Local variation of haemoparasites and arthropod vectors, and intestinal protozoans in spiny mice (*Acomys dimidiatus*) from four montane wadis in the St Katherine Protectorate, Sinai, Egypt

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Abstract

Haemoparasite infections and infestations with potential arthropod vectors were assessed in spiny mice *Acomys dimidiatus* from four wadis in the arid montane region of the southern Sinai in Egypt in late summer 2000. Five taxa of haemoparasites (*Haemobartonella* spp. 80%, *Hepatozoon* sp. 20.6%, *Trypanosoma acomys* 17.5%, *Bartonella* spp. 2.5% and *Babesia* sp. 1.9%) were recorded. Additionally, infections with two intestinal protozoa, *Cryptosporidium* cf. *parvum* and *Giardia* sp., were quantified, both with similar prevalence (17.0 and 17.6%, respectively). 17.9% of mice carried fleas (*Parapulex chephrensis* and *Xenopsylla dipodilli*) and 32.1% had lice (*Polyplax oxyrrhyncha* and *Polyplax brachyrrhycha* combined). Marked differences in the prevalence and abundance of infections were detected between the four wadis, particularly with respect to *T. acomys*, *Hepatozoon* sp. and fleas, which were largely aggregated in just two of the four sites (Wadis Gharaba and Tlah). In contrast, the intestinal protozoa were more common, and abundance was higher, in Wadi El Arbaein. Intrinsic factors also contributed to a variation in prevalence, with strong age-dependent increases in the prevalence and abundance of *Hepatozoon* sp., higher mean species richness, prevalence of *Cr.* cf. *parvum,* and abundance of *Giardia* sp. and *Hepatozoon* sp. in female mice. *Haemobartonella* spp. showed an age-dependent reduction in abundance and higher abundance among male mice. A weak association was found between the prevalence of *T. acomys* and its putative flea vector. The single extrinsic factor in the study, site of capture, was more important than the intrinsic factors in explaining variation in the prevalence and abundance of haemoparasites, intestinal protozoa and arthropod vectors. In the high mountains of southern Sinai, the parasite fauna of spiny mice is distinct in each wadi, and hence we expect the parasites to exert spatially different co-evolutionary pressures on their hosts, with a resultant variation in host life histories.

Introduction

Fragmentation of the environment has important consequences for the distribution of local flora and fauna, and human activities in particular have often exaggerated the effects of naturally occurring barriers to animal movement and hence gene flow, through agriculture and construction (e.g. of towns, major roads; Gerlach & Musolf, 2000). Isolated or semi-isolated subpopulations of animals may differ in the stresses to which they are subjected in each site, including pathogens, and hence experience different selection pressures created by the specific conditions in their home range (the geographical mosaic theory of co-evolution; Thompson, 1994).

In earlier papers we showed that the helminth communities of bank voles vary markedly between subpopulations of voles living in forest patches that are ecologically very similar but segregated from each other by natural barriers (Behnke *et al.*, 2001; Barnard *et al.*, 2002, 2003*a*), and that the key indicators of helminth community structure are stable in the medium term (Bajer *et al.*, 2005). Similarly, helminth communities in spiny mice *Acomys dimidiatus* differ profoundly between neighbouring but isolated wadis in the mountains of the Sinai Peninsula (Behnke *et al.*, 2000,

2004; Barnard *et al.*, 2003*b*). In contrast to studies of rodent helminths, there are few studies of site-specific variation in haemoparasitic infections or in protozoan infections of the intestinal tract. Even less is known about haemoparasites of wild rodents from tropical and subtropical zones.

Building on the resources collected in our expedition to the Sinai in 2000 and the resultant database on natural infections in wild spiny mice, we report here on haemoparasites and their potential arthropod vectors and on two intestinal protozoa (*Cryptosporidium* cf. *parvum* and *Giardia* sp.), selected on the basis of their potential medical importance. Apart from arthropod vectors, the remaining parasites in this study have been poorly studied to date, particularly in their wild natural hosts, and hence identification of taxa beyond genus is still uncertain. Our objectives were to (1) assess the overall identity, prevalence and intensity of infection with haemoparasites, the two selected intestinal protozoa and potential arthropod vectors, (2) provide quantitative data on infections in four neighbouring and varyingly separated sites that differ from one another in subtle aspects of their ecology (Gilbert *et al.*, 1996; Zalat *et al.*, 2001) and (3) assess whether the prevalence and abundance of haemoparasites and arthropod vectors in the population as a whole, and in specific wadis in particular, are interdependent. Our data provide a baseline for studies focusing on the ecology of haemoparasites, intestinal protozoa and arthropod vectors of hosts living in semi-isolated, xeric habitats about which little is currently known.

Materials and methods

Fieldwork was conducted over a 4-week period in August–September 2000 and was based at the Environmental Research Centre (ERC) of Suez Canal University, located on the periphery of the town of St Katherine, South Sinai, Egypt. Trapping was carried out in four sites in the vicinity of St Katherine. The local environment and general features of the four study sites, as well as their spatial relationships with one another, were described by Behnke *et al.* (2004).

In our earlier papers (Behnke *et al.*, 2000, 2004; Barnard *et al.*, 2003*b*), we referred to the host spiny mouse as *Acomys cahirinus dimidiatus*. Here we refer to the host as *Ac. dimidiatus*, in line with the insights on relationships within the genus *Acomys* obtained using molecular markers (Barome *et al.*, 2001). At each site, rodents were caught live in Sherman traps, and placed selectively among the rocks and boulders around walled gardens and occasionally along the lower slopes of wadis. These were set out at dusk, and inspected in the early morning before exposure to direct sunlight. All traps were brought into the local camp or the ERC, where the animals were removed, identified and processed. Traps were re-set the following evening.

All trapped animals were sexed, weighed, measured and scrutinized for obvious lesions as described by Behnke *et al.* (2004). Ectoparasites visible during field examination were removed and placed in 70% ethanol, and fur and spines were carefully parted and examined with a hand lens for the presence of lice, mites and tick larvae. Blood and faecal samples were taken and animals were then either fur marked individually and released close to the point of capture, or returned to the ERC at St Katherine for autopsy. A small proportion of released animals was subsequently recaptured, but samples were only taken if the first sampling was inadequate in some way. For statistical analysis, only one sample per animal was included in the database, and this was usually that taken on first capture. A maximum of 40% of the captured mice from each site were culled (by agreement with the St Katherine National Protectorate authorities).

Thin blood smears were prepared from drops of blood taken from the tail vein, air dried and fixed in the field in 100% methanol within 1–2 h. They were stained for 45 min in Giemsa's stain (diluted 1:3 in buffer, pH 7.2) on arrival in Nottingham. Each smear was examined, with thorough coverage of the smear, under oil immersion (using the same Olympus AX70 microscope with a magnification of $\times 100$ in the objective lens and $\times 10$ in the eyepiece lens). Initially, sufficient fields of vision (a minimum of 200) from the tail region of the smear were examined to enable up to 50 leucocytes (both lymphocytes and monocytes) to be inspected for the presence of *Hepatozoon* sp. Each field of vision was also examined for the presence of other taxa, although these were not quantified at this stage. If the blood smear revealed the presence of other taxa, an additional 200 fields of vision were inspected and the number of cells infected with *Bartonella*, *Babesia* and *Haemobartonella* spp. per 200 fields of vision was recorded. The concentration of trypanosomes was also expressed per 200 fields of vision.

Individual faecal samples were collected from traps immediately after retrieval of the captured rodent. A few pellets were broken up in sufficient drops of water over a 5–10 min period to soften them and create a paste, which was used to prepare thin faecal smears. These were stained according to a modified Ziehl–Neelsen technique (Henriksen & Pohlenz, 1981) after drying and fixation in methanol. Then, at least 200 fields of vision under $\times 400$ magnification were carefully examined on each slide for the presence or absence of *Cryptosporidium* oocysts. These were identified on the basis of their characteristic size ($4–5 \times 3.5–4.5 \, \mu m$), general morphology and bright red/pink colour as *Cr.* cf. *parvum*. For some animals, only this method provided evidence of infection and in such cases we recorded a minimum detectable intensity, entered into the quantitative analysis as 200 oocysts per 1 ml of concentrated sample (see below).

For identification of genus and quantification of infection, we used a commercially available immunofluorescence assay (IFA) capable of labelling oocysts and cysts of the protozoa [MerIFluor Cryptosporidium/Giardia (Meridian Diagnostics Inc., Cincinnati, OH, USA)]. For *Cr.* cf. *parvum*, this provided additional information, but *Giardia* sp. infections were quantified only by this method. Where available, one faecal sample (weighing between 0.3 and 1 g) was concentrated using a modified Sheather's sucrose flotation method (Garcia & Bruckner, 1988). The volume of concentrated material was estimated by comparison with

calibrated Eppendorf vials and the pellet was re-suspended (1:3, v/v, pellet:10% formalin; dilution factor = 4). Suspension (20 μL) was used for the IFA test, which was carried out according to the manufacturer's instructions. Identification was aided by comparison with positive control samples provided in the kit. Wells were examined under $\times 400$ magnification, and the numbers of *Cr.* cf. *parvum* oocysts and *Giardia* sp. cysts were recorded. For estimation of abundance of infection, the total numbers of oocysts/cysts detected were multiplied by 200 (dilution factor $\times$ 50 = oocysts/cysts per mL) to give the number per 1 mL of concentrated sediment. Thus, the lowest limit of detection was 200 oocysts/cysts per 1 ml of concentrated sediment.

Autopsied animals, which were killed by overexposure to chloroform, were examined for ectoparasites immediately after a blood sample was taken, and usually within 2–3 min of death. All ectoparasites were removed systematically into 70% ethanol for later examination. For animals examined in the field and subsequently released, all ectoparasites seen during handling and examination were also removed and preserved for subsequent identification. Although this approach was accurate and reliable for highly mobile and relatively large ectoparasites such as fleas and ticks, mites and lice in particular were probably under-represented.

Animals were allocated to three age classes, on the basis of body weight, nose-to-anus length, anus-to-tail tip length, mean hind foot length and skull width. These measurements were reduced by principal components analysis, and principal component 1 was used to guide allocation of animals to three age classes. Full details of the methods used and statistical verification of the age classes are given in Behnke *et al.* (2004). Age class 1 comprised the youngest animals, mostly weanlings and very young juveniles, age class 2 comprised juveniles and young adults, and age class 3 comprised the adult and oldest animals in the study.

The frequency distribution of infracommunity species richness was tested for goodness of fit to the positive binomial distribution (assumption of the null model is a regular distribution), the Poisson distribution (assumption of the null model is a random distribution), the negative binomial model (assumption of the null model is an aggregated distribution) and the null model of Janovy *et al.* (1995) (the assumption of the null model is that, in the absence of associations and interactions between species, the frequency distribution of infracommunity species richness is predicted by prevalence values of all the species comprising the component community). All distributions were tested for goodness of fit by χ^2.

Prevalence data (percentage of animals infected) are shown with 95% confidence limits, calculated as described by Rohlf & Sokal (1995), using bespoke software. Prevalence was analysed by maximum likelihood techniques based on log-linear analysis of contingency tables using the software package Statgraphics version 7. Full factorial models incorporated age (three age classes), site (four levels), sex (two levels, males and females) and infection as a binary factor (present/absent). Beginning with the most

complex model, involving all possible main effects and interactions, the combinations that did not contribute significantly towards explaining variation in the data were eliminated in a stepwise fashion beginning with the highest level interaction. A minimum sufficient model was then obtained, for which the likelihood ratio of χ^2 was not significant, indicating that the model was sufficient in explaining the data. The importance of each term (i.e. interactions involving infection) in the final model was assessed by the probability that its exclusion would alter the model significantly.

Summary figures for parasite abundance are expressed as arithmetic means $\pm$ SEM, although $\log_{10}(x+1)$ means are also given where statistical analysis required this transformation. These means reflect the abundance of infection as defined by Margolis *et al.* (1982) and Bush *et al.* (1997) and include all subjects within the specified group, infected and not infected, for which relevant data were available.

The degree of aggregation in the data was calculated by the index of discrepancy (D) as described by Poulin (1993) (a value of 0 indicates an even distribution of counts across all hosts and a value of 1 indicates all parasites aggregated in a single host) and the index of dispersion (I, variance to mean ratio, where values >1 indicate over-dispersed data). Frequency distributions of individual taxa were also tested for goodness of fit to negative binomial, positive binomial and Poisson models by χ^2 as described by Elliott (1977), and the negative binomial exponent k is given as appropriate.

Parasite abundance was analysed by generalized linear interactive modelling (GLIM) (GLIM 4, PC version, Royal Statistical Society 1993) as described previously (Abu-Madi *et al.*, 1998). Where data conformed to negative binomial distributions, we first evaluated models with negative binomial error structures as models of choice. If these did not converge satisfactorily, models with normal errors were fitted after normalization of the data by $\log_{10}(x+1)$ transformation (Crawley, 1993; Wilson & Grenfell, 1997; Behnke *et al.*, 1999). Site (four levels), host age (three levels) and host sex (two levels) were entered as factors. In all cases, we began with full factorial models, including all main effects and interactions, and then progressively simplified them by deletion of terms, beginning with the highest order interactions and progressing to the main effects. The three-way interaction was removed first and the change in deviance was noted. Two-way interactions were then deleted and reinstated in turn until all three had been evaluated. All two-way interactions were then removed, and the procedure was repeated with the main effects. Finally, minimum sufficient models were fitted, entering only the significant terms, to obtain probabilities, and the residuals from these were checked for approximately negative binomial or normal distribution, respectively, as appropriate.

Correlations between continuous variables were analysed by the non-parametric Spearman's correlation coefficient test. To control for the confounding effects of extrinsic and intrinsic factors on infection intensity, we also examined the correlations between the residuals from minimum sufficient

ANOVAs, in each case entering only data from animals that carried both taxa of the pair concerned.

Results

Acomys dimidiatus

A total of 168 spiny mice was sampled from the four study sites. The structure of the host population by site, host sex and age has been described previously (Behnke *et al.*, 2004). Table 1 summarizes the numbers of samples available from each of the sites for blood smears and for analysis of *Cryptosporidium* spp. in faecal samples. For analysis of *Giardia* spp., fewer samples were available as priority was given to *Cryptosporidium* spp. when faecal material was limited ($n = 148$, and these data are not tabulated). For all three datasets, there were significant differences in the numbers of animals sampled by wadi ($\chi^2 = 16.0$, d.f. = 3, $P = 0.0011$; $\chi^2 = 17.5$, d.f. = 3, $P = 0.0006$; $\chi^2 = 13.9$, d.f. = 3, $P = 0.003$, respectively; most mice were from Wadi El Arbaein and fewest were from Wadi Gharaba). There was also a significant interaction between sex and age class (Table 1, $\chi^2 = 6.8$, d.f. = 2, $P = 0.034$; $\chi^2 = 7.29$, d.f. = 2, $P = 0.026$; $\chi^2 = 6.63$, d.f. = 2, $P = 0.036$, respectively), reflecting significant differences in the distribution of sexes and ages of mice collected across different wadis. The number of mice examined for ectoparasites was 162. These various datasets were not identical because it was not possible to bleed all animals; some did not provide faecal material for analysis, and others insufficient for analysis of both intestinal taxa. Moreover, ectoparasites were not examined on animals that had died in traps.

Measures of component community structure of haemoparasites and intestinal protozoa

Total species richness

Five taxa of haemoparasites were recorded in total and both intestinal microparasites were also present in the mice. One hundred and thirty-eight mice (86.3%, $n = 160$) carried at least one taxon of haemoparasite and 39 (26.4%, $n = 148$) carried at least one of the intestinal taxa. Among the haemoparasites, *Haemobartonella* spp. were the most prevalent (Table 2) and *Babesia* sp. the least. Both *Cr*. cf. *parvum* and *Giardia* sp. showed similar prevalence (Table 2). However, there were marked differences in the prevalence rates between sites.

Total species richness by site

Of the five blood haemoparasites, four were recorded in Wadis Gharaba, El Arbaein and Tlah but only two were recorded in Wadi Gebal. Both intestinal taxa were recorded in each of the four wadis (Table 2).

Table 1 Numbers of *Acomys dimidiatus* examined by site, and host sex and age

| Site | Sex | Age class | | | | | | | | | |
| | | Blood smears | | | | | Faecal samples (*Cryptosporidium* spp.) | | | | |
		Class 1	Class 2	Class 3	Total by sex	Total by site	Class 1	Class 2	Class3	Total by sex	Total by site
El Arbaein	Male	6	15	7	28		7	16	7	30	
	Female	11	8	11	30		10	8	13	31	
	Combined	17	23	18		58	17	24	20		61
Gebal	Male	3	7	2	12		3	9	2	14	
	Female	3	5	8	16		4	6	8	18	
	Combined	6	12	10		28	7	15	10		32
Gharaba	Male	1	5	5	11		1	4	5	10	
	Female	2	6	9	17		2	6	8	16	
	Combined	3	11	14		28	3	10	13		26
Tlah	Male	4	9	11	24		4	9	11	24	
	Female	4	5	13	22		4	5	13	22	
	Combined	8	14	24		46	8	14	24		46
Total by sex											
	Male	14	36	25	75		15	38	25	78	
	Female	20	24	41	85		20	25	42	87	
Total by age		34	60	66			35	63	67		
Grand total						160					165

Statistical analysis: the minimum sufficient models for:
(1) blood smears = sex × age class+site ($\chi^2 = 12.5$, d.f. = 15, $P = 0.64$, $n = 160$),
(2) faecal samples [*Cryptosporidium* spp. = sex × age class+site ($\chi^2 = 12.6$, d.f. = 15, $P = 0.64$, $n = 165$)],
(3) faecal samples [data not tabulated above, *Giardia* spp. = sex × age class+site ($\chi^2 = 10.8$, d.f. = 15, $P = 0.77$, $n = 148$)].
The significance of omitting each term, respectively, is given in the text.

Table 2 Prevalence (% infected) of haemoparasites, intestinal taxa and ectoparasites by wadi

Site	El Arbaein		Gebal		Gharaba		Tlah		Total	
Parasite	n^a	% Infected ± 95 CL[b]	n	% Infected ± 95 CL	n	% Infected ± 95 CL	n	% Infected ± 95 CL	n	% Infected ± 95 CL
Intestinal parasites										
Cryptosporidium cf. *parvum*	61	31.1 (21.3, 44.5)	32	6.3 (1.4, 20.8)	26	3.8 (0.2, 18.8)	46	13.0 (6.5, 27.2)	165	17.0 (11.9, 23.6)
Giardia sp.	55	27.3 (17.3, 41.1)	31	9.7 (2.9, 26.0)	24	12.5 (3.5, 31.0)	38	13.2 (5.8, 28.2)	148	17.6 (12.6, 25.0)
Blood parasites	58		28		28		46		160	
Hepatozoon sp.		0		0		39.3 (22.9, 59.1)		47.8 (33.7, 62.8)		20.6 (15.2, 27.9)
Trypanosoma acomys		1.7 (0.2, 9.7)		0		21.4 (9.8, 40.9)		45.7 (32.3, 60.7)		17.5 (12.7, 24.7)
Babesia sp.		3.4 (0.9, 12.6)		0		0		2.2 (0.4, 12.9)		1.9 (0.6, 5.7)
Bartonella spp.		3.4 (0.9, 12.6)		3.6 (0.2, 17.5)		3.6 (0.2, 17.5)		0		2.5 (1.2, 6.9)
Haemobartonella spp.		75.9 (63.3, 85.6)		82.1 (64.3, 92.7)		89.3 (71.8, 97.0)		78.3 (64.7, 88.8)		80.0 (73.1, 85.6)
Ectoparasites										
Fleas	56	3.6 (0.9, 12.9)	28	0	28	46.4 (28.2, 64.5)	46	30.4 (19.2, 45.8)	162	17.9 (12.8, 24.6)
Lice	56	32.1 (21.7, 46.1)	32	12.5 (4.9, 29.1)	28	39.3 (22.9, 59.1)	46	41.3 (28.5, 56.8)	162	32.1 (26.2, 40.7)

[a]Sample size for the following subset of data.

[b]95% confidence limits (CL) are given as the lower and upper values, respectively.

Measures of infracommunity structure of haemoparasites and intestinal protozoa

Mean species richness

The overall mean number of microparasite taxa per host (both haemoparasites and intestinal, $n = 140$) was 1.54 ± 0.082 (variance to mean ratio $= 0.61$), of which 1.17 ± 0.063 was accounted for by haemoparasites and 0.371 ± 0.056 by intestinal taxa. Mean species richness was highest in Wadi Tlah and lowest in Wadi Gebal (Fig. 1a), and this difference between the wadis was significant (three-way ANOVA with negative binomial errors and site, host age and sex as factors, main effect of site $\chi^2_3 = 13.0$, $0.005 > P > 0.001$). Mean species richness among haemoparasites was high in Wadis Gharaba and Tlah and comparably low in Wadis El Arbaein and Gebal (Fig. 1b). However, the mean species richness among the intestinal taxa was markedly higher in Wadi El Arbaein and lower in the other wadis (Fig. 1c).

There was also a significant main effect of host sex ($\chi^2_1 = 5.53$, $0.025 > P > 0.001$), with female mice showing a higher overall mean species richness (1.65 ± 0.12) compared with males (1.42 ± 0.11). This female bias was reflected in higher values for females in all four wadis (Fig. 1a) and was also evident with respect to haemoparasites in three of the four wadis (Fig. 1b) and intestinal taxa in all four wadis (Fig. 1c).

Frequency distributions of species richness

The species density distributions for all four sites combined are shown in Fig. 2. As can be seen, most mice harboured one or two haemoparasite taxa or, in the case of intestinal taxa, were not infected. These distributions were significantly different from the binomial, Poisson and normal distributions ($P < 0.005$ in all three cases). In each case, the closest fit was the negative binomial, although for haemoparasites this distribution was not adequate ($\chi^2_3 = 18.0$, $P < 0.001$; Fig. 2). Each dataset was also compared with the distribution predicted by the null model for interactions of parasite species in an assemblage (Janovy et al., 1995). For haemoparasites, there was no significant difference ($\chi^2_3 = 8.0$, $P = 0.09$) between observed and predicted species distributions, but for intestinal taxa the difference was highly significant ($\chi^2_2 = 24.1$, $P < 0.001$), arising principally from more mice than expected harbouring both taxa concurrently.

Prevalence of haemoparasites and intestinal protozoa

The prevalence data for each taxon by wadi are summarized by site in Table 2. *Hepatozoon* sp. showed an overall prevalence of 20.6%. As can be seen from Table 2, none of the mice in Wadis El Arbaein or Gebal were found to be infected, whereas Wadis Gharaba and Tlah showed a similar high prevalence ($> 39\%$). There was also a consistent age-dependent increase in prevalence (Fig. 3a), which was highly significant ($\chi^2_2 = 12.9$, $P = 0.0016$).

The prevalence of *Trypanosoma acomys* was only affected by site (Table 2, $\chi^2_3 = 45.8$, $P < 0.0001$). Again, none of the mice from Wadi Gebal were infected, although the parasite was identified in a single animal from Wadi El Arbaein (1.7%). Prevalence among mice from Wadi Tlah was more than twice that from Wadi Gharaba. For this species, the minimum sufficient model included site $\times$ presence/absence of *T. acomys* + age $\times$ sex (for goodness of fit, $\chi^2_{35} = 30.1$, $P = 0.70$).
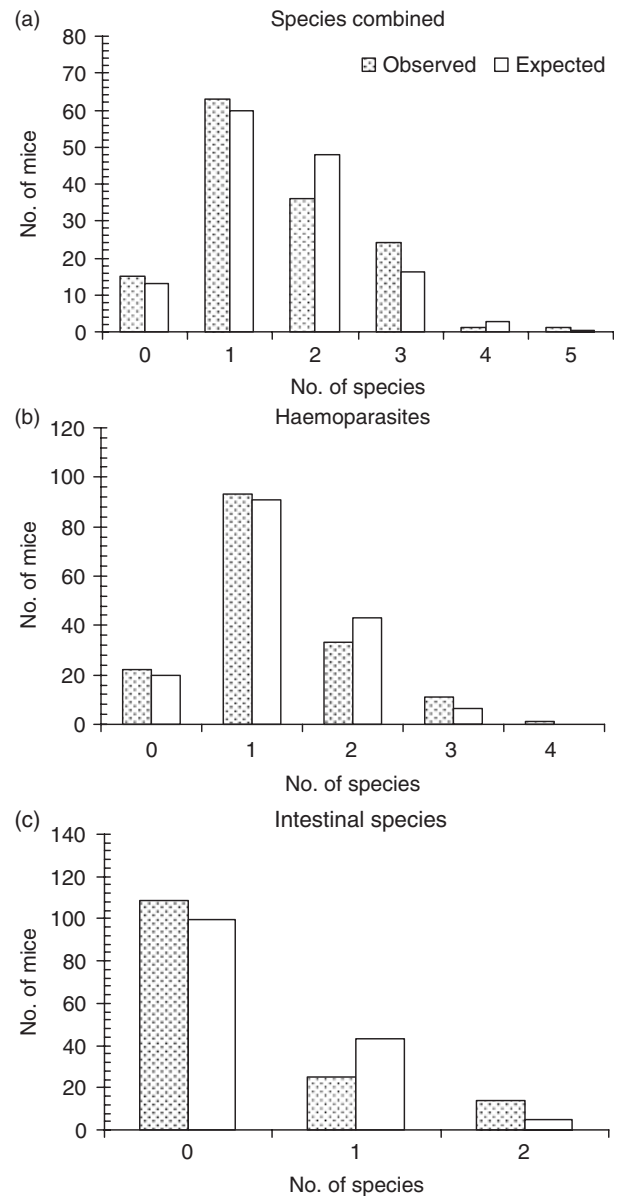
Babesia and *Bartonella* spp. infections were the most rare (three and four mice infected, respectively), and these were not examined further statistically. *Haemobartonella* spp. was the most prevalent taxon (Table 2), but none of the
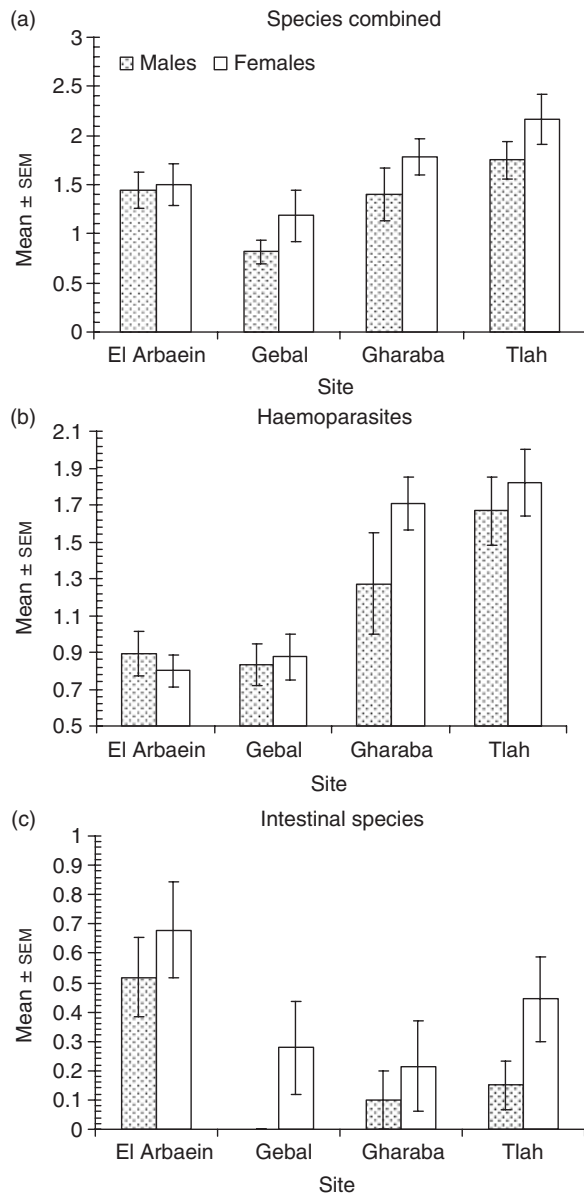
Figure 1 Site-dependent variation in mean species richness: (a) taxa combined (*n*=140), (b) haemoparasites (*n*=160), (c) intestinal taxa (*n*=148).

Figure 2 Frequency distribution of infracommunity species richness for the combined data (a; *n*=140) and for haemoparasites (b; *n*=160) and intestinal species (c; *n*=148) separately. The observed data are in the spotted columns and that predicted by the null model of Janovy *et al.* (1995) are in the open columns. See text for a full explanation and statistical analysis.

factors entered into the analysis affected prevalence. Whereas mice infected with *Haemobartonella* spp. were found in all wadis, those with *Bartonella* spp. were recorded in all wadis expect Wadi Tlah, whereas those with *Babesia* sp. came from two wadis (El Arbaein and Tlah).

Cryptosporidium cf *parvum* showed marked differences in prevalence between the wadis (Table 2, $\chi^2_3 = 15.5$, $P = 0.0014$), with a high prevalence in Wadi El Arbaein. However, there was also an independent difference in prevalence between the sexes (overall prevalence in males = 11.5% and females = 21.8%), which was just outside significance ($\chi^2_1 = 3.17$, $P = 0.075$) and this sex effect on prevalence was evident in all four wadis (Fig. 3b).

Giardia sp. varied between the wadis with the highest prevalence in Wadi El Arbaein (Table 2), but the site-specific variation was also dependent on host sex (interactions site × sex × presence/absence of *Giardia* spp., $\chi^2_3 = 9.62$, $P = 0.022$). In two of the wadis, prevalence was clearly higher among female mice, but in Wadis El Arbaein and Gharaba there was little difference between the sexes. In Wadi Tlah prevalence among female mice was comparable with that of both sexes in Wadi El Arbaein (Fig. 3c). Overall prevalence was higher in females (males = 12.9% and

Table 3 Measures of aggregation for individual species of haemoparasites and intestinal protozoa by site

Species	Wadi El Arbaein k^a ($\pm$ SEM[d])	I^b	D^c	Wadi Gebal k^a ($\pm$ SEM[d])	I^b	D^c	Wadi Gharaba k^a ($\pm$ SEM[d])	I^b	D^c	Wadi Tlah k^a ($\pm$ SEM[d])	I^b	D^c
Hepatozoon sp.	$-^e$	–	–	$-^e$	–	–	0.108[g,i,j] (0.001)	56.4	0.794	0.149[g,i,j] (0.001)	55.7	0.700
Trypanosoma acomys	0.020[f,h]	6	0.966	–	–	–	0.058[g,h] (0.0006)	55.4	0.893	0.150[g,h] (0.001)	57.8	0.778
Haemobartonella spp.	1.04[g,h] (0.075)	4.6	0.507	0.744[f,i,j] (0.049)	19.5	0.580	2.252[f,i,j] (0.792)	3.4	0.386	1.113[g,h] (0.107)	3.92	0.491
Cryptosporidium cf. *parvum*	0.094[g,h] (0.0006)	54.5	0.904	0.029[f,h] (0.0004)	4.13	0.917	0.021[f,i,k] (0.0004)	3.0	0.926	0.036[g,h] (0.0002)	32.8	0.930
Giardia sp.	0.071[g,h] (0.0004)	80.5	0.896	0.020[f,h] (0.0001)	49.9	0.907	0.024[f,i,j] (0.0001)	120.9	0.917	0.031[f,h] (0.0002)	51.6	0.922

[a]Negative binomial exponent.
[b]Index of dispersion = variance to mean ratio.
[c]Index of discrepancy (Poulin, 1993).
[d]Standard error of the mean estimate.
[e]Too few infected animals to calculate statistic.
[f]Not possible to test for goodness of fit to negative binomial distribution.
[g]Not significantly different from negative binomial distribution.
[h]Significantly different from positive binomial and Poisson distributions.
[i]Not possible to test for goodness of fit to Poisson distribution.
[j]Significantly different from positive binomial distribution.
[k]Not possible to test for goodness of fit to positive binomial distribution.

females = 21.8%), but there was no independent significant effect of host sex.

Frequency distributions and measures of aggregation

The frequency distributions of all taxa for which quantitative analysis was possible were examined, and the summary statistics are presented in Table 3. It was not possible to fit distributions to all because in some cases there were very few animals carrying infection. Of the 17 distributions listed, nine did not differ significantly from the negative binomial. In 13 cases, the value of D equalled or exceeded 0.7, and in all cases where it was possible to calculate I, the values exceeded 1, supporting the idea that parasite distributions were aggregated.

Abundance of infection

Table 4 summarizes the mean abundance values for individual taxa by wadi. However, intrinsic factors confounded the data and some of these relationships are illustrated in Fig. 4.

Hepatozoon sp. varied significantly between sites (three-way ANOVA on $\log_{10}(x+1)$-transformed data, main effect of site $F_{3,156} = 13.57$, $P < 0.001$). This taxon was only found in Wadis Gharaba and Tlah and its abundance was twice as high in Wadi Tlah. With site and sex taken into account, there was a significant increase in abundance with increasing age (Fig. 4a; three-way ANOVA, main effect of age $F_{2,155} = 3.43$, $0.05 > P > 0.025$), and abundance was almost twice as high in female compared with male mice [mean $\log_{10}(x+1) = 0.36 \pm 0.077$ and 0.22 ± 0.062; arithmetic means, 11.55 ± 3.17 and 5.36 ± 1.77, respectively], but this difference was just outside significance (three-way ANOVA, main effect of sex $F_{1,154} = 3.12$, $0.1 > P > 0.05$).

The abundance of *Haemobartonella* spp. also varied significantly between sites (three-way ANOVA with negative binomial errors, main effect of site $\chi^2_3 = 12.1$, $0.01 > P > 0.005$), but there was also a highly significant interaction with host age (Fig. 4b; three-way ANOVA, $\chi^2_6 = 43.8$, $P < 0.0005$) and a significant main effect of age (three-way ANOVA, $\chi^2_2 = 7.09$, $0.05 > P > 0.025$). This interaction arose primarily because of the very high abundance of infection in the youngest age class from Wadi Gebal. In Wadis Gharaba and Tlah, abundance was also highest in the youngest age class. However, the differences between age classes were not as prominent, and overall, with age, host sex and the interaction between site and age taken into account, there was a significant decline with increasing mouse age (mean abundance in age classes 1, 2 and $3 = 6.97 \pm 1.84$, 4.70 ± 0.61 and 4.67 ± 0.52, respectively). The abundance of infection was higher in male compared with female mice (mean $= 5.73 \pm 0.94$ and 4.67 ± 0.46, respectively; three-way ANOVA, main effect of sex $\chi^2_1 = 6.19$, $0.025 > P > 0.001$).

The abundance of *T. acomys* varied significantly between sites [three-way ANOVA on $\log_{10}(x+1)$-transformed data with normal errors, main effect of site $F_{3,159} = 12.98$, $P < 0.001$], and again the highest abundance was found in
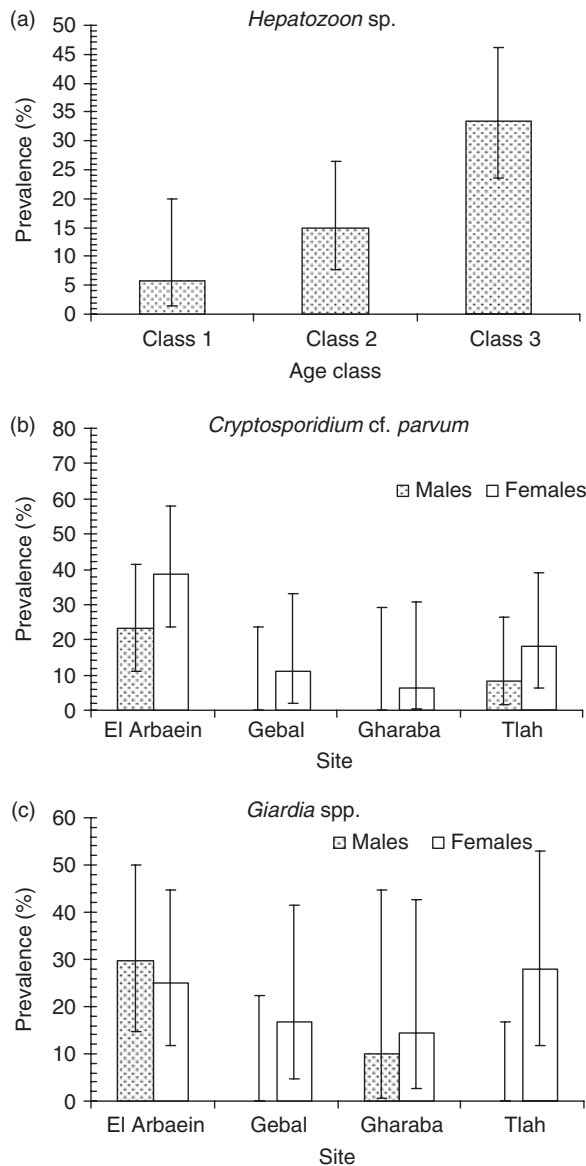
Figure 3 Age-dependent variation in the prevalence ($\pm 95\%$ confidence limits) of *Hepatozoon* sp. (a), site- and sex-dependent variation in *Cryptosporidium* cf. *parvum* (b) and *Giardia* sp. (c). The minimum sufficient model for *Hepatozoon* sp. included age $\times$ infection + site $\times$ infection + sex $\times$ age (goodness of fit, $\chi^2_{33} = 18.62$, $P = 0.98$), for *C. parvum* site $\times$ infection + sex $\times$ age (goodness of fit, $\chi^2_{35} = 29.4$, $P = 0.73$), and for *Giardia* sp. site $\times$ sex $\times$ infection + sex $\times$ age (goodness of fit, $\chi^2_{28} = 21.4$, $P = 0.81$). For significance of the individual effects, see text.

Wadi Tlah (Table 4). Neither *Babesia* nor *Bartonella* spp. were analysed further because there were very few infected animals in the dataset.

Although the abundance of *Giardia* sp. did not differ significantly between wadis, that of *Cr.* cf. *parvum* did [three-way ANOVA on $\log_{10}(x+1)$-transformed data and normal errors, main effect of site $F_{3,164} = 3.06$, $0.05 > P > 0.025$]. As

Table 4 shows, the abundance of *Cr. parvum* was greatest in Wadi El Arbaein and lowest in Wadi Gharaba. The abundance of both taxa was greatest in female hosts but was only significant in the case of *Giardia* sp. (for *Giardia* sp., males $= 345.7 \pm 285.9$ and females $= 1443.6 \pm 527.0$, main effect of sex $F_{1,147} = 5.22$, $0.025 > P > 0.01$; for *Cr.* cf. *parvum*, males $= 305.1 \pm 170.0$ and females $= 485.1 \pm 248.1$, main effect of sex $F_{1,159} = 2.2$, $P = NS$).

Arthropod vectors

Fleas

Most of the fleas recovered from mice were *Parapulex chephrensis*, although one mouse from Wadi El Arbaein was found infested with *Xenopsylla dipodilli*. No fleas were found on the mice from Wadi Gebal, and only two mice from Wadi El Arbaein were found with fleas. Mice from Wadis Gharaba and Tlah showed markedly higher flea infestations (Table 2). This difference between wadis was highly significant [the minimum sufficient model included site $\times$ presence/absence of fleas + age $\times$ sex (overall goodness of fit of model, $\chi^2_{35} = 20.7$, $P = 0.973$) and for the two-way interaction, site $\times$ presence/absence of fleas, $\chi^2_3 = 39.8$, $P < 0.0001$]. Similarly, abundance was affected only by site (Table 4, three-way ANOVA on $\log_{10}(x+1)$-transformed data, main effect of site $F_{3,161} = 9.43$, $P < 0.001$).

Lice

Two species of lice were recorded (*Polyplax oxyrrhyncha* and *Polyplax brachyrrhyncha*), and where they were distinguished reliably, most specimens proved to be *Po. brachyrrhyncha*. However, the two species were not counted separately on all animals and hence they were treated together as one taxon for analysis. The minimum sufficient model was found to be sex $\times$ age $\times$ presence/absence of lice + site $\times$ presence/absence of lice (for overall goodness of fit of the model, $\chi^2_{30} = 25.0$, $P = 0.73$). Table 2 shows that infestations with lice were most frequent in Wadis Gharaba and Tlah and least frequent in Wadi Gebal (for the site $\times$ presence/absence interaction, $\chi^2_3 = 9.0$, $P = 0.029$). The sex $\times$ age $\times$ presence/absence interaction ($\chi^2_2 = 6.8$, $P = 0.034$) arose because infestations were lower in juveniles compared with older mice and because juvenile females showed a higher prevalence than males (0 and 19% among juvenile, age class 1, male and female mice, respectively), whereas among young adults (age class 2) prevalence was very similar in both sexes (37.8 and 41.7%, respectively) and among older mice (age class 3) prevalence was higher in males (48.0 vs. 29.3%, respectively).

Arachnids

Two highly active mite taxa were recorded, the gamasid *Allodermanyssus sanguineus* and a *Haemolaelaps* sp. close to the *Haemolaelaps* sp. recorded from gerbils from

Table 4 Abundance of parasites by wadi

Site	El Arbaein		Gebal		Gharaba		Tlah		Total	
		$x \pm$ SEM		$x \pm$ SEM		$x \pm$ SEM		$x \pm$ SEM		$x \pm$ SEM
Parasite	*n*	Range	*n*	Range	*n*	Range	*n*	Range	*n*	Range
Intestinal parasites										
Cryptosporidium cf. *parvum*	61	790.2 ± 375.7 0–19 600	32	50.0 ± 35.9 0–1000	26	23.1 ± 23.1 0–600	46	339.1 ± 220.0 0–8000	165	400.0 ± 153.3 0–19 600
Giardia sp.	55	1232.7 ± 600.7 0–26 400	31	677.4 ± 467.0 0–11 000	24	1075.0 ± 1040.5 0–25 000	38	584.2 ± 398.4 0–14 000	148	924.3 ± 311.2 0–26 400
Blood parasites	58		28		28		46		160	
Hepatozoon sp.		0		0		12.9 ± 5.1 0–102		22.2 ± 5.2 0–181		8.7 ± 1.9 0–181
Trypanosoma acomys		0.1 ± 0.1 0–6		0		3.8 ± 2.7 0–76		12.1 ± 3.9 0–150		4.2 ± 1.3 0–150
Babesia sp.		0.3 ± 0.2 0–12		0		0		0.02 ± 0.02 0–1		0.11 ± 0.08 0–12
Bartonella spp.		0.03 ± 0.02 0–1		0.07 ± 0.07 0–2		0.11 ± 0.11 0–3		0		0.04 ± 0.02 0–3
Haemobartonella spp.		4.3 ± 0.6 0–24		7.1 ± 2.2 0–62		6.2 ± 0.9 0–18		4.5 ± 0.6 0–18		5.2 ± 0.5 0–62
Ectoparasites	56		32		28		46		162	
Fleas		0.05 ± 0.04 0–2		0 –		0.79 ± 0.24 0–6		0.76 ± 0.21 0–5		0.37 ± 0.08 0–6
Lice		1.73 ± 0.57 0–18		0.44 ± 0.23 0–5		4.21 ± 2.30 0–63		2.65 ± 1.06 0–37		2.17 ± 0.54 0–63

Cryptosporidium cf. *parvum* and *Giardia* sp. are given as oocysts ml^{-1} and cysts ml^{-1} of concentrated faeces, respectively. *Hepatozoon* sp. is given as the number of infected leucocytes (lymphocytes and monocytes) per 200 fields of vision under oil immersion; *T. acomys*, *Babesia* sp., *Bartonella* spp. and *Haemobartonella* spp. are all given as the number of parasites or infected erythrocytes per 200 fields of vision under oil immersion.

St Katherine by Hoogstraal & Traub (1965*a*). An unidentified trombiculid was present at a very high prevalence and intensity. This attached to the skin surface and appeared immobile. Given the life cycle of trombiculids, which are parasitic at only one stage of their life cycle, and the almost universal occurrence of this taxon on spiny mice, it has been excluded from further analyses.

Only three ticks were found (species indet.). These individuals (two nymphs and one larva) were attached to mice from Wadi Gebal. In view of their rarity, they have also been excluded from further analyses.

Associations between haemoparasites and between intestinal protozoa

Haemoparasites

The possibility of associations between the five haemoparasite taxa was tested in a log-linear model that incorporated all five taxa and the factors site, sex and age. The minimum sufficient model was complex and included seven terms, but none of these involved interactions between any taxa.

Quantitative analysis by Spearman's rank order test on pairs of haemoparasites, but in each case only involving mice that were infected with both taxa in a given pair, revealed only one borderline relationship in the raw data. This was a negative relationship between *Hepatozoon*

sp. and *T. acomys* ($r_s = -0.56$, $n = 13$, $P = 0.049$); however, when we controlled for extrinsic and intrinsic factors by examining the correlation between the residuals of minimum sufficient ANOVAs for each taxon, the relationship became much weaker and was no longer significant ($r_s = -0.36$, $n = 13$, $P = 0.23$).

Intestinal protozoa

Log-linear analysis of the co-occurrence of *Cr. parvum* and *Giardia* sp. revealed two interactions that included both parasites in the minimum sufficient model (overall goodness of fit of model, $\chi^2_{42} = 4.76$, $P = 1.0$).

The simpler of these interactions included site and presence/absence of both taxa ($\chi^2_3 = 12.5$, $P = 0.0058$). The prevalence of *Cr.* cf. *parvum* was 53.9% among mice with *Giardia* sp. ($n = 26$), but only 9.8% among mice without *Giardia* sp. ($n = 122$). In Wadis Gebal and Gharaba, all *Cr.* cf. *parvum* infections were detected only in mice carrying *Giardia* sp. (66.7 and 33.3%), but this was based in both cases on very small sample sizes (one mouse from Wadi Gharaba and two from Wadi Gebal were infected with *Cr.* cf. *parvum*, out of three in each case, compared with 28 and 21 mice, respectively, that carried neither parasite). In Wadis El Arbaein and Tlah, the prevalence of *Cr.* cf. *parvum* was 66.7% ($n = 15$) and 20% ($n = 5$), respectively, among
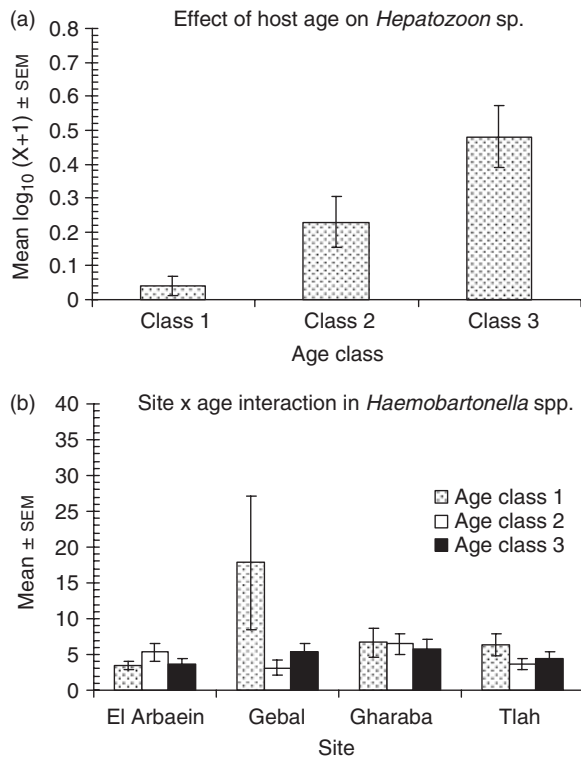
Figure 4 (a) Age-dependent variation in the abundance of *Hepatozoon* sp. [mean $\log_{10}(x+1)$ infected cells per 200 fields of vision] and (b) the site × age interaction in abundance of *Haemobartonella* spp. (arithmetic mean of number of infected cells per 200 fields of vision). For statistical analysis, see text.

mice with *Giardia* sp., but only 20% ($n = 40$) and 12.1% ($n = 33$), respectively, among those without *Giardia* sp. The second interaction was more complex, including again both taxa and host sex and age ($\chi^2_2 = 9.24$, $P = 0.01$), but this was not explored further.

Quantitative analysis by Spearman's rank order test of animals carrying both taxa did not reveal a significant correlation in the raw data, nor after controlling for intrinsic and extrinsic factors by applying the test to the residuals of minimal sufficient ANOVAs ($r_s = 0.42$, $n = 14$, $P = 0.14$, two-tailed test).

Associations between arthropod vectors and haemoparasites

Fleas and *T. acomys*

The overall prevalence of *T. acomys* among mice with its likely flea vector was 44.8% ($n = 29$) compared with just 12% among mice without fleas ($n = 125$), and there was a weak but significant overall association which was sex and age dependent (for the sex × age × presence/absence of fleas × presence/absence of *T. acomys* interaction, $\chi^2_2 = 6.3$, $P = 0.044$). This is illustrated in Fig. 5, where the age and sex effects are shown separately for clarity. The prevalence of
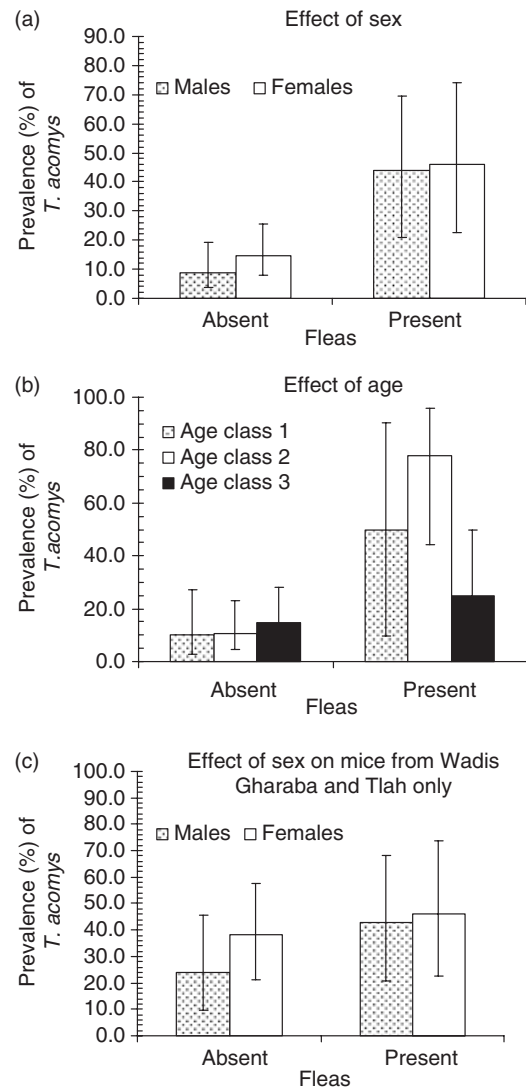
Figure 5 Sex- (a) and age- (b) dependent association between fleas and *Trypanosoma acomys* in the full dataset and (c) the sex effect confined to mice from Wadis Gharaba and Tlah, where both species were largely aggregated (prevalence ± 95% confidence limits).

T. acomys was three to four times higher in mice of both sexes harbouring fleas compared with those without fleas, but whereas prevalence was almost identical in both sexes among mice with fleas, it was marginally higher among females without fleas compared with males without fleas (Fig. 5a). Although there was no apparent age effect among mice without fleas, among mice with fleas prevalence peaked in age class 2 and then dropped in the oldest mice in the study (Fig. 5b).

However, as *T. acomys* and fleas were both highly aggregated in Wadis Gharaba and Tlah, infrequently present in Wadi El Arbaein and absent from Wadi Gebal (Table 2), this association may have arisen in part indirectly (although site was taken into account in the model) through fleas and *T. acomys* both being more prevalent in Wadis

Gharaba and Tlah than in Wadis El Arbaein and Gebal. Therefore, we repeated the analysis, confining it to mice from Wadis Gharaba and Tlah. This time, sex, age, presence/absence of fleas and presence/absence of *T. acomys* were fitted into the model. However, the model could not be simplified (four-way interaction, $\chi^2_2 = 6.6$, $P = 0.038$), indicating that there was a significant association between these taxa but that it was dependent on both host sex (Fig. 5c) and age (not illustrated). Quantitative analysis by Spearman's rank order test on raw data and residuals from minimum sufficient ANOVAs, confined to mice with both taxa ($n = 13$), did not indicate any correlation between the intensity of infections with these taxa.

Fleas and *Hepatozoon* sp.

The prevalence of *Hepatozoon* sp. among mice with fleas was 41.4% ($n = 29$) in contrast to 16.8% ($n = 125$) among mice without fleas. However, when the site, sex and age effects were controlled for, no significant association was evident between these taxa that was independent of the association arising from focused occurrence of both taxa in subsets of mice (e.g. like *T. acomys*, both were largely aggregated in Wadis Gharaba and Tlah; Table 2). Similarly, neither analysis of raw data nor that of residuals of minimum sufficient ANOVAs by Spearman's rank order test indicated any evidence for significant correlations between these taxa.

Lice and *Haemobartonella* spp.

No significant association was evident between lice and *Haemobartonella* spp. Prevalence ranged from 63.2% (Wadi Tlah) to 100% (Wadis Gebal and Gharaba) among mice with lice, and varied from 81.5% (Wadi Gebal) to 88.9% (Wadi Tlah) among those without lice, so no consistent pattern emerged. No quantitative associations between lice and *Haemobartonella* spp. based on Spearman's rank order test were evident.

Discussion

The data presented in this paper show that in the St Katherine area of the Sinai peninsula of Egypt, spiny mice are hosts to a gut community of protozoan microparasites, an assemblage of protozoan and bacterial haemoparasites, and a group of blood-feeding arthropods. This is the first detailed study combining all these communities in naturally occurring spiny mice in the region. However, the picture was not uniform throughout, the exact combination of taxa and their relative prevalence and abundance varying markedly between wadis and hence conferring a distinctive component community of parasites on mice in each of our study sites. It is pertinent therefore to explore the possible underlying reasons.

Most of the protozoan and bacterial taxa were identified using morphological criteria only, although *Cr*. cf. *parvum* and *Giardia* spp. were also identified using an IFA. The taxonomy of these taxa infecting spiny mice in particular, and of desert rodents in general, is poorly understood, and therefore, although identifications to the genus level are likely to be correct, strain and species identities remain uncertain. Even among the much better studied haemoparasites of European rodents, the situation appears far more complex than had hitherto been appreciated. Genera such as *Bartonella* and *Trypanosoma* are now known to comprise a range of species that can only be differentiated by molecular techniques (Birtles *et al.*, 2001; Noyes *et al.*, 2002; Rolain *et al.*, 2003). These taxa can cause mixed infections and are not rigidly host specific (as had been considered previously), and therefore no prior assumptions as to specific identity can be made. Our current analysis, although based only on morphological distinctions, nevertheless provides a foundation upon which future studies, exploiting molecular differentiation of the constituent species, can probe the factors regulating protozoan and arthropod parasites in xeric hosts.

The five haemoparasites that were recorded represent the same range of taxa that occur in European rodents (Bajer *et al.*, 2001; Pawełczyk *et al.*, 2004) and some have been recorded previously from African rodents (e.g. *Bartonella* and *Babesia* in *Psammomys obesus*; see Fichet-Calvet *et al.*, 2000); however, there were some notable differences as well as similarities in their epidemiology. Overall, the prevalence of *Haemobartonella* was much higher than recorded previously in *Ac. dimidiatus* in Egypt (80% compared with 3.8% noted by Nasr & Arafa, 1977), but it was similar to that typically encountered in *Apodemus* spp. and *Mus spretus* (A. Bajer & J. M. Behnke, unpubl. data) in Europe. Prevalence was similar in mice from all four wadis (range 75.9–89.3%), and lice, which are considered important vectors of Haemobartonellae (Kreier, 1977), were also present although, paradoxically, the percentage infested with lice was markedly lower in Wadi Gebal, where the prevalence of *Haemobartonella* was high. *Polyplax brachyrrhyncha* and *Po. oxyrrhyncha* were both recorded from this site, but it is also possible that the ubiquitous mite *Al. sanguineus* acted as a vector.

In comparison, both *Babesia* and *Bartonella* spp. infections were very rare in spiny mice, contrasting markedly with both European rodents and Tunisian *Ps. obesus,* for both of which late summer is the season of highest prevalence, that of *Bartonella* spp. sometimes rising to 60% or more (Fichet-Calvet *et al.*, 2000; Bajer *et al.*, 2001; Pawełczyk *et al.*, 2004). *Bartonella* spp. are believed to be transmitted by fleas (Kreier, 1977; Bown, Bennett & Begon, 2004), which were present in three of the four wadis studied, but there was no evidence of significant co-occurrence of these taxa (but see below). Tick larvae may also play a role in transmitting *Bartonella* spp. (Sanogo *et al.*, 2003), and both larvae and nymphs are the main vectors of *Babesia* sp. In our study, they were found very infrequently on *Ac. dimidiatus,* which might explain the very low prevalence of infections with *Babesia* sp. at this time of year. *Bartonella* and allies are important, emerging zoonoses of humans, and rodent *Bartonella* infections of humans have been reported

from both America and Europe (Bown *et al.*, 2004). Given the increasing importance of ecotourism in the St Katherine National Park (Zalat & Gilbert, 1998), with trekking western tourists sleeping within the gardens of local farmers where they may encounter *Acomys* and its ectoparasites, a review of the potential of these *Bartonella* spp. for human zoonoses might be worthwhile.

Both *Hepatozoon* sp. and *T. acomys* were markedly more prevalent and abundant than reported previously in Egypt (Nasr & Arafa, 1977) and, in our study, showed clear site-specific co-occurrence with the flea *Pa. chephrensis*, a known vector for *T. acomys* (Vilensky, 1960; Abdallah, Abdel-Hafez & Al-Yaman, 1989). European fleas can act as vectors for *H. erhardovae* (Krampitz, 1981) and so *Pa. chephrensis* may also be the vector for the *Hepatozoon* sp. infecting *Ac. dimidiatus*. Alternatively, in the absence of experimental evidence, mites such as *Al. sanguineus* may transmit *Hepatozoon*. However, the mites were more uniformly distributed throughout the four wadis, and no obvious correlation between abundance of mites and *Hepatozoon* prevalence was noted. Both protozoa were more prevalent and abundant in mice from Wadis Gharaba and Tlah, which had a far higher proportion of rodents also infested with fleas (30–46%). By comparison, *Pa. chephrensis* were rare in Wadi El Arbaein and absent from Wadi Gebal. *Hepatozoon* sp. was completely absent from these wadis, whereas only one mouse from Wadi El Arbaein carried *T. acomys*. These close correlations between the prevalence of *T. acomys* and the presence of *Pa. chephrensis* and *Hepatozoon* sp. at the component community level are consistent with the idea that *Pa. chephrensis* is a vector of these pathogens within the St Katherine's wadi system. At the infracommunity level, we detected a weak but significant association between *T. acomys* and fleas, the first statistically sound, field-based evidence in support of this parasite–vector relationship (but see Rifaat *et al.*, 1976; Smith *et al.*, 2005). *Xenopsylla* fleas, collected from *Acomys* in Wadi Gebal, appear not to transmit *T. acomys*, and the role of the winter-active *Nosospyllus* fleas (Krasnov *et al.*, 1997) as disease vectors has not been considered. Associations between parasites and their vectors, whether based on presence/absence data as here, or on quantitative data, are difficult to detect in the field because of the different biologies of ecto- and haemoparasites, including differences in the times needed for haemoparasites to become patent in the bloodstream [from 48 to 72 h in the case of *T. acomys* (Abdallah *et al.*, 1989) to a few weeks for *Hepatozoon* sp. (Krampitz, 1964)] and differences in the residence time of feeding vectors. For these reasons, it is rare to establish statistically significant evidence of a relationship from co-occurrence data. Vectoring relationships are more likely to be detected in longitudinal studies where a lag time between the occurrence of fleas and haemoparasites can be factored into the analysis (Smith *et al.*, 2005). Nevertheless, in our study the aggregation of fleas in two wadis created an opportunity to detect an association convincingly, although in the case of *Hepatozoon,* even with this advantage, we failed to detect any significant relationship at the level of infracommunities.

Herpetosoma-type trypanosomes, such as *Trypanosoma lewisi* and *Trypanosoma musculi*, do not normally cause mortality in healthy laboratory hosts, but heavy infections may cause abortion or embryo resorption (Molyneux & Ashford, 1983). More subtle effects have been suggested recently in field voles *Microtus agrestis* infected with *T. microti,* including reduced likelihood of holding territory in the breeding season (Smith *et al.*, 2005). Given the life history of *Ac. dimidiatus*, with a small number of embryos nurtured to an advanced stage of development (Young, 1976), effects of this sort on morbidity or fertility caused by *T. acomys* could have a major selective impact on the rodent population. A further feature of *T. acomys* is the extent of the patent period in spiny mice. Both *T. lewisi* and *T. musculi* have short patent periods when transmission to the flea vector is possible. *T. acomys,* however, has a long (100 days plus, Abdallah *et al.*, 1989) period when parasitaemia may exceed 1000 trypanosomes per ml peripheral blood and transmission is presumably possible. This may represent an adaptation facilitating transmission in this arid environment when flea density is low. The long patent period explains the high prevalence of infection with *T. acomys* in mice of age class 2, but the decline in the oldest mice (age class 3) suggests either the action of some form of immunity in later life or selective mortality of infected older mice (Fig. 5b). An immune response certainly occurs in *T. lewisi* and *T. musculi*, and is suggested by the data of Abdallah *et al.* (1989) for *T. acomys*, which show clearance from peripheral blood after 150 days, although a mechanism for this has not been identified. The potential of fleas other than *Pa. chephrensis* to transmit *T. acomys* has not been evaluated, but if species such as *Nosopsyllus* sp. and *X. dipodilli* do have annual life cycles in this extreme environment (Krasnov *et al.*, 2002b; but see also Smith *et al.*, 2005), the discontinuity of their life cycles may reduce transmission to below break-point for the trypanosome in sites where they act as principal vectors.

Our data represent the first report of *Cr.* cf. *parvum* from *Ac. dimidiatus*, extending the many reports of its presence in other rodents (Fayer, Morgan & Upton, 2000; Bajer *et al.*, 2002). The prevalence of *Cr.* cf. *parvum* and *Giardia* sp. (overall about 17%) was surprisingly high for such an arid area. As natural water resources are scarce in the four wadis, and water for agriculture is drawn from deep underground, the probability of waterborne transmission must be very low, although sporadic winter rain can result in localized standing water during the spring. Nevertheless, direct and foodborne transmission routes seem more likely. Perhaps pertinently, the prevalence and abundance of both protozoa were markedly higher in Wadi El Arbaein, the busiest wadi because of the camel supply route supporting tourism on Mt Sinai and because of human activity in the lower wadi adjacent to St Katherine town. Camel dung forms a food resource within Wadi El Arbaein for invertebrates, birds and rodents. Middens of ruminant dung accumulate under rocks, the result of winnowing by Sinai rose finches *Carpodacus synoicus* searching for food, and around the entrances to rodent refuges in the walls of the Bedouin gardens as well

as near burrows. These accumulations of dung may create a more favourable moist microhabitat for transmission of both *Cr*. cf. *parvum* and *Giardia* spp. Camels *Camelus bactrianus* are suitable hosts for these intestinal parasites (Fayer *et al.*, 2000), although no studies have as yet compared the taxonomy of operational taxonomic units from *Acomys* with those from ruminants including camels. Goats and sheep are grazed throughout the wadi and may be alternate hosts, but interestingly the infected mice were highly aggregated around one of the Bedouin gardens in the upper wadi adjoining a large captive colony of hyrax *Procavia capensis*, which has existed for almost two decades in this location. Hyrax dung is used extensively to fertilize this garden, and although nothing is known currently about their suitability as reservoir hosts for *Cr*. cf. *parvum* and *Giardia*, it is possible that these animals may be the source of *Acomys* infections. An assessment of the role of both camels and hyrax in the context of transmission, and in particular whether rodent-, ruminant- and human-infectious strains are involved (Morgan *et al.*, 1999), is currently being undertaken.

A distinctive arthropod ectoparasite fauna, dominated by the flea *Pa. chephrensis*, the lice *Po. oxyrrhyncha* and *Po. brachyrrhyncha*, and the mite *Al. sanguineus*, was collected from *Ac. dimidiatus* in St Katherine. All are well-known ectoparasites of *Ac. dimidiatus* (Hirst, 1914; Keegan, 1956; Hoogstraal & Traub, 1965*a,b*; Lewis, 1967) and appear specific, although the mite *Al. sanguineus* has also been recorded from a range of other rodents. A trombiculid larva was also prevalent (almost 100%) on *Ac. dimidiatus* from all sites, but the taxonomy of this species has not been fully resolved. As this mite was abundant at all sites, it is assumed that its selective influence was similar in all wadis.

Other ectoparasites from *Ac. dimidiatus* are primarily parasites of other rodents, particularly gerbils (genera *Gerbillus* and *Seekatomys*). These include the flea *X. dipodilli* and a *Haemolaelaps* species. Hoogstraal & Traub (1965*b*) noted a *Haemolaelaps* sp. on gerbils from St Katherine, and we also recorded these mites abundantly from *Gerbillus*. Hoogstraal & Traub (1965*b*) recorded an unidentified *Nosopsyllus* species from *Acomys* at St Katherine, and suggested that this might replace *Pa. chephrensis* at high altitude. *Nosopsyllus theodori* was also found by Krasnov *et al.* (1997) from this host in the Negev. We have found no evidence for *Nosopsyllus* at St Katherine (including in wadis not considered in this paper). However, our studies were conducted entirely in summer at temperatures of 30–35 °C, and *N. theodori* has been shown in the Negev (Krasnov *et al.*, 1997) to occur only in the winter months. This species is believed to have an annual life cycle in the Negev, aestivating as pupae through the summer months (Krasnov *et al.*, 2002*b*).

Clear differences were noted in the ectoparasite fauna of the different wadis. In particular, the complete absence of the flea *Pa. chephrensis* from Wadi Gebal was notable, and this flea showed a gradient of abundance that was to some extent correlated with altitude and environmental temperature. The only fleas found on *Ac. dimidiatus* within Wadi Gebal were *X. dipodilli*, which had probably transferred

from gerbils. On the other hand, *Pa. chephrensis* was most abundant within Wadi Gharaba, the hottest, lowest wadi. This distribution of flea species with altitude may be correlated with temperature and humidity (Krasnov *et al.*, 2001*a,b*) or may be related to the availability of suitable substrates for pupation; Krasnov *et al.* (2002*a*) noted differences in the larval survival of *Xenopsylla* species parasitizing *Meriones,* depending on substrate texture.

As in previous studies of protozoan haemoparasites and gut parasites (e.g. Turner, 1986; Bajer *et al.*, 2001), a small and relatively predictable assemblage of protozoan and bacterial pathogens was recorded in spiny mice. Most mice supported only a subset of these taxa, the maximum coexisting in one animal being four. The community structure of haemoparasites in *Ac. dimidiatus* is actually very similar to that of *Clethrionomys glareolus* in northern European woodlands; total species richness, as discernable by morphology on slides, in both hosts is 5, with an average of 1.4 parasite taxa per host in bank voles (Bajer *et al.*, 2001) and 1.22 in spiny mice. This is despite the considerable differences in ecology and life-history strategies of the two host rodents. *Clethrionomys glareolus* is a high-fecundity, short-lived species experiencing large population oscillations and high mortality of young animals (Alibhai & Gipps, 1985). *Acomys dimidiatus,* on the other hand, has low fecundity, with an extensive gestation period (Young, 1976), and is thought to be long-lived and fairly sessile (Elvert *et al.*, 1999; Shargal, Kronfeld-Schor & Dayan, 2000; E. Sayed, pers. comm.). The similarity between the two species in protozoan parasite diversity is probably due to two opposing processes. In the first place, acquisition of infections in north temperate woodlands is probably much faster than in the Sinai desert. Opportunities for vector transmission are greater, there is free access to water facilitating transfer of gut pathogens and rodent density is high by the end of the summer. Within the northern woodlands, voles therefore acquire infections much more readily than spiny mice in the desert. On the other hand, vole life span is short, with up to 60–70% mortality in the first 6 weeks of life (Alibhai & Gipps, 1985). Hosts therefore die before they have the opportunity to acquire a more complex protozoan fauna. In the Sinai, *Acomys* probably acquire protozoan infections relatively slowly, but they live longer, and so have the potential to acquire more complex protozoan faunas in this montane desert. This is seen most clearly in the case of *Hepatozoon* infections (Fig. 3a), in which prevalence increases throughout life, presumably as a direct result of a steady rate of vector challenge. There is also evidence of haemoparasites partitioning exploitation of spiny mice according to age. Whereas *Hepatozoon* was most prevalent in the oldest mice (Fig. 3a), *Haemobartonella* and *T. acomys* did not show this increase with age, and in Wadi Gebal *Haemobartonella* spp. were more abundant in the youngest mice (Fig. 4b), although this may have represented a local transmission effect. Such well-evidenced age-specific effects have not been observed in earlier studies of northern boreal voles (e.g. Turner, 1986; Bajer *et al.*, 2001; Pawełczyk *et al.*, 2004), possibly because these voles do not live long enough,

but recently Smith *et al.* (2005) reported a convex age-prevalence curve for *T. microti* in a longitudinal study of *M. agrestis* in the UK. Similarly, neither haemoparasites nor intestinal protozoa of voles have shown consistent variation associated with the sex of the host (Turner, 1986; Chalmers *et al.*, 1997; Sturdee, Chalmers & Bull, 1999; Bajer *et al.*, 2001; Smith *et al.*, 2005). In the present study, however, a marked sex effect was noted for *Cr.* cf. *parvum* and *Giardia* spp. (females had higher prevalence and hence were more important as reservoirs of these parasites) and for *Haemobartonella* spp. (males had higher abundance). In this case, the sex effects were probably more obvious because of the relatively low random mortality experienced by *Ac. dimidatus* relative to voles, and because of the highly specialized reproductive ecology of this rodent. Mature females give birth to relatively few advanced offspring, and live together in family groups (Shargal *et al.*, 1999), generating greater opportunities for transmission from parents to offspring. *Acomys dimidiatus* males are aggressive and individuals within enclosures fight (Shargal *et al.*, 1999). Sex-linked differences in aggression and dispersal may create sufficient differences in physiology to allow sex-based differences in susceptibility to parasites to become apparent (Klein & Nelson, 1999).

Despite these age and sex differences, the most important differences in parasite component community structure related to the wadis in which the mice were trapped, backing up observations on the helminth parasites of these rodents presented by Behnke *et al.* (2004). As in that paper, mice from the high-altitude Wadi Gebal had an impoverished parasite fauna, lacking both the flea *Pa. chephrensis* and the trypanosome *T. acomys*, in addition to the dominant nematode *Protospirura muricola* (Behnke *et al.*, 2004). In contrast, mice from the low-level hot Wadi Gharaba were heavily infected with *Pr. muricola*, *Pa. chephrensis* and *T. acomys*. The intestinal parasites *Giardia* sp. and *Cr.* cf. *parvum* were most common in Wadi Arbaein. *Acomys dimidiatus* is a relatively sedentary rodent (E. Sayed, pers. comm.) and mice within wadis are effectively segregated from their conspecifics in other wadis. Indeed, if this were not the case, these differences between wadis would not be discernable. Such differences might lead to local adaptation of mice to their prevailing parasite fauna, a phenomenon that appears to be taking place in relation to androgen metabolism and intra-specific social behaviour in *Ac. dimidatus* populations (Barnard *et al.*, 2003*b*). Indeed, it may be the case that populations of mice within wadis (which are usually associated with Bedouin gardens) are locally specialized to a particular parasite fauna. It remains to be seen what will happen to local mouse and parasite populations as increasing human activity within the national park breaks down barriers to movement.

Acknowledgements

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