth species richness. There was no significant independent effect of body weight, when site of capture, sex and age were taken into account.

Sex ratio of the spirurid nematodes and D. kuntzi

A total of 183 spirurid nematodes were removed from the 23 infected mice giving a mean worm burden of 8.0 for infected animals. Forty seven worms could not be sexed and were designated as immature larvae (L3, and probably mostly L4s), 50 were males and 86 females. The male/female ratio of spirurid worms was therefore 0.58 with 36.7% of the adult worm population represented by males. The three mice which carried *M. muris* appeared to have just this species and no *P. muricola*. The sex ratio was 0.57 with 36.4% male worms and for

Table 4. The prevalence of infection with spirurid nematodes in *Acomys cahirinus dimidiatus* as detected by faecal analysis, in relation to host sex, age and site of capture.

Site	Sex	Age	No +ve	Total examined	Prevalence in adult mice
Wadi El Arbain	Male	Adult	8	14	
	Female	Adult	6	13	51.9
Wadi Tofaha	Male	Juvenile	0	4	
	Male	Adult	1	5	
	Female	Juvenile	0	3	
	Female	Adult	2	12	17.6
Wadi Abu Seylah	Male	Juvenile	0	1	
	Male	Adult	2	3	
	Female	Adult	3	4	71.4
Wadi Sheikh	Male	Adult	1	1	
Wadi Gebal	Female	Adult	1	1	
Total			24	61	

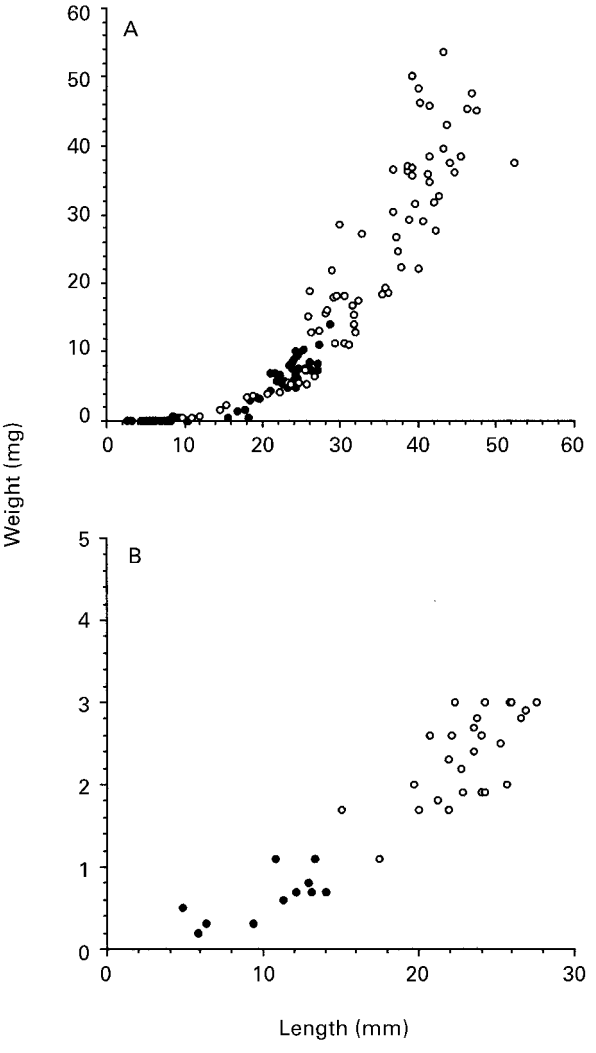

Fig. 4. Weight for length relationship of (A) the spirurid nematodes (*Mastophorus muris* and *Protospirura muricola*, combined) and (B) *Dentostomella kuntzi*. *Mastophorus muris* and *P. muricola* were combined because they could not be accurately separated in many specimens, especially the larval worms. The vast majority of worms which were confidently speciated were *P. muricola*. See text for full details. ●, Male worms; ○, female worms.

P. muricola, separately, the values were 0.58 and 36.8%, respectively.

Sixteen mice yielded a total of 79 *D. kuntzi* with a mean worm burden among infected animals of 4.9 worms. Eleven worms were male and 30 female giving a male/female ratio of 0.37 and males representing 26.8% of the adult population.

Weight/length of the spirurid nematodes and D. kuntzi

The lengths of 161 spirurid worms (43 larvae, 47 males and 71 female worms) were measured, the remaining worms being incomplete or punctured. Forty eight males and 76 females were also weighed. Most of the larvae were too small to weigh (< 0.1 mg). Eleven male and 26 female *D. kuntzi* were also measured and weighed. The relationships between length and weight of these worms are illustrated in fig. 4 and frequency distributions of length and weight are presented in fig. 5.

In this sample of mice, male spirurids rarely grew to a length in excess of 28 mm although, at 50 mm, female worms achieved a length almost twice as long. The maximum weight for males was 14.1 mg and for females 28.7 mg. *Dentostomella kuntzi* was a shorter, and considerably lighter nematode with a maximum length of 13.34 mm for males and 27.5 mm for females and maximum weights of 1.1 mg and 3 mg, respectively.

The spirurids, therefore, achieved a considerably greater biomass in the mice, and this is clearly shown in fig. 6 where the frequency distribution of the biomass of each of these taxa in the 27 autopsied animals is compared. One female mouse from Wadi El Tofaha carried a spirurid biomass (probably mostly *M. muris*) of 392.2 mg, representing 0.87% of its total body weight. The same animal had a *D. kuntzi* biomass of 4.6 mg. The highest value for mice carrying only *P. muricola* was 297.6 mg, representing 0.47% of total body weight.

Relationship between faecal egg counts and worm burden

The eggs of the spirurid worms were easily differentiated from the other species, but not from each other, and could be reliably quantified in faecal specimens only as spirurid eggs. Reassuringly, there were no false positives, but there were several false negatives. Of the 27 mice examined, eight had worms without detectable eggs in their faeces. Three of these had no female worms, but the remaining five did, and one had seven adult female worms.

We examined the relationship between eggs per ml of faeces (EPM) and various measures of parasite burden including total number of worms, number of female worms, number of male worms, total biomass, female worm biomass, etc. Stepwise partial regression analysis incorporating the total spirurid worm burden, length and weight of male and female worms and host body size (nose to anal length) as independent variables showed that EPM was predicted mainly by the total biomass of worms ($t_{23} = 11.78$, $P < 0.01$) with no other variables entering the equation (fig. 7).

Although the eggs of *D. kuntzi* were distinct enough for us to be certain about their identity, they were infrequently encountered. Of the 16 animals carrying this species, eggs were only detected in two, so no further analysis was possible. As in the case of the spirurids and *D. kuntzi*, the eggs of *A. africana* were distinct. Tapeworm eggs were treated collectively, although among the limited material available for examination the only species present was *R. negevi*.

Analysis of helminth burdens by faecal egg counts

As table 1 shows, faecal samples were examined from sixty one mice in total. The eggs of *D. kuntzi* were identified in only four mice (6.6%), those of *A. africana* in only one (1.6%) and cestode eggs in only five (8.2%) mice, limiting the scope for any further analysis of these species.

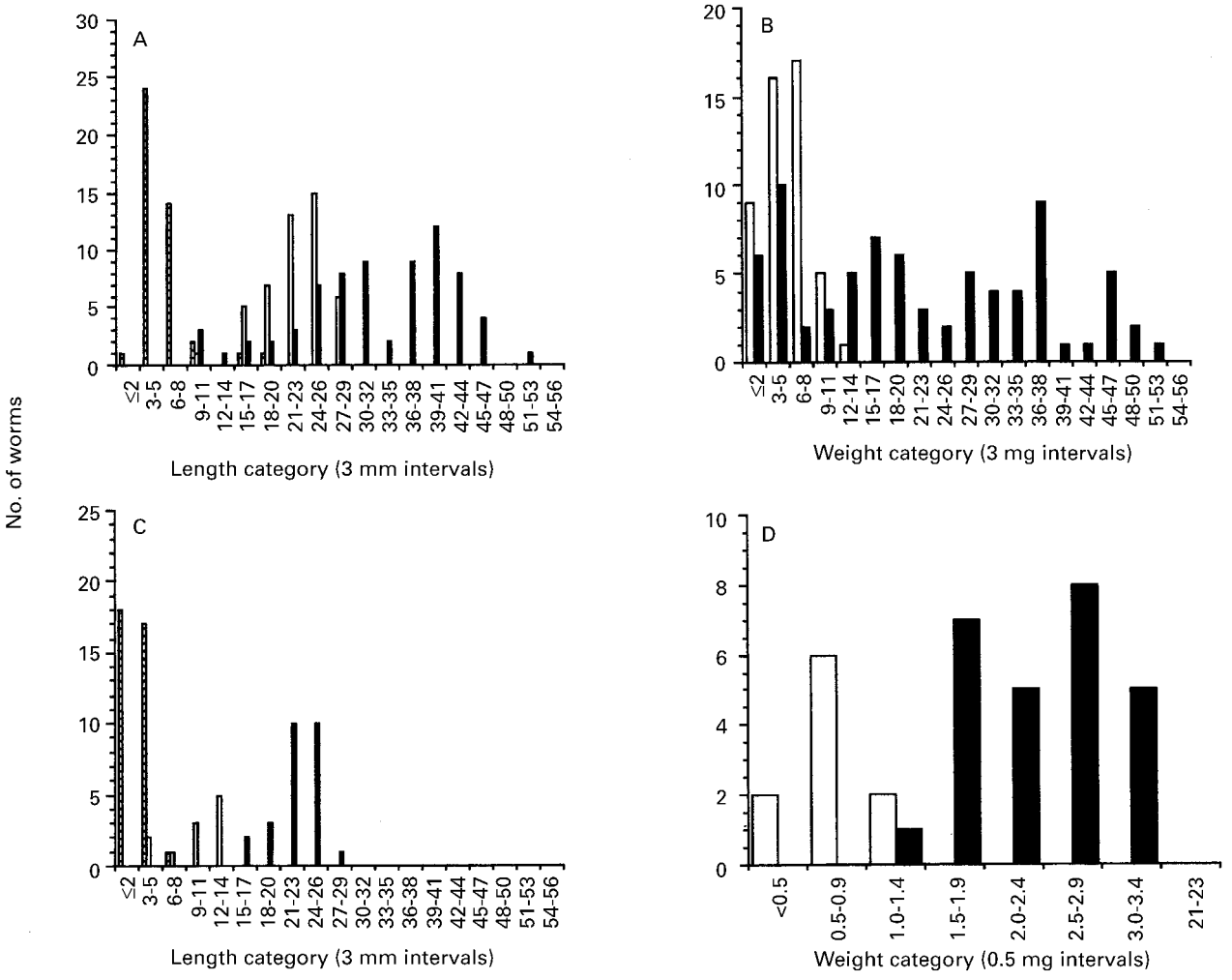

Fig. 5. Frequency distribution of the length (A and C) and weight (B and D) of larval, male and female spirurid nematodes (A and B) and *Dentostomella kuntzi* (C and D). ▤, Larvae; □, males; ■, females.

However, spirurid eggs were identified in 24 mice (39.3%), sufficient for more detailed analysis. The frequency distribution is shown in fig. 8, and prevalence by site of capture is summarized in table 4. The statistical analyses were again confined to the three wadis which yielded multiple captures of mice. Log-linear analysis of the prevalence of spirurid nematodes by maximum likelihood techniques revealed that three independent interactions explained the data: age × site, site × infection and age × infection (likelihood ration $\chi^2 = 5.091$, dof = 14, $P = 0.985$). The age × site interaction arose because juvenile mice were mainly from Wadi Tofaha. The age × infection interaction arose because the 24 positive samples all came from adult mice. The site × infection interaction indicated that the differences in prevalence between the wadis (table 4) were significant.

Quantitative analysis was again by a multifactorial analysis of variance for these three sites, taking age, sex and body weight into account and this revealed a significant main effect of site on EPM ($F_{2,53} = 3.38$, $P = 0.042$), with egg counts lowest in Wadi Tofaha, and highest in Wadi Abu Seylah (fig. 9). No significant effect of host age, weight or sex emerged from this analysis.

Discussion

Although the helminth parasites of *Acomys* spp. from Egypt have been studied previously, most published reports are taxonomic or species lists from surveys (Myers *et al.*, 1962; Kuntz & Myers, 1968; Ashour, 1980). Some give the prevalence of infection (Greenberg, 1969; Wertheim & Greenberg, 1970) in *Acomys* spp. in relation to habitat type but, to our knowledge, none provide detailed quantitative information on helminth component community structures, range of variation in infracommunity structures nor probe the underlying ecology of the host–parasite systems involved in depth. Our quantitative analyses of parasite burdens, and of faecal egg counts as measures of prevalence and abundance of adult spirurid nematodes, therefore build on the earlier studies by Wertheim & Greenberg (1970), making novel contributions to the understanding of the ecology of the helminths

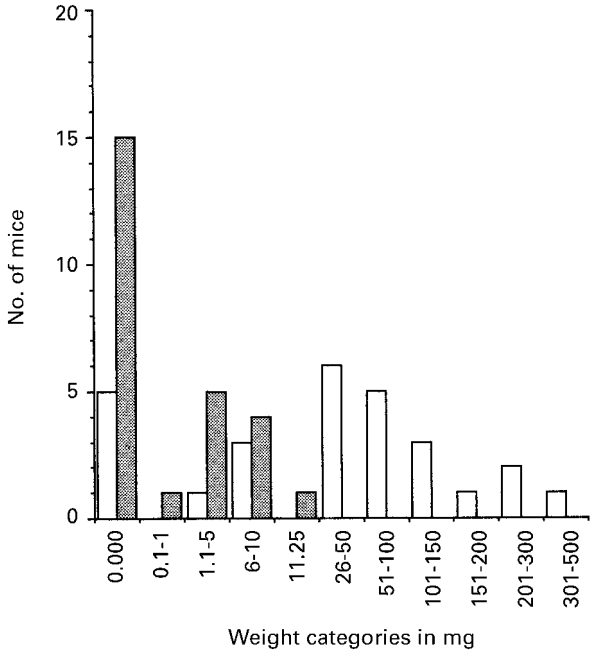

Fig. 6. Frequency distribution of the total worm biomass of spirurid nematodes (white columns) and *Dentostomella kuntzi* (grey columns) in the autopsied animals ($n = 27$).

of *A. cahirinus dimidiatus* inhabiting the harsh, fragile environment in the mountains of the Sinai peninsula.

All of the helminths recovered from the autopsied animals have been previously recorded from *Acomys* spp. in the Sinai (Wertheim & Greenberg, 1970) and the Middle East (Greenberg, 1969; Myers, 1954, 1961; Myers *et al.*, 1962; Kuntz & Myers, 1968). *Protospirura muricola* has a very wide host, ecological and geographical range, having been recorded from many different rodent species (Baylis, 1928) including the Zambian mole rat (Scharff *et al.*, 1997), commensal rodents (Tubangui, 1931; Baylis, 1928) and even primates (*Perodicticus potto*, Baylis, 1928; *Cebus capucinus*, Foster & Johnson, 1938, 1939). *Mastophorus muris* shows a global distribution in rodents (Bangs, 1985) and is known to occur in spiny mice in Egypt (Ashour, 1980). Our specimens of *Syphacia* corresponded to the brief description given by Greenberg (1969) and those *of A. africana* clearly belonged to the subgenus *Pseudoaspiculuris* Akhtar, 1955. The six species we identified constitute only a fraction of the total helminth fauna (17 species) reported from *A. dimidiatus* sampled right across the Sinai peninsula (Wertheim & Greenberg, 1970) but our sample was more limited and it is well recognized that parasite species richness in a given host community increases with sampling effort (Walther *et al.*, 1995). Moreover, although Wertheim & Greenberg (1970) sampled in the region of St Katherine, their analysis was based on the pooled data from all sites across the Sinai, and it may be that the helminth species richness at St Katherine is more limited than in the Sinai as a whole.

Perhaps the most interesting aspect of our findings was the marked dominance of the helminth component community of *A. cahirinus dimidiatus* by the spirurid

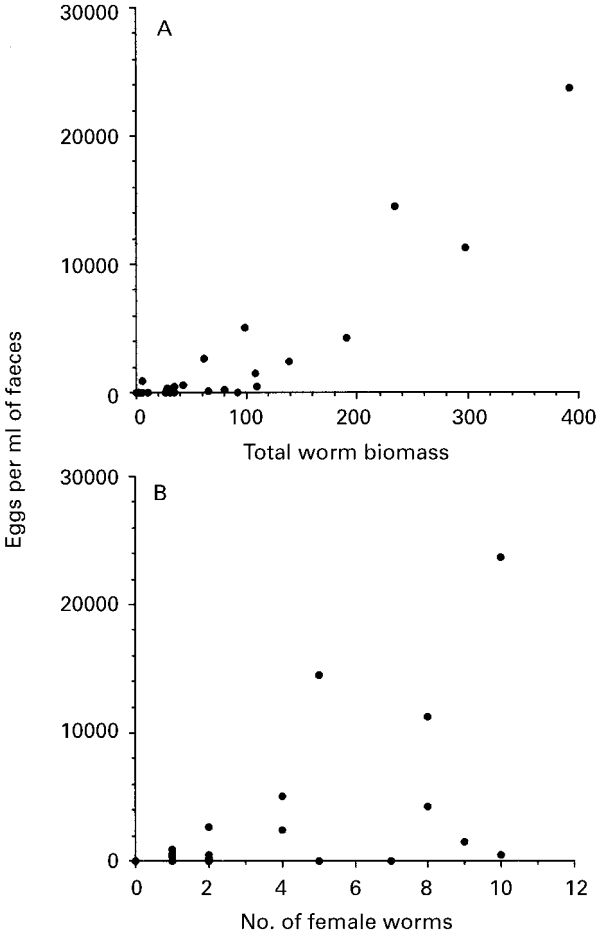

Fig. 7. Relationship between the concentration of eggs per ml of faeces and (A) total spirurid biomass and (B) the number of spirurid females recovered.

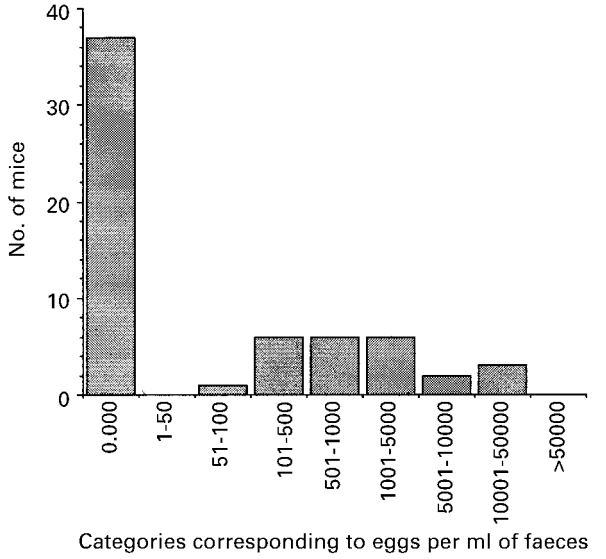

Fig. 8. Frequency distribution of spirurid faecal egg counts ($k = 0.228 \pm 0.063$, $\chi^2 = 0.29$, dof = 2, $P = 0.867$).

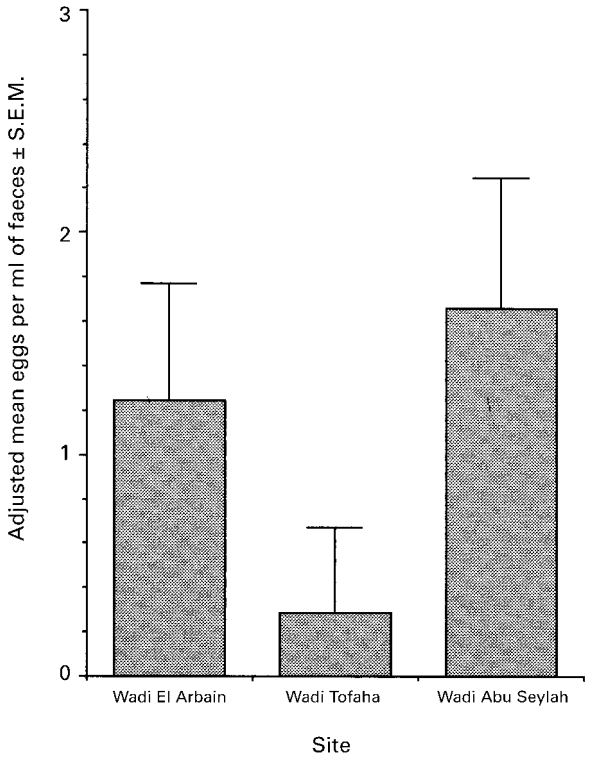

Fig. 9. Variation in spirurid faecal egg counts of mice captured from different wadis. The figure shows the adjusted means as fitted by a 3-way ANOVA (site + sex + age) with weight as a covariate on faecal egg counts (Log_{10} $(x+1)$ transformed). For full statistical analysis see text.

nematodes (85.2% prevalence), and particularly by *P. muricola* (74.1% prevalence). Earlier studies found an overall prevalence with *P. muricola* of only 19% and *M. muris* 5%, in a sample of six species of rodents from the whole of the Sinai (Wertheim & Greenberg 1970). However, these authors also detected a higher prevalence among *A. dimidiatus* from 'artificial habitats' (56.9 and 9.3%, respectively) compared with arid regions (6.1 and 6.1%, respectively). For the most part, our quantitative analysis of worm burdens did not distinguish between these two species because the two genera are very similar to each other and there is some confusion in the literature (Chitwood, 1938; Chabaud, 1975; Ashour, 1980; Scharff *et al*., 1993). *Protospirura muricola* and *M. muris* have very similar life cycles and host–parasite relationships but exploit different hosts. The developmental cycle of *P. muricola* has been described from limited experimental infections of rodents such as *Praomys jacksoni*, *Hybomys univittatus* and *Thamnomys* spp. (Quentin, 1969), laboratory rats and black-handed spider monkeys (*Ateles geoffroyi*) (Campos & Vargas, 1978) and from captive white-faced monkeys, *Cebus capucinus* (Foster & Johnson, 1939). That of *M. muris* has been reported from murid rodents (*Apodemus sylvaticus*, *Mus musculus* and *Calomys callosus*) (Quentin, 1970) and from laboratory rats (Shogaki *et al*., 1972). Quentin (1969) found that *P. muricola* had a prepatent period of 40 days although the prepatent period of the related species *Mastophorus columbiana* (previously, *Protospirura columbiana*, Chitwood, 1938) is about 2–3 months in duration (Cram, 1926) whilst that of *M. muris* is only about 28 days (Quentin, 1970). Scarff *et al*. (1997) list cockroaches, fleas and scarabeid beetles as the intermediate hosts of *P. muricola*. Foster & Johnson (1939) found that only one species of cockroach, *Leucophaea maderae*, harboured larvae and this was largely confirmed by Campos & Vargas (1977), however, Quentin (1969) reported earwigs (Dermaptera) as suitable hosts. Cram's (1926) attempts to infect cockroaches with *M. columbiana* suggests that some 5–6 weeks of development are necessary to reach infectivity in the intermediate host, although Quentin (1969) reported encysted third stage larvae of *P. muricola* in earwigs within 23 days of infection, and those of *M. muris* in locusts (*Locusta migratoria*), earwigs (*Labidura riparia*) and cockroaches (*Periplaneta americana*) within 4 weeks (Quentin, 1970), while Dyer & Olsen (1967) found that *Mastophorus numidica* reached infectivity in insect hosts only after 38 days.

The comparatively long period of development in the intermediate host and the long prepatent periods in definitive hosts, imply that *Mastophorus* and *Protospirura* are long-lived genera (Kirschenblatt, 1938; Rausch & Tiner, 1949), investing initially in growth and then a long period of fecundity. Our finding that only adult mice carried fecund worms and harboured a wide range of worm sizes are consistent with the idea that worm burdens accumulate in the stomachs of susceptible hosts over prolonged periods of time. Such a strategy would suit the environment in the Sinai, where insect life is highly seasonal and dependent on narrow windows when temperatures are not excessive and water is available. In this context Kirschenblatt (1938) concluded that the intensity of infection was not season-dependent although subsequently Grundman (1957) reported seasonal prevalence of *P. numidica* in various desert rodents in Utah, relating this to the seasonal abundance of insect intermediate hosts. Our expedition was limited to a two week period in late May–early June, and it is quite clear from the wide range of worm sizes that transmission had been occurring, probably for several months, preceding our sampling period. In fact, May–June are the last months when some rain is expected in the region following the wet season in December to February.

It is possible that worm burdens accumulate to levels which may exert some metabolic cost to the host. In one mouse we found 392.2 mg of biomass from 17 worms representing 0.87% of the body weight of the host. Four other animals also had over 100 mg of parasite burden. In these hosts the knot of stomach worms occupied a significant proportion of the volume of the stomach, and it will be interesting to determine whether such heavy worm burdens have consequences for appetite, frequency of feeding and efficiency of the digestive processes. However, we never found worms outside the stomach, as reported by Foster & Johnson (1939) who, in their heavily infected monkeys, observed worms both more anteriorly and more distally in the intestine, as well as throughout all the visceral organs.

Although *Acomys* spp. are the main hosts of *D. kuntzi* (Myers, 1961) incidental infections have also been recorded from *Arvicanthis niloticus* (Nile kusu grass rat), *Rattus*

rattus (Ashour & Lewis, 1982) and *Mus musculus* (Myers *et al*., 1962). In common with other oxyuroids, this species is probably transmitted directly, but if it were to be transmitted by host contact as in murine pinworms we might have expected to see a higher focal prevalence. In fact worm burdens were low (range 1–12 worms) suggesting that the eggs of this species are liberated in host faeces and acquired during foraging. Moreover, since very few eggs were observed in the faecal samples even when female worms were present, it is conceivable that egg production is discontinuous, perhaps following an intermittent circadian or even longer-term rhythm, as in *S. muris* and *A. tetraptera* (Phillipson, 1974; Lewis & D'Silva, 1980).

With respect to our second objective, on several criteria mice living in Wadi Abu Seylah were more heavily parasitized than those in other sites. Thus, helminth species richness, mean nematode abundance, the prevalence and abundance of spirurids (faecal egg counts) and *D. kuntzi* were all higher than elsewhere. Wadi Tofaha was similar to Wadi Abu Seylah in terms of mean helminth species richness, intermediate with respect to nematode abundance, but quite clearly the poorest on the basis of spirurid faecal egg counts. These differences between the wadis may reflect the relative abundance of intermediate hosts and possibly, host intrinsic factors such as genetically determined differences in resistance to parasitic helminths. The underlying mechanisms are intriguing and will hopefully be clarified by our continuing studies in the region.

For intestinal helminths of humans and domestic animals faecal egg counts (FEC) are the only non-invasive technique widely used for quantifying infections. However, FEC are fraught with problems and their accuracy has often been questioned (Keymer & Slater, 1987) because release of eggs may show circadian and longer-term rhythms, the techniques themselves show wide intra-sample variability and only infections with patent female worms can be detected. Alternatives, immunological assays such as ELISA for detecting circulating or faecal antigens, require the necessary specific reagents (Johnson *et al*., 1996), have only been refined for a few species and were not available for the parasites in this study. Faecal egg counts were therefore the only feasible non-invasive technique available, and this was an issue of paramount importance because this study, and the associated longer-term programme, was based in a fragile environment of immense conservation value. In the event, only one of the helminth taxa showed promise for detection via FEC, quantitative egg counts strongly predicting spirurid worm biomass. This encouraged us to believe that comparative studies of the spirurid burdens among the different species of rodents inhabiting the wadi systems, and in relation to host community structure, would be possible in the future without need for animals to be culled. Indeed, spirurid FEC revealed a significant difference between sites of capture (in contrast to spirurid abundance as detected by autopsy) but the relative importance of the wadis was different to that identified for nematode abundance. In agreement with spirurid autopsy data, but contrasting with mean helminth species richness and nematode abundance, spirurid faecal egg counts did not show a host age effect. On the basis of these results we conclude that use of FEC as a non-invasive method of quantifying parasite burdens showed some promise but further refinement is still necessary.

Finally, this paper has reported for the first time, quantitative worm burden data on the helminths infecting *A. cahirinus dimidiatus* from the mountain region of the Sinai. The dominance of spirurid nematodes in this host population is an interesting phenomenon. Because of the size of these parasites and their likely metabolic cost, we expect host fitness to be affected and, in consequence, these parasites may play a significant role in determining host life history strategy. How life histories vary in relation to parasite burdens and the specific hazards presented by the contrasting environments in disparate wadis remains to be elucidated.

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