

1 **Long-term spatiotemporal stability and dynamic changes in**
2 **helminth infracommunities of spiny mice (*Acomys dimidiatus*)**
3 **in St. Katherine's Protectorate, Sinai, Egypt**

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21 Running head : Helminth communities in spiny mice from the Sinai, Egypt

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33 SUMMARY

34 The importance of parasites as a selective force in host evolution is a topic of current interest.
35 However, short-term ecological studies of host-parasite systems, on which such studies are usually
36 based, provide only snap-shots of what may be dynamic systems. We report here on four surveys,
37 carried out over a period of 12 years, of helminths of spiny mice (*Acomys dimidiatus*), the
38 numerically dominant rodents inhabiting the dry montane wadis in the Sinai Peninsula. With host
39 age (age-dependent effects on prevalence and abundance were prominent) and sex (female bias in
40 abundance in helminth diversity and in several taxa including Cestoda) taken into consideration, we
41 focus on the relative importance of temporal and spatial effects on helminth infracommunities. We
42 show that site of capture is the major determinant of prevalence and abundance of species (and
43 higher taxa) contributing to helminth community structure, the only exceptions being
44 *Streptopharaeus* spp. and *Dentostomella kuntzi*. We provide evidence that most (notably the
45 Spiruroidea, *Protospirura muricola*, *Mastophorus muris* and *Gongylonema aegypti*, but with
46 exceptions among the Oxyuroidea e.g. *Syphacia minuta*), show elements of temporal-site stability,
47 with rank order of measures among sites remaining similar over successive surveys and hence some
48 elements of predictability in these systems.

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50 Key words: helminth infracommunities, spiny mice, *Acomys dimidiatus*, helminths, nematodes,
51 cestodes, site-specific parasite variation.

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55 INTRODUCTION

56 Helminth communities of rodents have been studied mostly through short-term surveys usually
57 limited to one to three years in duration, corresponding to typical PhD studentships and
58 conventionally awarded research grants and are mostly based on destructive, cross sectional
59 sampling of the host population over these periods of time (Lewis, 1968; Montgomery and
60 Montgomery, 1988; Behnke *et al.* 2001; Bajer *et al.* 2005; Jackson *et al.* 2014). Data from such
61 studies are then used to test hypotheses, for example about the role of particular parasite species or
62 even communities in host evolution, in modifying host life history parameters and affecting their
63 immunological profiles (Barnard *et al.* 2002, 2003; Jackson *et al.* 2014; Babayan *et al.* 2018).
64 Quantitative studies of rodent helminth communities, spanning longer periods of time are rare in the
65 literature but examples include the work of Kisielewska (1970a) in Poland, Haukisalmi, Henttonen
66 and Tenora (1988) in Finland, Tenora and Staněk (1995) in the Czech Republic and more recently
67 Grzybek *et al.* (2015) in Poland. Of these, only Haukisalmi *et al.* (1988) and Grzybek *et al.* (2015)
68 subjected their data to rigorous statistical scrutiny; both studies concentrating on bank voles
69 (*Myodes glareolus*). As far as we are aware, there are no long-term studies of other rodent helminth
70 communities from other parts of the world, including Africa and the Middle East that specifically
71 address the issue of temporal changes in helminth communities over timespans of a decade or
72 longer (but see Spickett *et al.* 2017).

73 In European rodents, relatively stable patterns of infection with dominant helminths have
74 been reported through short-term monitoring (~ three years) of host populations (Montgomery and
75 Montgomery, 1990; Bajer *et al.* 2005) and gastro-intestinal parasite communities seem to remain
76 relatively stable even in experiments in wild populations that have been manipulated by
77 intervention with anthelmintics (Knowles *et al.* 2013). In contrast rarer species, with lower
78 prevalence in the population, appear to fluctuate more unpredictably (Montgomery and

79 Montgomery, 1990; Bajer *et al.* 2005; Kisielewska, 1970a; Knowles *et al.* 2013). Nevertheless,
80 derived measures of community structure such as diversity indices and species richness appear to be
81 more influenced by minor fluctuations in the common species and these are primarily responsible
82 for among-year variation in these parameters (Behnke *et al.* 2008b). More marked dynamic changes
83 in some measures of component and infracommunity structure, including cyclic changes over
84 seasons and years, have also been recorded in particular helminth species (Tenora, Wiger and
85 Barus, 1979; Tenora and Staněk, 1995; Haukisalmi, Henttonen and Tenora, 1988; Montgomery and
86 Montgomery, 1990; Behnke *et al.* 1999; Behnke *et al.* 2008a).

87 Longer-term studies, lasting over ecologically and evolutionarily relevant periods of time,
88 are important, however, if we are to establish the robustness of some of the epidemiological trends
89 that have been detected in particular host-parasite systems (e.g. relative temporal stability of
90 prevalence and abundance, of dominant helminth species, and dynamic changes in other species).
91 Long-term studies allow documentation of aspects of systems that cannot be recorded over shorter
92 periods of time, including the repeatability of trends and the extent to which they constitute typical
93 features of these host-parasite systems (or perhaps represent unpredictable ephemeral events). By
94 testing the robustness and repeatability of spatial trends in measures of helminth communities over
95 time, their broader relevance and role in shaping parasite communities becomes apparent. Studies
96 that last over a decade or longer might also allow cycles/fluctuations in helminth communities to be
97 observed fully, and linked to host demographic changes over time (Tenora *et al.* 1979), marked
98 cycles in population density being one of the characteristic features of rodent populations (Elton,
99 1924; Lambin *et al.* 2000; Gouveia *et al.* 2015). Unidirectional temporal trends in measures of
100 parasite communities can also be related to gradual climatic and environmental changes, both of
101 which are of current public concern (Hudson *et al.* 2006; Brooks and Hoberg, 2007; Houghton,
102 2009; Marohasy, 2017). Duly processed empirical data derived from long-term monitoring, can
103 inform computer models used to make predications within scrutinised systems (e.g. the growing

104 interest in spatial epidemiology; Eisen and Wright, 2001; Ostfeld *et al.* 2005;), but also in the
105 wider frame for human health and livestock agriculture arising from, for example, the consequences
106 of climate change, alterations in landscape structure and environmental fragmentation from
107 increasing urbanization (Zell, 2004; Ostfeld *et al.* 2005; Bradley and Altizer, 2006; Morgan and
108 Wall, 2009; Huntley *et al.* 2014). Monitoring longer-term temporal trends therefore is important.

109 Building on our previously published long-term series of surveys of helminths of bank voles
110 in Poland (Behnke *et al.* 2008; Grzybek *et al.* 2015), we report here in a parallel study on four
111 successive cross-sectional surveys of the helminth parasites of spiny mice conducted over a twelve
112 year period (2000, 2004, 2008 and 2012) in the arid wadis that transect the mountains located in the
113 South Sinai Peninsula of Egypt. The helminth communities of spiny mice in this geographical
114 location are relatively depauperate in terms of component community species richness (Greenberg,
115 1969; Wertheim & Greenberg, 1970; Barnard *et al.* 2003; Behnke *et al.* 2000, 2004) compared with
116 hosts living in some other regions of the world (Brouat *et al.* 2007; Spickett *et al.* 2017). In this
117 respect they bear much similarity to those of bank voles in Europe and therefore constitute an ideal
118 system through which to examine the generality of some of the conclusions from work on European
119 rodents, this time in an ecologically contrasting environmental system typified primarily by aridity
120 and intense summer temperatures. The work was conducted in the same four sites at the same time
121 of year on each occasion in order to assess the relative importance of temporal versus spatial
122 factors, and their interaction, in affecting the structure of helminth infracommunities in spiny mice
123 in this region of the Middle East.

124

125 MATERIALS AND METHODS

126 *Study sites*

127 The local environment in this part of Egypt has been described by Hobbs (1995) and Zalat and
128 Gilbert (1998). The study sites utilised in the current work have been described comprehensively in
129 our earlier papers (Behnke *et al.* 2000, 2004) and subtle differences in aspects of their ecology have
130 been documented (Gilbert *et al.* 1996; Zalat *et al.* 2001). They are located in the mountains of the
131 South Sinai, two within the vicinity of St. Katherine, bordering on the town periphery (Wadis El
132 Arbaein and Tlah), and two somewhat further afield (Wadis Gebal and Gharaba), but all within 15
133 km of the town centre (See Behnke *et al.* 2004, for GPS data and full descriptions of each site).
134 These sites are separated from one another by the town of St. Katherine and also by high ridges and
135 therefore we consider them to be isolated from one another in ecological time, although the host
136 species is panmictic and genetic studies have revealed some gene flow among the three populations
137 (Alfudhala 2015). The sites were sampled at the same time of year in each year of the study (last
138 two weeks of August and the first two weeks of September).

139

140 *Terminology and collection of spiny mice*

141 In this paper we refer to *Acomys dimidiatus* (Cretzschmar, 1826) for eastern spiny mice from this
142 region of Egypt following Cassola (2016a) and not *A. cahirinus* (Geoffroy, 1803) (Cairo spiny
143 mouse; Cassola, 2016b) as in some earlier studies from the region (Myers 1961; Greenberg, 1969;
144 Ward and Nelson, 1967), since the latter species is now known to occur across N. Africa, rather
145 than on the north-eastern side of the Suez Canal. The methods used for trapping rodents, and for
146 sampling and processing trapped animals have all been fully described previously (Behnke *et*
147 *al.* 2004). Age categories were established as described earlier using principal components analysis
148 of a range of morphological measures including body weight and dried eye lens weight (Behnke *et*
149 *al.* 2004) and two age classes were established. Age class 1 mice were immature juveniles, while
150 age class 2 mice were all young and breeding adults.

151

152 *Identification and quantification of endoparasites*

153 The entire alimentary tracts were brought back to the University of Nottingham in either 70%
154 ethanol (2012) or in 10% formalin (2000, 2004 and 2008) for dissection. The fixed intestines were
155 opened carefully in water or Hanks' saline and examined under a dissecting microscope. All
156 parasite specimens were identified with the help of relevant literature on rodent helminths from the
157 region (Greenberg, 1969; Myers, 1954, 1961; Quentin, 1966; Ward and Nelson, 1967; Chabaud,
158 1975; Quentin and Wertheim, 1975; Ashour and Lewis, 1982; Lewis and Ashour, 1983; Wertheim,
159 1993), sexed and stored in tubes containing 70% ethanol. Tapeworms were stained using borax
160 carmine, dehydrated in ethanol and mounted in Canada Balsam for microscopical examination.

161

162 *Statistical analysis*

163 Prevalence values (percentage of animals infected, based on presence/absence of parasites
164 and hence binomially distributed data) are given with 95% confidence limits (CL₉₅), calculated by
165 bespoke software based on the tables of Rohlf and Sokal (1995). Abundance of infection (including
166 both infected and non-infected animals) is summarised by arithmetic means and standard errors of
167 the mean (S.E.M.).

168 The degree of aggregation in the data was calculated by the index of discrepancy (*D*) as
169 described by Poulin (1993) and the index of dispersion (*I*, variance to mean ratio). Frequency
170 distributions of raw values from individual taxa were tested for goodness of fit to Gaussian,
171 negative binomial, positive binomial and Poisson models by χ^2 as described by Elliott (1977) and
172 the negative binomial exponent *k* is given as appropriate (See Table 1 in supplementray material).
173 The acceptability of parametric models was evaluated through the goodness of fit of residuals from

174 minimum sufficient GLM models to the distributions listed above, through Q-Q plots and through
175 estimation of the total deviance accounted for.

176 The statistical approach adopted has been documented comprehensively in our earlier
177 publications (Behnke *et al.* 2004, 2008a,b; Bajer *et al.* 2005). For analysis of prevalence we used
178 maximum likelihood techniques based on log linear analysis of contingency tables in the software
179 package IBM SPSS Statistics Version 22 (IBM Corporation). This approach is based on categorical
180 values of the factors of interest, which are used to fit hierarchical log linear models to
181 multidimensional cross-tabulations using an iterative proportional-fitting algorithm that detects
182 associations among the factors, one of which may be presence/absence of infection. Initially, full
183 factorial models were fitted, incorporating as factors SEX (two levels, males and females), AGE
184 (two levels, immature and mature animals), YEAR of study (four levels, 2000, 2004, 2008, 2012),
185 and SITE (four levels, Wadis El Arbein, Gebal, Gharaba and Tlah). The presence or absence of
186 parasites (INFECTION) was considered as a binary factor. All these five factors were fitted initially
187 to all models that were evaluated. For each level of analysis, beginning with the most complex
188 model involving all possible main effects and interactions, those combinations that did not
189 contribute significantly to explaining variation ($\alpha = 0.05$) were eliminated stepwise beginning
190 with the highest level interaction (backward selection procedure). A minimum sufficient model was
191 then obtained, for which the likelihood ratio of χ^2 was not significant, indicating that the removal of
192 all remaining parameters significantly reduced the fit of the model. The importance of each term in
193 interactions involving INFECTION in the final model was assessed by the probability that its
194 exclusion would alter the model significantly and these values are given in the text, assessed by
195 likelihood ratio test between nested models with and without each factor of interest.. The remaining
196 terms in the final model that did not include INFECTION (for example, variation among sites in the
197 number of animals of each sex sampled [SITE x SEX]) are not given but can be made available

198 from the authors on request. For each taxon in turn we also fitted models with each factor alone plus
199 INFECTION.

200 For analyses of quantitative data conforming to Gaussian distributions we used general
201 linear models (GLM) with normal errors implemented in R version 2.2.1 (R Core Development
202 Team) and the residuals were checked for approximate goodness of fit to the Gaussian distribution.
203 When the residuals failed to meet the requirements of Gaussian models we used generalised linear
204 models with negative binomial or Poisson error structures. Full factorial models that converged
205 satisfactorily were simplified using the STEP procedure and tested for significance using deletion of
206 terms beginning with the highest order interaction by comparing models with or without that
207 interaction, then models based on main effects plus 2-way and 3-way interaction by deletion of 3-
208 way interactions in turn, and so on until each main effect was evaluated in a model that only
209 comprised all main effects. Changes in deviance (*DEV*) are given for models based on Poisson
210 errors (interpreted by χ^2), for models based on Gaussian errors we give *F* and for those based on
211 negative binomial errors the likelihood ratio (*LR*). Minimum sufficient models (*MSM*) were then
212 fitted (all significant interactions and main effects plus any main effects that featured in
213 interactions) and the process was repeated to obtain values for changes in deviance, test statistics
214 and probabilities. The percentage of deviance accounted for by each significant main effect or
215 interaction was calculated as recommended by Xu (2003) and reported earlier by Behnke *et. al*
216 (2008) and more recently by Grzybek *et al.* (2015).

217 Throughout the analyses, our primary focus was on the temporal and spatial effects on
218 parasites communities as reflected in YEAR (reflecting overall change with time), location in which
219 the animals were sampled (SITE) and the interaction between these (YEAR x SITE on INFECTION
220 or abundance of worms), the latter in particular indicating whether the prevalence or abundance of
221 specific taxa showed a consistent hierarchical relationship across sites over time (rank order

222 remained the same), or fluctuated without direction. For this reason we also present values for some
223 non-significant outcomes of model parameters as these underscore the robustness of stability among
224 sites.

225 If the data did not meet the assumptions of parametric tests, we employed non-parametric
226 tests in IBM-SPSS 22 (Kruskal Wallis test for k levels in a specified factor (SITE and YEAR) and
227 the Mann Whitney U -test where factors only had 2 levels, e.g. SEX and AGE) and in these cases
228 interactions could not be tested.

229 We used canonical discriminant function analysis (CDFA) in IBM-SPSS as an additional
230 approach to evaluating the relative importance of the influence of site and year on parasite burdens.
231 Quantitative parasite data for each of 15 species of helminths were first standardized by $\log_e(x+1)$
232 transformation of individual worm burdens for each species, then subtraction of mean \log_e value for
233 each species and division by the standard deviation before analysis. After fitting in CDFA, of the 15
234 resulting canonical discriminant functions, functions 1 and 2, which accounted for most of the
235 variation in data (See results below), were plotted against one another.

236

237 **Results**

238 *Numbers of mice caught, trapping effort and numbers autopsied*

239 Table 1 shows the numbers of spiny mice caught by year of survey and by site, and summarizes the
240 trapping effort and resulting success, as calculated by the number of mice caught per 100 trap hours
241 (th) and the percentage of traps deployed that were occupied by spiny mice overnight. The total
242 number of individual mice was 857 and although there was some variation in trapping effort among
243 surveys and sites depending on local and year specific constraints, the only significant effect
244 (Kruskal-Wallis test with either YEAR or SITE as the explanatory factor on each of the variables in

245 Table 1) was that of YEAR, reflecting increasing numbers of trap hours over successive surveys
246 ($\chi^2_3=11.5$, $P= 0.009$).

247 Of the total caught, we autopsied 431 animals (50.3% of caught spiny mice) and the
248 distribution of these by year, site, sex and age is show in Table 2. Inevitably, there was significant
249 variation in the numbers taken for autopsy among years of survey ($\chi^2_3=28.4$, $P< 0.001$), site
250 ($\chi^2_3=13.4$, $P= 0.004$) and between the two age classes ($\chi^2_1=32.2$, $P< 0.001$) but not between the
251 sexes and there were no significant interactions between these factors. These differences are taken
252 into account in the analyses that follow.

253

254 *Prevalence and abundance of combined helminths*

255 The overall prevalence of helminths (all species combined) across the whole period was 91.2%
256 (86.77-94.21). Prevalence values were generally high throughout (Table 3 and Fig. 1A), but
257 nevertheless varied significantly among the wadis (SITE x INFECTION $\chi^2_3=17.9$, $P<0.001$; Table
258 3), with the highest values recorded among spiny mice from Wadis Gharaba and Tlah. The YEAR x
259 SITE x INFECTION interaction term was not significant ($\chi^2_9=12.6$, $P=0.18$) suggesting that site
260 differences in prevalence were stable through time and overall there was no significant change in
261 prevalence of helminths over time (YEAR x INFECTION $\chi^2_3=3.0$, $P=0.4$). Fig. 1A shows that the
262 relatively high prevalence among mice from Wadi Tlah was evident in all four surveys and those
263 from Wadi Gharaba likewise, but with only one exception in 2008, when prevalence values for
264 mice from this wadi and those from Wadis El Arbaein and Gebal were all identical (90.0%).
265 Prevalence did not vary significantly between the two sexes (Table 3), but there was a significant
266 difference in prevalence between the two age classes (AGE x INFECTION $\chi^2_1=7.94$, $P=0.005$;

267 Table 3) values being higher among the older mice (8.2% higher). There were no significant
268 interactions between any of the explanatory factors.

269 The overall abundance of helminths (all species combined) was 37.5 ± 7.17 worms per
270 mouse. All four main effects were highly significant (Table 4; for YEAR $LR_{3,422}=15.7$, $P=0.0013$,
271 highest in 2004; for SITE $LR_{3,422}=48.7$, $P<0.00001$, highest in Wadi Tlah; for SEX $LR_{1,422}=23.9$,
272 $P<0.00001$, highest in female mice; for AGE $LR_{1,422}=34.5$, $P=0.00001$, highest in older mice) but of
273 these, SITE was the most important in explaining deviance in the MSM (Table 5). However, there
274 was also a highly significant 2-way interaction (SITE x YEAR, $LR_{9,410}=41.8$, $P<0.00001$) which is
275 illustrated in Fig. 1B and which was of secondary importance in explaining deviance and YEAR
276 even less so (table 5). As can be seen, abundance of helminths was relatively steady across the
277 period in three wadis, with highest mean abundance in Wadi Gharaba, then El Arbaein and lowest
278 in Wadi Gebal, and there was no overlap during the period for mean abundance values from spiny
279 mice from these three wadis, their relative rank order remaining the same at each survey. The
280 interaction was attributable to the variable worm burdens among mice from Wadi Tlah, which in
281 three years ranked among the typical values derived from mice from the other three wadis, but
282 showed a huge peak in 2004, more than three times higher than the highest mean worm burden
283 recorded from mice elsewhere. Fig. 2A also shows that that while in Wadis El Arbaein, Gharaba
284 and Tlah, the abundance of helminths was higher in female mice, this was not the case for mice
285 from Wadi Gebal, where male and female mice essentially harboured comparable but low worm
286 burdens (SITE x SEX, $LR_{3,410}=7.6$, $P=0.06$).

287

288 *Species Richness*

289 The overall mean species richness (MSR) was 2.09 ± 0.063 . Analysis by a model with Poisson
290 errors showed that none of the possible interactions and only three of the main effects were

291 significant (Table 4; for YEAR, $DEV_3 = -12.01$, $P = 0.0074$, highest value in 2004 and lowest in
292 2008; for SITE, $DEV_3 = -12.84$, $P = 0.005$, highest value for Wadi Tlah and lowest for Wadi El
293 Arbaein). The temporal changes across surveys were mostly consistent and in the same direction in
294 all four sites (Fig. 2A; for SITE x YEAR $Dev_9 = 5.24$, $P = 0.8$), except in Wadi Gebal between 2008
295 and 2012 when species richness fell across the period, while showing stability or in an increase in
296 the other three sites. Of the three main effects, AGE accounted for the highest percentage of
297 deviance in the MSM (Table 5; for AGE, $DEV_1 = -29.97$, $P < 0.00001$, higher among older mice).

298

299 *Species Diversity*

300 The overall value of Brillouin's index of diversity (BID) was 0.31 ± 0.015 . The two strongest
301 effects on BID were the significant increase in its value with host age (Table 4; main effect of AGE,
302 $F_{1,422} = 17.49$, $P < 0.0001$) and the difference in value among surveys (Table 4; main effect of YEAR,
303 $F_{3,422} = 7.35$, $P < 0.0001$), this temporal change accounting for most of the deviance in the MSM as
304 shown in Table 5 and thereby, indicating overall fluctuation with time. However, the rank order of
305 the values of BID for sites was mostly consistent from year to year (no significant 2-way interaction
306 of SITE x YEAR), with the exception of mice from Wadi Gebal (Fig. 2B) which showed the
307 greatest change in value and rank order. There were also significant but weaker effects of study site
308 (Tables 4 and 5; main effect of SITE, $F_{3,422} = 2.92$, $P = 0.034$) and host sex (main effect of SEX,
309 $F_{1,422} = 4.06$, $P = 0.044$), but there were no significant interactions.

310

311 *Frequency distributions and measures of aggregation*

312 Frequency distributions were fitted to all higher taxa and individual species for which
313 quantitative data were available, by site, by year and in relevant combinations. These were then

314 tested for goodness of fit to the Gaussian, Poisson and to the positive and negative binomial
315 distributions. For brevity we do not report these values here (but see supplementary materials, Table
316 1). However, all parasite burdens were over-dispersed (based on values of I and D) and conformed
317 best to the negative binomial distribution. Indeed, some were so aggregated that even GLM with
318 negative binomial error structures failed to converge.

319

320 *Prevalence and abundance of nematodes*

321 Overall, 89.3% (84.70-92.79) of the spiny mice were infected with nematodes, and these were
322 mostly from the two Orders Spirurida (Superfamily Spiruroidea) and Oxyurida (Superfamily
323 Oxyuroidea). As with the prevalence of combined helminths, values for prevalence of nematodes
324 were consistently high throughout (exceeding 85% in all surveys, Table 3 and Fig. 1C). Analysis of
325 this data subset generated much the same results as that of combined helminths, because the
326 helminth assemblage was so dominated by nematodes (93.1% of all the recovered helminths were
327 nematodes). Thus prevalence values also varied significantly among the wadis (Table 3; SITE x
328 INFECTION $\chi^2_3=25.2$, $P<0.001$), and the difference among the wadis was maintained over time
329 (no significant YEAR x SITE x INFECTION interaction, $\chi^2_9=14.3$, $P=0.11$) and no significant
330 change in prevalence with time (YEAR x INFECTION $\chi^2_3=5.3$, $P=0.15$). Prevalence did not vary
331 significantly between the two sexes (Table 3), but there was a significant difference in prevalence
332 between the two age classes (AGE x INFECTION $\chi^2_1=8.6$, $P=0.003$; Table 3), with a higher
333 prevalence among the older mice (an increase of 8.2%).

334 Abundance of nematodes (for all species combined the mean worm burden was 34.9 ± 7.12)
335 was analysed as above for all helminths, with much the same outcome. In addition to the significant
336 main effects of YEAR (Table 4; $LR_{3,422}=15.78$, $P=0.0013$) and SITE ($LR_{3,422}=46.15$, $P<0.00001$,

337 which accounted for most deviance in the MSM, Table 5) and the interaction between these (Fig.
338 1D; $LR_{9,410}=42.42$, $P<0.00001$), the main effects of AGE (Table 4; $LR_{1,422}=28.7$, $P<0.00001$) and
339 SEX (Table 4; $LR_{1,422}=21.6$, $P<0.00001$) were also significant. There was also a borderline
340 significant interaction between SEX and SITE (not illustrated; $LR_{3,410}=7.67$, $P=0.053$), much as
341 described above and illustrated in Fig. 2A for the abundance of helminths.

342

343 **Spiruroid nematodes**

344 Spiruroid nematodes accounted collectively for 33.7% of all nematodes that were recovered, and
345 had an overall prevalence of 69.6% [63.46-75.16]. Five species were identified and all five were
346 stomach dwelling worms. *Pterogodermatites witenbergi* Quentin & Wertheim, 1975 was only
347 found on one occasion in one mouse, a mature male mouse, captured in Wadi El Arbaein in 2004.
348 Analysis of all five species combined showed that prevalence did not vary across years (Table 6;
349 YEAR x INFECTION, $\chi^2_3=1.38$, $P=0.7$), but there was a highly significant effect of wadi (SITE x
350 INFECTION, $\chi^2_3=34.4$, $P<0.001$), with a higher prevalence in the mice from Wadis Gharaba and
351 Tlah, compared with El Arbaein and Gebal (Table 6). The overall temporal consistency of this
352 difference among the wadis is evident through the lack of a significant SITE x YEAR x
353 INFECTION interaction ($\chi^2_9=14.2$, $P=0.12$) and therefore prevalence can be considered to have
354 been stable over time. Fig. 4A shows that prevalence among mice from Wadi Gebal exceeded that
355 of mice from Wadi Tlah on only one occasion (2008) but never that of mice from Wadi Gharaba.
356 Prevalence did not vary between the sexes (SEX x INFECTION, $\chi^2_1=0.2$, $P=0.65$) but was
357 significantly higher among the older age class (Table 6; AGE x INFECTION, $\chi^2_1=101.0$, $P<0.001$),
358 although the age-related pattern, while always showing a higher prevalence among older mice,

359 varied in extent among sites and across years (YEAR x SITE x AGE x INFECTION, $\chi^2_9=24.2$,
360 $P=0.004$, not illustrated).

361 The mean abundance of combined spiruroid nematodes was 11.8 ± 1.15 and abundance was
362 also stable across the years (Table 7; main effect of YEAR, $LR_{3,422}=4.01$, $P=0.26$). However, there
363 was a highly significant difference in mean worm burdens among sites (Table 7, main effect of
364 SITE, $LR_{3,422}=91.5$, $P<0.00001$, highest worms burdens in Wadi Gharaba). SITE accounted for
365 most of the explained deviance in the MSM (Table 5) and overall the rank order of sites across
366 surveys remained stable (Fig. 4A, for SITE x YEAR $LR_{9,400}=9.70$, $P=0.38$). Worm burdens were
367 greater in female (main effect of SEX, $LR_{1,422}=13.3$, $P=0.00026$) and older mice (Table 7, main
368 effect of age, $LR_{3,422}=69.9$, $P<0.00001$). There was also a significant 3-way interaction (SITE x
369 YEAR x AGE, $LR_{24,397}=55.0$, $P=0.0003$) arising from the AGE effect varying in extent but not
370 directions in particular years in some sites as illustrated in Fig. 2C. A weaker 2-way interaction
371 (SEX x AGE, $LR_{1,421}=4.71$, $P=0.03$) similarly reflected variation in the extent of the age effect, but
372 in this case between male and female mice (Fig. 2B).

373 Two of the lumen dwellers, *Protospirura muricola* and *Mastophorus muris*, accounted for
374 94.95% of all the spiruroids and since these two species are overtly very similar in appearance to
375 one another but quite different to the other three species, we could not distinguished convincingly
376 some immature specimens. Therefore, we also analysed a taxon that included a combination of
377 these two species, and as the data in Table 6 and Fig. 4B show, prevalence values for data subsets
378 were much the same as when all spiruroids were pooled in one taxon, with only minor changes to
379 their values. Log-linear analysis of prevalence also revealed the same outputs as those for all
380 spirurids collectively, again with only very minor changes to model parameters (not shown). Much
381 the same turned out to be the case for analysis of abundance as Table 7 shows, with the outcome of
382 the statistical analysis very similar to that for all spiruroid nematodes.

383

384 ***Protospirura muricola***

385 The majority of spiruroids were identified as *P. muricola* ($n=4520$ and 89.1% of all spiruroids). The
386 overall prevalence of this species was 52.9% (46.50-59.31) and was very similar in each year of the
387 study varying only between 47.8 and 55.7% (Table 6), and not surprisingly there was no significant
388 difference across years and no SITE x YEAR x INFECTION interaction (Fig.4C, $\chi^2_9=7.1$, $P=0.6$),
389 indicating consistent and stable differences among the mice from different wadis over the four
390 surveys. Prevalence was highest in Wadi Gharaba, and the species was virtually absent from Wadi
391 Gebal, where only one mouse was found to carry this species in 2012, so there was a huge site
392 effect (Table 6; SITE x INFECTION, $\chi^2_3=164.0$, $P<0.001$). Older mice were more likely to be
393 infected (Table 6, AGE x INFECTION, $\chi^2_1=68.3$, $P<0.001$), and although prevalence was 7.6%
394 higher among female mice, the difference between sexes was not significant ($\chi^2_1=2.4$, $P=0.12$).

395 Quantitative analysis also revealed a highly significant main effect of SITE (Table 7; $LR_{3,422}$
396 $=166.8$, $P<0.00001$), which accounted for most of the explained deviance in MSM (Table 5), but
397 not of YEAR ($LR_{3,422}=3.78$, $P=0.29$) and no SITE x YEAR interaction (Fig. 2D), indicating
398 stability in the rank order of sites across years of survey. Worm burdens were highest in mice from
399 Wadi Gharaba, substantially lower in Wadis El Arbaein and Tlah, and the species was rare in Wadi
400 Gebal, where, as indicated above, only one mouse was found to be infected with *P. muricola*. In
401 contrast to prevalence, abundance of *P. muricola* was significantly higher among female mice
402 (Table 7; $LR_{1,422}=12.6$, $P=0.0004$) and as expected was much higher among the older mice (Table
403 7, main effect of AGE, $LR_{1,422}=44.4$, $P<0.00001$). There was also a significant 3-way interaction,
404 illustrated in Fig. 2D, (SITE x YEAR x AGE, $LR_{24,395}=47.9$, $P=0.0026$), showing that in wadis
405 where *P. muricola* was abundant, older mice always had higher worm burdens than younger mice,

406 but the relative difference in abundance between the age classes varied from year to year and from
407 site to site.

408

409 *Mastophorus muris*

410 *Mastophorus muris* accounted for only 5.7% of the spiruroids, with an overall prevalence of
411 17.4 % [12.97-22.82], and as Table 6 shows prevalence was highest among mice from Wadi Gebal,
412 with much lower values for the other three wadis (SITE x INFECTION, $\chi^2_3=66.0$, $P<0.001$).

413 Although overall prevalence of this species was stable across the four surveys, varying only
414 between 14.1 and 20.7% (Table 6; YEAR x INFECTION, $\chi^2_3=2.18$, $P=0.5$), with consistent rank
415 order of prevalence values across the four surveys (YEAR x SITE x INFECTION, $\chi^2_9=11.0$,
416 $P=0.3$), Fig. 4D shows nevertheless that 2008 was a peak year in Wadi Gebal with 75.0% [52.55 -
417 89.59%] of mice from this wadi infected. Age also affected prevalence (Table 6; AGE x
418 INFECTION, $\chi^2_3=34.1$, $P<0.001$), with a more than 5 times higher value among the older compared
419 with younger mice, but the difference in prevalence between the sexes was not significant. Analysis
420 also identified two significant interactions, the first of which reflected that while prevalence was
421 always higher among older mice, there was variation in the relative difference between younger and
422 older mice in the four surveys (Not illustrated; AGE x YEAR x INFECTION, $\chi^2_3=9.0$, $P=0.029$)
423 and the second reflected the same effect but for SITE rather than year of survey (AGE x SITE x
424 INFECTION, $\chi^2_3=9.0$, $P=0.029$).

425 As expected from the above analysis, abundance of *M. muris* varied hugely among sites
426 (Table 7; $LR_{3, 422}=60.6$, $P<0.00001$) and accounted for most of the explained deviance (Table 5).
427 This species was mostly encountered in mice from Wadi Gebal (67.4% of all worms of this species)
428 where *P. muricola* was extremely rare. As with prevalence there was relative stability in abundance

429 across years (Table 7; main effect of YEAR, $LR_{3,422}=1.36$, $P=0.72$) and no significant YEAR x
430 SITE interaction (Fig. 3E) and no difference in abundance between the sexes (Table 7, $LR_{1,422}$
431 $=0.12$, $P=0.73$). Most worms were recovered from the older age class of mice (Table 7, main effect
432 of AGE $LR_{1,422}=18.3$, $P<0.0001$), but the relative difference in abundance between the age classes,
433 whilst always in the same direction, showed some variation across years (YEAR x AGE, $LR_{3,416}$
434 $=12.9$, $P=0.0048$), and among sites (SITE x AGE, $LR_{3,416}=8.65$, $P=0.034$).

435

436 *Streptopharagus spp.*

437 The predominant species was *S. greenbergi* (Myers, 1954) Wertheim, 1993, although in our
438 survey in 2000 we also recorded *S. numidicus*, so here we combine both species and refer to
439 *Streptopharagus spp.* The overall prevalence was 20.4% [16.09-25.45], and nematodes of this
440 genus accounted for 4.4% of all the spiruroids recovered. In contrast to *P. muricola* and *M. muris*,
441 these spiruroids showed significant variation in prevalence across the surveys (Table 6; YEAR x
442 INFECTION, $\chi^2_3=17.4$, $P=0.001$) but overall no significant difference in prevalence among the
443 wadis (Table 6; SITE x INFECTION, $\chi^2_3=4.58$, $P=0.2$). Prevalence was higher in 2004 and 2012,
444 than in the intervening years (Table 6). However, the data in Fig. 4E show that prevalence increased
445 steadily across the whole period only among mice from Wadi Gharaba (0% in 2000, but up to
446 40.5% in 2012). Prevalence also rose sharply in 2012 among mice from Wadi Gebal, and varied
447 more modestly among those from Wadis El Arbaein and Tlah, and but overall there was no
448 significant YEAR x SITE x INFECTION interaction, ($\chi^2_9=16.0$, $P=0.067$). There was no difference
449 in prevalence between the sexes, but there was significant age effect in the expected direction
450 (Table 6; AGE x INFECTION, $\chi^2_1=22.2$, $P<0.001$).

451 The mean worm burden of *Streptopharagus* spp. was just 0.52 ± 0.105 . Analysis of
452 quantitative data by models with negative binomial errors and other models failed to converge
453 satisfactorily or failed to give acceptable distributions of residuals, so we used non-parametric tests
454 to assess the main effects. As with prevalence there was a highly significant difference in
455 abundance across the surveys (Table 7; Kruskal-Wallis test, effect of YEAR, $\chi^2_3=18.6$, $P<0.001$)
456 with peak abundance in 2012. Despite the variation in mean abundance among mice from different
457 wadis, the differences were not significant (effect of SITE, $\chi^2_3=5.5$, $P=0.14$). Abundance did not
458 differ significantly between the sexes (Table 7), but the older mice carried heavier worm burdens
459 compared with the younger individuals (Table 7; Mann-Whitney *U* test, $z=4.35$, $P<0.001$).
460 Temporal changes in mean worm recovery for each site in turn are illustrated in Fig. 3F, where it
461 can be seen that mean worm burdens rose steadily over successive surveys in mice from Wadi
462 Gharaba, but showed lower and overlapping values for recovery from mice from the other three
463 wadis.

464

465 ***Gongylonema aegypti***

466 *Gongylonema aegypti* was a much rarer parasite to the above four species accounting for
467 only 0.61% of the spiruroids recovered and with an overall prevalence of just 4.2% [2.18-7.53]. No
468 worms of this species were recovered in 2000 and most (89%) in 2012, when the overall prevalence
469 rose to 11.3% (Table 6; YEAR x INFECTION, $\chi^2_3=26.8$, $P<0.001$). *G. aegypti* was predominantly
470 recovered from mice from Wadi Gharaba (67% of all worms recovered) and this site effect was
471 significant (Table 6; SITE x INFECTION, $\chi^2_3=15.5$, $P=0.001$) but there was no SITE x YEAR x
472 INFECTION interaction ($\chi^2_9=3.31$, $P=0.95$). As with the other spiruroids there was also an age
473 effect (Table 6; AGE x INFECTION, $\chi^2_1=6.2$, $P=0.013$), but no difference between the sexes.

474 Too few animals were infected to permit analysis of abundance by GLM, but non-
475 parametric tests showed that worm burdens differed cross the years of survey (Table 7; Kruskal-
476 Wallis test, $\chi^2_3=26.5$, $P<0.001$), with peak abundance in 2012, and heaviest mean worm burdens in
477 mice from Wadi Gharaba (Table 7, for SITE $\chi^2_3=15.5$, $P=0.001$). Worm burdens did not differ
478 significantly between the sexes, but on average were twice higher among female mice (Table 7;
479 Mann-Whitney U test, $z=2.27$, $P=0.023$).

480

481 **Oxyuroid nematodes**

482 The three species of oxyuroid nematodes collectively accounted for 63% of all the nematodes
483 recovered, with an overall prevalence of 61.0% (54.63-67.01). Prevalence varied across years of
484 survey (Table 8; $\chi^2_3=14.7$, $P=0.002$), peaking in 2004, and among sites ($\chi^2_3=11.9$, $P=0.008$) with
485 highest prevalence among mice from Wadi Tlah, but there was no SITE x YEAR interaction (Fig.
486 5A; $\chi^2_9=11.0$, $P=0.28$). There was a significant difference between the age classes ($\chi^2_1=14.3$,
487 $P<0.001$) but in contrast to the spirurid nematodes, for the oxyuroid species prevalence was higher
488 among the young mice (age class 1 in Table 8). Prevalence did not differ between the sexes.

489 Mean abundance was 22.1 ± 6.98 , and all the main effects significantly influenced
490 abundance (Table 9). Abundance was highest in 2004 and lowest in 2000 (main effect of YEAR,
491 $LR_{3, 422}=14.18$, $P=0.0027$), highest in mice from Wadi Tlah (main effect of SITE, $LR_{3, 422}=35.9$,
492 $P=0.00001$), higher in female mice (main effect of SEX, $LR_{1, 422}=9.82$, $P=0.0017$) and in the older
493 animals (main effect of AGE, $LR_{1, 422}=4.23$, $P=0.04$). Moreover, the difference in abundance among
494 sites varied significantly across the four surveys (2-way interaction, YEAR x SITE, $LR_{9, 413}=39.01$,
495 $P<0.00015$) and this is illustrated in Fig. 6A. Abundance was generally low with overlapping values
496 for mice from Wadis El Arbaein, Gebal and Gharaba across the period, varying from a mean

497 abundance of 2.3 in mice from Wadi El Arbaein in 2000, to 14.8 in the same wadi in 2008, but as
498 illustrated in Fig. 6A, there were two prominent peaks among mice from Wadi Tlah, one in 2004
499 and another in 2012.

500

501 *Syphacia minuta*

502 The overall prevalence of *S. minuta* was 27.1% (21.81-33.26) and varied significantly
503 among mice from different wadis (SITE x INFECTION, $\chi^2_3=14.4$, $P=0.002$), with the highest
504 prevalence recorded in mice from Wadi Gebal (Table 8). There was also significant temporal
505 variation (YEAR x INFECTION, $\chi^2_3=13.5$, $P=0.004$) with the highest value in 2004. However, the
506 rank order of prevalence among mice from some wadis, but not all, changed across the years of
507 survey (YEAR x SITE x INFECTION, $\chi^2_9=21.6$, $P=0.010$) as illustrated in Fig. 5B. Prevalence
508 among mice from Wadi Gebal was always higher than that among mice from Wadi El Arbaein, but
509 more variable among mice from Wadis Gharaba and Tlah. The difference in prevalence values
510 between the two sexes was not significant (Table 8) but prevalence was higher overall among older
511 mice ($\chi^2_1=4.8$, $P=0.028$) although the extent of this age effect differed between the two sexes (Fig.
512 7A; SEX x AGE x INFECTION, $\chi^2_1=4.0$, $P=0.046$).

513 As Fig. 6B shows, the peaks of abundance of oxyuroid nematodes in 2004 and 2012 among
514 mice from Wadi Tlah were largely attributable to unusually high mean worms burdens with *S.*
515 *minuta* in those years. One mouse from Wadi Tlah harboured 2,786 *S.minuta* and in 2012 another
516 mouse from the same wadi had 675 worms. Of the 11 heaviest worm burdens among the 117 mice
517 from which we recovered *S.minuta*, nine were from mice from Wadi Tlah. The high mean values
518 for worm recovery were heavily swayed by the worm burden of the mouse carrying 2,786 *S. minuta*
519 which was an adult female from Wadi Tlah in 2004. With such extreme variation in worm burdens,

520 values were clearly overdispersed ($I=1075$, $D=0.93$) and models with negative binomial and other
521 error structures all failed to provide acceptable residuals, so further analysis was by non-parametric
522 tests. These showed that there was significant overall variation across surveys (Kruskal-Wallis test,
523 for effect of YEAR, $\chi^2_3=13.0$, $P=0.005$, Table 9), among sites ($\chi^2_3=14.9$, $P=0.002$) and between the
524 age classes (Mann-Whitney U Test, $z=2.0$, $P=0.41$), but not between the two sexes.

525

526 *Aspiculuris africana*

527 *Aspiculuris africana* was recovered from 21.6% (16.70-27.24) of the mice and as with the
528 other two oxyuroid nematodes, 2004 was a year of peak prevalence for this species also (Table 8).
529 Prevalence varied significantly across the surveys (YEAR x INFECTION, $\chi^2_3=12.6$, $P=0.006$) and
530 also among sites, with the highest value recorded among mice from Wadi Tlah and lowest among
531 those from Wadi Gebal (Table 8; SITE x INFECTION, $\chi^2_3=18.1$, $P<0.001$). Despite variation across
532 years, this difference in prevalence between mice from these two wadis was maintained across all
533 four surveys (Fig. 5C). There was less temporal variation in prevalence among mice for the other
534 two wadis, but their rank order varied more, nevertheless the YEAR x SITE x INFECTION
535 interaction was just on the wrong side of the cut off for significance ($\chi^2_9=16.4$, $P=0.059$),
536 suggesting some element of stability over the years. Prevalence was very similar in both sexes and
537 only just higher among the younger mice (Table 8; $\chi^2_1=3.83$, $P=0.05$).

538 Variation in worm burdens with this species was far less extreme than that for *S. minuta*
539 ($I=8.3$, $D=0.89$), but nevertheless still best described by the negative binomial model (goodness of
540 fit, $\chi^2_6=4.8$, $P=0.56$). As with prevalence there was a significant effect of YEAR ($LR_3=9.89$,
541 $P=0.020$), a stronger effect of SITE ($LR_3=19.27$, $P=0.0002$), and a weak interaction between these
542 two main effects (YEAR x SITE, $LR_9=17.79$, $P=0.038$). Although this model reflected well the

543 summary data in Table 9 and Fig. 6C, the residuals were not ideally distributed. However, a
544 *posteriori* analysis using non-parametric tests confirmed the significance of these main effects
545 (YEAR by Kruskal-Wallis test, $\chi^2_3=13.4$, $P=0.004$; SITE, $\chi^2_3=20.1$, $P<0.001$). Both approaches
546 confirmed the significance of the age effect ($LR_1=7.25$, $P=0.007$ and Mann-Whitney U test, $z=2.29$,
547 $P=0.022$). There was no significant difference in prevalence between the sexes.

548

549 *Dentostomella kuntzi*

550 Prevalence of *D. kuntzi* showed a distinct pattern. Overall prevalence was 40.1% (33.94-
551 46.53) and did not differ significantly among mice from the four wadis (Table 8; SITE x
552 INFECTION, $\chi^2_3=6.7$, $P=0.082$). Moreover, this similarity of prevalence among sites was
553 maintained over time (YEAR x SITE x INFECTION, $\chi^2_9=4.83$, $P=0.85$). However, there was a
554 significant overall change in prevalence with time (YEAR x INFECTION, $\chi^2_3=16.85$, $P=0.001$),
555 and the data in Table 8 and Fig. 5D show that there was a consistent fall in prevalence among mice
556 in all four wadis from peak values in 2004, through 2008 to 2012. As with *A. africana*, prevalence
557 of this species was significantly higher among younger mice (Table 8; AGE x
558 INFECTION, $\chi^2_1=37.4$, $P<0.001$), but not between the sexes (SEX x INFECTION, $\chi^2_1=0.19$,
559 $P=0.89$). Moreover, whilst in the same direction, the extent of this age effect varied significantly
560 between the two sexes (Fig. 7B; SEX x AGE x INFECTION, $\chi^2_1=7.94$, $P=0.005$) being more
561 extensive among male mice. It also varied among mice from different sites, and whilst clearly
562 apparent among those from Wadis El Arbaein, Gharaba and Tlah, there was no difference in
563 prevalence of the two age classes among mice from Wadi Gebal (Fig. 7C; SITE x AGE x
564 INFECTION, $\chi^2_3=13.4$, $P=0.004$).

565 As with prevalence, abundance did not differ significantly among mice from different sites
566 (Table 9), but there was a significant temporal change in abundance (main effect of YEAR,
567 $LR_3=10.15$, $P=0.017$) and the significant SITE x YEAR interaction ($LR_9=18.91$, $P=0.026$) indicates
568 that the rank order of abundance changed across years. Therefore, for this species there was a lack
569 of temporal stability in abundance and this is clearly shown in Fig. 6D. Abundance was higher
570 among the younger mice overall (Table 9; for main effect of AGE, $LR_1=12.63$, $P=0.0004$) and in
571 mice from three wadis but as Fig. 7D shows not for those from Wadi Gebal (SITE x AGE,
572 $LR_3=8.76$, $P=0.033$). There was no difference in abundance between the sexes.

573

574 **Other species of nematodes**

575 In total 451 nematode larvae were recovered, which could not be identified with any degree of
576 certainty. These were included in analyses of higher taxa (Combined helminths and combined
577 nematodes) but not in other combinations. Of these 401 were recovered from 18 mice and found
578 encysted in the lower intestinal walls, mostly in the colon (Range = 1 – 171). These were most
579 likely to be the same as recorded by Greenberg (1969) from *A. dimidiatus* (= *cahirinus*) from Israel
580 and ascribed by him/her to the Spiruridae, but we could not be certain about our specimens. Eight
581 were recovered from mice from Wadi El Arbaein, seven from Wadi Tlah, two from Wadi Gharaba
582 and the remaining one from Wadi Gebal, and mostly in 2004 ($n=11$) and 2008 ($n=6$). Thirty
583 unencysted larval nematodes from 18 mice could not be identified and one mouse from Wadi
584 Gharaba harboured 20 unencysted nematode larvae in its liver.

585

586 *Prevalence and abundance of cestodes*

587 Prevalence of cestodes (intestinal dwelling adults + larvae combined) was 16.5% (12.16-21.76)
588 overall. As with combined helminths and combined nematodes, there was a highly significant
589 difference in prevalence among mice from different wadis (SITE x INFECTION $\chi^2_3=23.8$,
590 $P<0.001$; Table 3), but no significant change in prevalence with year of survey (YEAR x
591 INFECTION $\chi^2_3=1.15$, $P=0.76$), nor was the YEAR x SITE x INFECTION interaction significant
592 ($\chi^2_9=10.8$, $P=0.29$) and thus overall prevalence was relatively stable across the period (Fig. 1E).
593 While prevalence in three wadis was essentially similar, that among mice from Wadi Gharaba was
594 much lower, and consistently so. There was a significant difference in prevalence between the two
595 age classes (AGE x INFECTION $\chi^2_1=20.7$, $P<0.001$; Table 3), with a 3.5 fold higher prevalence
596 among the older mice and in contrast to nematodes, a strong effect of host sex (SEX x
597 INFECTION, $\chi^2_1=11.0$ $P=0.001$; Table 3) with prevalence among female mice twice as high as that
598 among males. There were no interactions between the explanatory factors.

599 Negative binomial models in R did not converge and hence analysis of abundance was
600 carried out using non-parametric tests. Overall abundance was 1.68 ± 0.52 worms/mouse and
601 abundance did not vary significantly across surveys (Table 4; Kruskal-Wallis test, $\chi^2_3=1.5$,
602 $P=0.68$). Cestodes were more abundant in spiny mice from Wadis El Arbaein, Gebal and Tlah
603 compared with Wadi Gharaba (Table 4; Kruskal-Wallis test, $\chi^2_3=17.12$, $P=0.001$). Abundance
604 increased significantly with host age (Mann-Whitney U test, $z=4.32$, $P<0.001$) with much higher
605 abundance among the older animals (Table 4), and it differed also significantly between the sexes
606 (Mann-Whitney U test, $z=3.36$, $P=0.001$) with more than two-fold higher abundance among female
607 compared with male mice (Table 4).

608

609 *Prevalence and abundance of adult cestodes*

610 The intestinal-dwelling adult cestode population comprised four species but was dominated by one,
611 *Rodentolepis negevi* Greenberg, 1969, which represented 74.7% of all the adult stage cestodes
612 recovered and had an overall prevalence of 10.2%. *R. fraterna* comprised 3.4% of adult cestodes,
613 *Mathevotaenia rodentinum* (Joyeux, 1927) 16.3%, *Witenbergitaenia sinaica* Wertheim, Schmidt &
614 Greenberg, 1986 1.7% and we were not able to identify with certainty seven specimens (3.9%). The
615 overall prevalence of *M. rodentinum* was 1.6% and that of the other taxa considerably lower, so
616 these were not analysed quantitatively.

617

618 ***Rodentolepis negevi***

619 *R. negevi* was encountered predominantly in two of the four wadis (Table 8. Gebal and Tlah), never
620 being recovered from mice from Wadi Gharaba (Table 8; SITE x INFECTION, $\chi^2_3=31.9$, $P<0.001$).
621 Prevalence increased significantly with time, from a low in the first two surveys until 2012 (YEAR
622 x INFECTION, $\chi^2_3=9.09$, $P=0.028$) and this was evident in mice from all the three wadis in which
623 this species occurred (Fig. 5E) and therefore consistent across the period (YEAR x SITE x
624 INFECTION, $\chi^2_9=9.8$, $P=0.37$). Prevalence was higher in female (Table 8; SEX x INFECTION,
625 $\chi^2_1=14.0$, $P<0.001$) and older mice (AGE x INFECTION, $\chi^2_1=15.6$, $P<0.001$).

626 Overall abundance was low (mean worm burden = 0.31 ± 0.073), overdispersed ($I=7.4$;
627 $D=0.95$) and best accounted for by the negative binomial model ($\chi^2_3=3.3$, $P=0.35$), but with only 44
628 out of 431 mice infected, parametric models failed to converge satisfactorily, so we applied only
629 non-parametric tests. As with prevalence, abundance increased with successive surveys although in
630 contrast to prevalence, there was a noticeable drop in abundance in 2012 (Table 9), and peak
631 abundance in the three wadis where this species occurred was in 2008 (Fig. 6E; Kruskal-Wallis test,
632 $\chi^2_3=8.9$, $P=0.030$). Since the parasite was never found in mice from Wadi Gharaba, not

633 surprisingly, the difference in abundance among wadis was highly significant (Kruskal-Wallis test,
634 $\chi^2_3=21.8$, $P<0.001$). As with prevalence, abundance increased with host age (Table 9; Mann-
635 Whitney U test, $z= 3.6$, $P<0.001$) and was higher in female mice ($z= 3.7$, $P<0.001$).

636 The 29 specimens of *M. rodentinum* were recovered from only seven mice, all from Wadi El
637 Arbaein, five mice in 2012 and two in 2004. Five of these were females, one of which was a
638 juvenile. *R. fraterna* was recovered from five mice, four of which were from Wadi El Arbaein and
639 in this case four were males and two juveniles. One female mouse from Wadi Gebal was infected
640 with *W. sinaica*.

641

642 *Prevalence and abundance of larval stages of cestodes*

643 Larval cestodes were rare in these populations of spiny mice and were only recovered from 12 mice
644 in total (2.8% [1.28 – 5.78]). Eleven of these mice were infected with a *Mesocestoides* sp. which we
645 were unable to identify to species level (see discussion). The average worm burden among the
646 infected animals was 49 worms/mouse, ranging from eight to 173 worms. *Mesocestoides* sp. was
647 recovered in 2000 (three mice, one from Wadi Tlah and two from El Arbaein), 2004 (four mice, two
648 from Wadi Tlah, and one each from Wadis Gebal and Gharaba) and 2008 (four mice, three from
649 Wadi Gharaba and one from Wadi Gebal) but not in 2012. Additionally, one mouse from Wadi Tlah
650 was infected with five larval stages of *Joyeuxiella rossicum* in 2000.

651

652 *Prevalence and abundance of Acanthocephala*

653 *Moniliformis acomysi* was the only acanthocephalan recovered from the spiny mice with a
654 prevalence of 5.6% [3.26-9.25]. Prevalence was affected significantly by the wadi in which mice

655 were captured (Table 8; SITE x INFECTION, $\chi^2_3=33.9$, $P < 0.001$) but did not vary significantly
656 across years, and there was no SITE x YEAR x INFECTION interaction. Of the 24 mice that were
657 infected with this species, 18 were from Wadi Gharaba, and none from Wadi Gebal. Prevalence did
658 not vary between sexes or age classes of mice. Much the same outcome was found for analysis of
659 quantitative data by non-parametric tests. The only significant effect was that of SITE (Kruskal-
660 Wallis test, $\chi^2_3=34.2$ $P < 0.001$), and as Table 8 shows abundance was clearly much higher among
661 mice from Wadi Gharaba.

662

663 *Sources of variation in abundance data*

664 The data in Table 5 show the percentage of deviance accounted for by each of the specific factors
665 and their interactions, as fitted in minimal sufficient models (MSM) in GLMs. For three of the four
666 individual species in this analysis (*P. muricola*, *M. muris* and *A. africana*), SITE was clearly the
667 greatest source of deviance. For three higher order taxa SITE also proved to be the factor
668 contributing most to explaining deviance in MSMs (Total helminths, total nematodes and combined
669 spiruroids) and for the combined oxyuroid nematodes it was the interaction of SITE with YEAR (as
670 explained above), but SITE also contributed a substantial proportion of the explained deviance for
671 this taxon. For *D. kuntzi* AGE accounted for most of explained deviance, and AGE together with
672 interactions with AGE played an important role in explaining deviance in the case of *P. muricola*,
673 *M. muris*, combined spiruroids and also helminth species richness. For just one measure, YEAR
674 was the main source of deviance (BID) and in this case AGE was second in importance.

675

676 *Canonical Discriminant Function Analysis*

677 Canonical discriminant function (CDF) analysis generated 15 axes that cumulatively accounted for
678 100% of the variance in the data. Canonical discriminant function 1 (Eigen value =0.810) accounted
679 for 41.8 % of the variance and function 2 (Eigen value =0.273) for a further 13.8% of the variance.
680 Together these two axes accounted for 54.8% of the variance and since lower ranked axes
681 individually explained a low proportion of the residual variation they were not examined further.
682 the remaining axes were not examined further. Function 1 (Fig. 8) essentially contrasts *P. muricola*
683 (0.733) with *M. muris* (-0.667), hence the scatter of data points from Gharaba towards the positive
684 range of the Function 1 axis, and those from Gebal towards the negative range. There were
685 additional positive but minor contributions to this axis from *Streptopharagus* spp. (0.163), *A.*
686 *africana* (0.131) and *G. aegypti* (0.111) and negative from *S. minuta* (-0.285) and *Mathevotaenia*
687 sp. (0.175). Axis 2 contrasts *S. minuta* (0.473). *D. kunzi* (0.391), *P. muricola* (0.370) and *M. muris*
688 (0.327) with *Mathevotaenia* (-0.577) and *R. negevi* (-0.324). With reference to Table 9, the negative
689 values of centroids for all 4 estimates for mice from Wadi El Arbaein reflect the low abundance of
690 *S.minuta*, *D. kuntzi* and the spiruroid nematodes in mice from this wadi.

691 Fig. 8E shows that with one exception, the centroids plus their SEMs for values from each
692 wadi occupy space that is unique to each wadi. Those from Wadi Gharaba are to the right (positive)
693 on the Function1 axis and those from Wadi Gebal to the left. Centroids from Wadi Tlah occupy
694 central ground on the Function 1 axis but are generally high on the Function 2 axis and those from
695 Wadi El Arbaein are low (negative) on the Function 2 axis. The only overlap is between the values
696 from Wadi Tlah in 2008, and those from Wadi El Arbaein in 2000, 2004 and 2008 but not 2012.

697

698 DISCUSSION

699 In this paper, whilst taking into account intrinsic factors, we have focused primarily on the question
700 of whether there are significant, and therefore meaningful, differences in the helminth community
701 structures of spiny mice living in different sites among the wadis of the S. Sinai massif (the spatial
702 effect, reflected in SITE), and if so whether they are stable over time (the spatiotemporal effect,
703 reflected in the YEAR x SITE interaction). Inevitably there are likely to be some fluctuations over
704 time (the temporal effect, reflected in YEAR), but the key question is whether, despite these
705 between-year fluctuations, the rank order of values for each of our target parameters, including the
706 species composition, derived from the different study sites changes over time. In this context our
707 analysis shows that the YEAR x SITE interaction on INFECTION reflecting prevalence, was only
708 significant in one case, for *S. minuta*. Likewise, where acceptable GLMs could be fitted in the
709 analysis of abundance, the YEAR x SITE interaction was mainly confined to the oxyuroid
710 nematodes *A. africana* and *D. kuntzi*, although there were also significant interactions for combined
711 helminths and combined nematodes (probably mostly driven again in both cases by the oxyuroid
712 component), but not for any of the spiruroid nematodes.

713 Our analysis shows not only that differences among wadis were generally maintained over
714 time, but also that there were some profound differences in the combinations of parasites typically
715 encountered at each of the four sites. The SITE effect accounted for most deviance in six of the ten
716 taxa for which GLMs converged satisfactorily (Table 5) and the outcome of CDFA analysis showed
717 that the centroids for each wadi representing the mean values for canonical discriminant function 1
718 and function 2 together with their standard errors, irrespective of the year of survey, occupied
719 unique 2-dimensional space in Fig. 8E in all but one case. Moreover, prevalence varied among sites
720 in 12 of the 14 analyses that were conducted on specific tax (the only exceptions were *S. minuta* and
721 *D. kuntzi*). Therefore, in agreement with Behnke *et al.* (2000, 2004), we conclude that spiny mice
722 from each wadi had a unique composition of helminth species which at the population level

723 distinguished them from the inhabitants of other wadis, and that these differences among wadis
724 were mostly stable over time.

725 Differences among the helminth communities of spiny mouse from different wadi-
726 populations were best reflected in the occurrence of spiruroid nematodes, as for example *P.*
727 *muricola* only very rarely occurring in mice from Wadi Gebal, but dominating the helminth fauna
728 of spiny mice in Wadi Gharaba, and in contrast *M. muris* dominating the spiruroid component in
729 mice from Wadi Gebal, but occurring only rarely in mice from the other three wadis. In fact mice
730 from Wadi Gharaba also showed the highest prevalence of *G. aegypti* and the acanthocephalan *M.*
731 *acomysi*, which was totally absent from mice from Wadi Gebal. Perhaps unexpectedly Wadi
732 Gharaba mice were not infected with the cestode *R. negevi*, which was most abundant in mice from
733 Wadi Tlah. All three species of oxyuroid nematodes were also more prevalent and more abundant in
734 mice from Wadi Tlah than in those from the other wadis, whereas mice from Wadi El Arbaein
735 showed intermediate prevalence and abundance of most helminth species, and hence their year
736 centroids occupy central ground in Fig. 8.

737 At this stage we can only speculate as to why these differences among the populations of
738 mice living in the four wadis occur. For the spiruroid nematodes, cestodes and the
739 acanthocephalans, one obvious possibility resides in the local composition and availability of
740 invertebrate intermediate hosts, such as the Coleoptera as reported from this region of Egypt by
741 Semida *et al.* (2001) and other ground dwelling insects including cockroaches (Zalat *et al.* 2001).
742 Spiruroid nematodes, including *Streptopharagus greenbergi*, *M. muris* and *Gongylonema* sp., are
743 all known to exploit Coleoptera, such as tenebrionids in other regions (Montoliu *et al.* 2013). Zalat
744 *et al.* (2001) recorded the highest diversity and species richness of ground dwelling insects in Wadi
745 Gharaba, significantly higher than for example in Wadi Gebal, and our data (Table 4) for helminth
746 species richness and diversity show a trend in the same direction for these two wadis (i.e. highest

747 values in mice from Wadi Gharaba and lowest in those from Wadi Gebal)). *P. muricola*, the
748 dominant species in Wadi Gharaba exploits invertebrates as intermediate hosts including Coleoptera
749 (Quentin, 1969; Campos and Vargas, 1977), and tenebrionid beetles have been used to maintain an
750 Egyptian isolate of this species in the laboratory (Lowrie *et al.* 2004; Schutgens *et al.* 2015).
751 *Moniliformis aegypti* is most likely to be transmitted by cockroaches (Blattidae), and these were
752 particularly common around the human dwellings in Wadi Gharaba (*pers. obs.*), although not
753 recorded by Zalat *et al.* (2001) in their survey of ground dwelling insects in this particular wadi but
754 recorded elsewhere in the region by Zalat *et al.* (2008). Interestingly, as noted above, *R. negevi*,
755 whose life cycle has not been studied, but which like other hymenolepidid cestodes is likely to be
756 transmitted through insects such as Coleoptera and possibly Siphonaptera (Behnke, 2000), was
757 never recovered from mice from Wadi Gharaba. Among-site differences were also found for two of
758 the three species of Oxyuroidea; prevalence of *D. kunzti* did not vary significantly among sites
759 although some differences in abundance were apparent (Fig. 6D, SITE x YEAR interaction) but *A.*
760 *africana* clearly did vary in both prevalence and abundance, with highest values recorded for mice
761 from Wadi Tlah though little difference in abundance in mice from the other three wadis. Ground
762 temperature is likely to influence the rate of embryonation of eggs of species such as *A. africana*
763 that depend on a period in the external environment for their eggs to reach infectivity, but Wadi
764 Tlah is situated at an intermediate height above sea level, with Wadis Gebal and El Arbaein higher
765 (and hence colder) and Wadi Gharaba lower (and warmer), so environmental temperature cannot be
766 directly responsible for the higher abundance of *A. africana* in Wadi Tlah through its influence of
767 development of eggs, although it is possible that environmental temperature may have had a role in
768 affecting abundance of this species through immune trade-off in the mice (Lochmiller and
769 Deerenberg 2000). It may be that host genetics play a role here, since the mice from this and each of
770 the other wadis had a distinct genetic signature, although this has not been linked yet to
771 susceptibility/resistance to specific helminths (Alfudhala, 2015). Even within a genetically

772 homogenous population, however, other environmental factors might indirectly influence the
773 abundance and prevalence of helminths through trade-offs that the mice face, which for example,
774 could restrict immune investment in harsher environments in which priority may be given to other
775 needs for survival (Lochmiller and Deerenberg 2000). Tapeworms are known to be particularly
776 susceptible to intra- and inter-specific competition in currently infected hosts (Read, 1951; Holmes,
777 1961; Arai, 1980; Holland, 1961; Bush and Lotz, 2000), and as we have shown the mice from Wadi
778 Gharaba were associated with the highest abundance of helminths, including the spiruroid
779 nematodes and the acanthocephalan *M. muris*. Thus it may be that *R. negevi* was unable to survive
780 in that wadi, where host responses to the other species (Behnke *et al.* 1977) and competition for
781 host resources would have been intense.

782 Our analysis revealed marked age effects in most cases, and the majority of these reflected
783 higher prevalence and greater abundance of worms in the older mice. In fact the only taxon that
784 failed to show a significant age effect, even though values for prevalence and mean abundance were
785 in the expected direction, was *M. acomysi*. In all other invertebrate transmitted species, including all
786 the spiruroid nematodes and the adult cestodes, worm burdens were significantly heavier in the
787 older compared with the younger juvenile mice. This is much as predicted given that most
788 helminths generate chronic infections in their hosts, and the longer a host lives, the more likely it is
789 to be exposed to infective stages of helminths and hence to accumulate worms in its intestines with
790 increasing age (Anderson and Gordon, 1982; Pacala and Dobson, 1988). Our data are therefore
791 consistent with many other studies on wild rodent helminths which have established age as a highly
792 predictable feature of these host-parasite systems (Kisielewska, 1971; Montgomery and
793 Montgomery, 1989; Behnke *et al.* 1999; Bugmyrin *et al.* 2005; Janova *et al.* 2010; Loxton *et al.*
794 2017), and as we have done here, a factor that must be taken into consideration and controlled for in
795 assessing the importance of other explanatory factors.

796 We did find the opposite pattern in two cases, however, with the prevalence and abundance
797 of two oxyuroid nematodes being in the opposite direction, with higher values for both parameters
798 among the younger mice. This is not unexpected, since in contrast to the spiruroid nematodes,
799 oxyuroid species are directly transmitted with no dependence on intermediate hosts. Both *A.*
800 *africana* and *D. kuntzi* are transmitted by eggs liberated in the faeces of hosts with patent infections,
801 and although to the best of our knowledge, neither species has been investigated in the laboratory,
802 the host-parasite relationship of the related *Aspiculuris tetraptera* has been well documented.
803 Depending on external environmental temperature, eggs require a period of about 5-7 days to
804 become embryonated and fully infective (Anya 1966). Adult mice are most likely to exploit latrine
805 sites in close vicinity to their nests, and when juveniles begin to explore the local environment they
806 are exposed to infective eggs. The prevalence and abundance of *A. tetraptera* both peak in young
807 adult house mice before falling in older sectors of the population (Behnke, 1976). *Aspiculuris*
808 *tetraptera* generates acquired immunity in laboratory mice (Behnke, 1975), and if *A. africana* does
809 likewise, both parameters of infection would be expected to fall with host age as we have found and
810 as has been reported for other parasites of wild rodents that are known to elicit strong acquired
811 immunity in their hosts (Gregory, 1992; Gregory *et al.* 1992). Presumably much the same applies to
812 *D. kuntzi* but there are no laboratory studies on this parasite or on any close relative to enable
813 certainty.

814 Prevalence and abundance of helminths usually does not vary markedly between the sexes
815 in wild rodents (Abu-Madi *et al.* 2000; Bordes *et al.* 2012) and when it does the bias is more often
816 towards higher abundance and prevalence in male hosts (Poulin, 1996; Schalk and Forbes, 1997;
817 Moore and Wilson, 2002; Ferrari *et al.* 2004, 2007; Luong *et al.* 2009). Consistent with the
818 literature, in our data prevalence did not differ significantly between the sexes in most species, the
819 only exception being *R. negevi*. However, we found that abundance did vary between the sexes, and
820 surprisingly was mostly female biased. In two species in particular, *P. muricola* and *R. negevi*,

821 worm burdens were markedly higher in female mice. Although there was no significant difference
822 in abundance between the sexes for other species, in most cases the value for mean abundance of
823 worms was numerically higher for female mice and collectively these effects were sufficiently
824 robust to affect also the higher taxonomic orders as Tables 3, 4 and 6-9 show, suggesting that a
825 small sex bias was a robust phenomenon across the helminths in the current system. Grzybek *et al.*
826 (2015), also reported female biased helminth infections in bank voles in Poland and provided a
827 comprehensive discussion of other examples. In that study, *M. muris* was more prevalent and more
828 abundant in females, although for *M. muris* in the current study neither parameter varied between
829 the sexes.

830 As concluded earlier, the site of capture of spiny mice was the most important factor
831 affecting both prevalence and abundance of infection with most of the helminth species that we
832 identified. If not the most influential, then site of capture was certainly one of the key factors, in all
833 cases except *Streptopharagus* spp. and *D. kuntzi*. The former was one of the rarer species,
834 accounting for less than 5% of all spiruroid nematodes, but showed signs of rising prevalence and
835 abundance towards the end of our study period. For this species temporal effects were more marked
836 than spatial effects and these were evident in all four sites, and thus consistent, reflecting a similar
837 temporally increasing risk of exposure across the region, perhaps attributable to an influx of the
838 appropriate intermediate insect vector. This region of Egypt has experienced marked climatic
839 changes over the course of the decade over which these surveys were conducted, including
840 increasing aridity with resultant consequences for Bedouin gardens (See Alsarraf *et al.* 2016 for
841 discussion of recent local environmental changes). This is likely to have had a major effect on
842 invertebrates in the region, although we are unaware of any quantitative studies of insect and other
843 invertebrate populations across this period. *D.kuntzi* was likewise evenly distributed across sites,
844 and here again the temporal effect and the temporal changes across sites played a greater role than
845 the wadi in which the mice lived. Like *A. africana*, *D. kuntzi* is transmitted directly between hosts

846 via externally liberated eggs, and is one of the core species of *A. dimidiatus*. Its transmission
847 strategy is clearly highly efficient and appears to be independent of the environmental and other
848 influences that are responsible for among-site variation in transmission of the other helminths in this
849 study.

850 Intuitively, we might have expected intrinsic factors such as host age to play a major,
851 perhaps even decisive, role in determining parasite communities, since the longer an animal lives,
852 the greater its cumulative exposure to pathogens is likely to be. While clearly playing a significant
853 and highly predictable role in most cases, in this and other recent studies in which data analysis has
854 taken account of and controlled for confounding interactions between key quantified/identified
855 factors, intrinsic factors have been shown to be less influential in shaping helminth communities
856 compared with extrinsic factors (Decker *et al.* 2001; Calvete *et al.* 2004; Grzybek *et al.* 2015).
857 Where surveys have encompassed more than just a single site for sampling helminth communities,
858 the site effect has proved to be decisive and considerably more influential than intrinsic factors. Our
859 current study therefore contributes to the growing body of work that collectively has implicated the
860 location in which an animal lives, as the most important determinant of the parasites to which it is
861 likely to be exposed (Calvete *et al.* 2004; Booth, 2006; Brouat *et al.* 2007; Calabrese *et al.* 2011;
862 Young and MacColl, 2017). Whether sites differ markedly ecologically in terms of habitat structure
863 or are fundamentally similar appears to be less of an issue since site-specific differences in helminth
864 communities have been reported in both cases (Eira *et al.* 2006; Brouat *et al.* 2007; Froeschke *et al.*
865 2010; Grzybek *et al.* 2015; Dwużnik *et al.* 2017). In some, habitat qualities that impinge on
866 transmission efficiency of helminths have been quantified and suggested as explanations for among-
867 site differences (Kinsella, 1974; Mollhagan, 1978; Decker *et al.* 2001; Froeschke *et al.* 2010; Young
868 and MacColl, 2017). However, as Calabrese *et al.* (2011) wrote, it may just be bad luck for the
869 inhabitants of particular sites, and in their own specific example, for deer mice living in a site where
870 tick challenge was particularly heavy. Thus while the regional helminth fauna of a host meta-

871 population may be well documented, the structures and compositions of specific helminth
872 communities in host populations within the region may vary extensively from one another. Our data
873 show that in general these differences are dependent on the site of capture of an animal, are
874 maintained over time and are dominant effects shaping helminth communities.

875

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1203 Table 1. No. of spiny mice caught, trapping effort and success by site and year of
 1204 survey

1206	1207	1208	1209	1210	1211	1212
	Site	Year	mice	Trap hours	mice/100	trap
					trap hours	success (%)¹
1211	El Arbaein	2000	63	2723	2.31	32.0
1212		2004	43	3265	1.32	16.8
1213		2008	69	3714	1.86	25.3
1214		2012	67	3918	1.71	23.4
1215		Combined	242	13620	1.78	23.9
1217	Gebal	2000	32	1838	1.74	21.3
1218		2004	43	2112	2.04	27.4
1219		2008	43	3831	1.12	16.4
1220		2012	47	3675	1.28	17.2
1221		Combined	165	11456	1.44	19.6
1223	Gharaba	2000	28	2136	1.31	16.5
1224		2004	61	2913	2.09	29.2
1225		2008	54	4314	1.25	16.1
1226		2012	52	3989	1.30	17.2
1227		Combined	195	13352	1.46	19.2
1229	Tlah	2000	46	2199	2.09	27.5
1230		2004	70	2117	3.31	45.2
1231		2008	80	5344	1.50	20.1
1232		2012	59	3988	1.48	19.9
1233		Combined	255	13648	1.87	25.1
1235	Combined	2000	169	8896	1.90	24.7
1236		2004	217	10407	2.09	27.9
1237		2008	246	17203	1.43	19.3
1238		2012	225	15570	1.45	19.4
1241		Overall total	857	52076	1.65	22.0

1244 ¹. Trap success is the percentage of traps that were occupied by rodents after overnight deployment
 1245 in the field.

1247 Table 2. Number of spiny mice autopsied in successive surveys, by site, host age and sex
 1248

1249			Age class		Totals		
1250	Site	Year	Sex	1	2	Row	Site & year
1251				1	2		
1252	El Arbaein	2000	Male	5	5	10	
1253			Female	4	7	11	21
1254		2004	Male	4	9	13	
1255			Female	6	7	13	26
1256		2008	Male	5	10	15	
1257			Female	5	10	15	30
1258		2012	Male	6	12	18	
1259			Female	9	8	17	35
1260		Total males		20	36	56	
1261		Total females		24	32	56	
1262	Total combined sexes		44	68	112		
1263	Gebal	2000	Male	4	3	7	
1264			Female	3	4	7	14
1265		2004	Male	4	6	10	
1266			Female	5	6	11	21
1267		2008	Male	2	8	10	
1268			Female	1	9	10	20
1269		2012	Male	5	7	12	
1270			Female	3	8	11	23
1271		Total males		15	24	39	
1272		Total females		12	27	39	
1273	Total sexes combined		27	51	78		
1274	Gharaba	2000	Males	2	4	6	
1275			Females	2	5	7	13
1276		2004	Males	7	6	13	
1277			Females	6	8	14	27
1278		2008	Males	4	9	13	
1279			Females	5	12	17	30
1280		2012	Males	5	13	18	
1281			Females	6	18	24	42
1282		Total males		18	32	50	
1283		Total females		19	43	62	
1284	Total sexes combined		37	75	112		
1285	Tlah	2000	Males	3	6	9	
1286			Females	3	7	10	19
1287		2004	Males	7	11	18	
1288			Females	5	9	14	32
1289		2008	Males	8	11	19	
1290			Females	7	10	17	36
1291		2012	Males	7	12	19	
1292			Females	9	14	23	42
1293		Total males		25	40	65	
1294		Total females		24	40	64	
1295	Total sexes combined		49	80	129		

1300
 1301

1302	Total by year	2000	Males	14	18	32
1303			Females	12	23	35
1304			Both sexes	26	41	67
1305		2004	Males	22	32	54
1306			Females	22	30	52
1307			Both sexes	44	62	106
1308		2008	Males	19	38	57
1309			Females	18	41	59
1310			Both sexes	37	79	116
1311		2012	Males	23	44	67
1312			Females	27	48	75
1313			Both sexes	50	92	142
1314						
1315	Total by sex		Males	78	132	210
1316			Females	79	142	221
1317			Both sexes	157	274	431
1318						
1319						

Table 3. Prevalence (\pm 95% confidence limits) of higher taxa – all helminths combined, all nematodes combined and all cestodes combined by year, site, host sex and age class

	Helminths (all combined)	Nematodes (all combined)	Cestodes (all combined)	Cestodes (intestinal adults)	Cestodes (larval stages)
Year					
2000	94.0 (86.19-97.70)	91.0 (82.36-95.84)	13.4 (7.27-23.05)	9.0 (4.16-17.64)	6.0 (2.30-13.81)
2004	92.5 (87.73-95.48)	92.5 (87.73-95.48)	14.2 (9.74-19.81)	10.4 (6.63-15.56)	3.8 (1.72-7.52)
2008	91.4 (86.15-94.78)	90.5 (85.19-94.14)	17.2 (12.17-23.66)	13.8 (9.31-19.70)	3.4 (1.49-7.31)
2012	88.7 (82.42-93.13)	85.2 (78.41-90.27)	19.0 (13.29-26.36)	19.0 (13.29-26.36)	0 (0.00-2.66)
Site					
El Arbaein	84.8 (78.80-89.45)	81.3 (74.78-86.45)	23.2 (17.45-30.03)	22.3 (16.73-28.99)	1.8 (0.55-5.06)
Gebal	84.6 (73.73-91.86)	80.8 (69.30-88.79)	19.2 (11.21-30.70)	16.7 (9.14-27.71)	2.6 (0.43-9.91)
Gharaba	96.4 (92.62-98.42)	96.4 (92.62-98.42)	3.6 (1.58-7.38)	0 (0.00-2.10)	3.6 (1.58-7.38)
Tlah	96.1 (91.86-98.33)	95.3 (90.83-97.78)	20.2 (14.47-27.15)	17.1 (11.79-23.86)	3.1 (1.23-7.11)
Sex					
Males	90.5 (87.49-92.85)	89.0 (85.91-91.61)	10.5 (7.96-13.56)	8.6 (6.35-11.46)	1.9 (0.99-3.58)
Females	91.9 (88.94-94.06)	89.6 (86.44-92.14)	22.2 (18.55-26.22)	19.0 (15.66-22.86)	3.6 (2.22-5.72)
Age					
Class 1	86.0 (78.86-91.06)	83.4 (75.98-89.03)	6.4 (3.24-11.94)	6.4 (3.24-11.94)	0 (0.00-2.94)
Class 2	94.2 (91.30-96.14)	92.7 (89.61-94.95)	22.3 (18.31-26.73)	18.2 (14.62-22.50)	4.4 (2.71-6.93)

See text for detailed statistical analysis. Here all significant main effects are in bold.

Table 4. Helminth species richness, diversity and abundance of higher taxa (mean \pm standard error) – all helminths combined, all nematodes combined and all cestodes combined by year, site, host sex and age class.

	Species richness	Brillouin's Index of Diversity	Helminths	Nematodes	Cestodes (all combined)	Cestodes (intestinal adults)	Cestodes (larval stages)
Year							
2000	1.88 \pm 0.135	0.27 \pm 0.033	20.5 \pm 3.68	18.5 \pm 3.50	1.43 \pm 0.930	0.18 \pm 0.088	1.25 \pm 0.928
2004	2.41 \pm 0.122	0.39 \pm 0.031	63.2 \pm 26.87	60.3 \pm 26.76	1.60 \pm 0.900	0.11 \pm 0.034	1.49 \pm 0.901
2008	1.84 \pm 0.116	0.23 \pm 0.026	28.1 \pm 4.69	24.7 \pm 4.37	3.23 \pm 1.653	0.63 \pm 0.229	2.60 \pm 1.645
2012	2.16 \pm 0.120	0.35 \pm 0.028	34.0 \pm 7.23	32.1 \pm 7.16	0.57 \pm 0.143	0.57 \pm 0.143	0 \pm 0
Site							
El Arbaein	1.82 \pm 0.126	0.25 \pm 0.028	20.1 \pm 4.43	18.9 \pm 4.37	0.79 \pm 0.208	0.63 \pm 0.175	0.16 \pm 0.114
Gebal	1.83 \pm 0.152	0.30 \pm 0.039	11.7 \pm 1.91	10.8 \pm 1.84	0.90 \pm 0.365	0.53 \pm 0.257	0.37 \pm 0.269
Gharba	2.15 \pm 0.113	0.33 \pm 0.030	40.7 \pm 5.65	34.5 \pm 4.76	3.14 \pm 1.796	0 \pm 0	3.14 \pm 1.796
Tlah	2.42 \pm 0.114	0.37 \pm 0.026	65.4 \pm 22.94	63.8 \pm 22.93	1.64 \pm 0.710	0.52 \pm 0.150	1.12 \pm 0.701
Sex							
Males	1.96 \pm 0.088	0.28 \pm 0.021	22.2 \pm 3.21	20.7 \pm 3.15	0.90 \pm 0.439	0.14 \pm 0.040	0.75 \pm 0.439
Females	2.21 \pm 0.089	0.34 \pm 0.021	52.1 \pm 13.60	48.5 \pm 13.52	2.42 \pm 0.923	0.67 \pm 0.149	1.75 \pm 0.916
Age							
Class 1	1.61 \pm 0.088	0.24 \pm 0.023	17.7 \pm 3.35	17.4 \pm 3.32	0.18 \pm 0.075	0.18 \pm 0.075	0 \pm 0
Class 2	2.36 \pm 0.081	0.36 \pm 0.019	48.8 \pm 11.07	45.0 \pm 11.00	2.53 \pm 0.813	0.55 \pm 0.117	1.99 \pm 0.809

See text for detailed statistical analysis. Here all significant main effects are in bold.

Table 5. Percentage of variation in data (deviance) explained by extrinsic and intrinsic factors affecting the measures of infracommunity structure and diversity, and the abundance of helminths

Source of Variation	Percentage of deviance explained									
	MSR ¹	BID ²	Total Helminths	Total nematodes	Spiruroids	<i>P. muricola</i>	<i>M. muris</i>	Total-Oxyuroides	<i>A. africana</i>	<i>D. kuntzi</i>
Site	3.58	2.03	1.33	1.29	3.43	7.23	8.57	1.410	2.343	0.323
Year	3.35	4.97	0.43	0.45	0.16	0.18	0.21	0.561	1.216	0.725
Age	7.97	3.98	0.95	0.81	2.61	2.03	2.75	0.168	0.895	0.901
Sex	-	0.95	0.66	0.61	0.52	0.59	0.02	0.389	-	-
Site*age	-	-	-	-	-	-	1.36	-	-	0.640
Site*year	-	-	1.16	1.21	-	-	-	1.552	2.215	1.371
Site*sex	-	-	0.21	0.22	-	0.36	-	-	-	-
Year*age	-	-	-	-	-	-	2.02	-	-	-
Age*sex	-	-	-	-	0.18	-	-	-	-	-
Site*sex*age	-	-	-	-	-	-	3.35	-	-	-
Site*year*sex	-	-	0.50	-	-	-	5.39	-	-	-
Site*year*age	-	-	0.63	0.66	2.14	2.25	-	-	-	1.758

(In each case the output from the most parsimonious and appropriate minimum sufficient model is given. Thus, the significant main effects and interactions have been highlighted in bold. Non-significant main effects if a component of one of the interactions or interactions showing borderline significance have also been included but are not in bold. Models for total helminth burden and individual species are models with negative binomial error structures unless stated otherwise below. For further details of the statistical models, see the text. Note that some main effects, 2-way and 3-way interactions and the 4-way interaction are not given because these were not significant.)

1. Mean species richness (model based on Poisson errors); 2. Brillouin's index of diversity (model based on Gaussian errors).

Table 6. Prevalence (\pm 95% confidence limits) of spirurid nematodes, individually and in specific combinations by year, site, host sex and age class

	All spiruroids	<i>P.muricola</i> + <i>M. muris</i>	<i>P. muricola</i>	<i>M. muris</i>	<i>Streptopharagus</i> spp.	<i>G. aegypti</i>
Year						
2000	64.2 (52.83-74.31)	62.7 (51.33-72.91)	47.8 (36.52-59.16)	19.4 (11.81-29.90)	9.0 (4.16-17.64)	0.0 (0-5.02)
2004	72.6 (65.76-78.59)	68.9 (6.93-75.10)	55.7 (48.48-62.59)	17.0 (12.07-23.10)	17.0 (12.07-23.10)	0.9 (0.16-3.64)
2008	69.8 (62.59-76.28)	65.5 (58.06-72.29)	50.0 (42.51-57.49)	20.7 (15.16-27.33)	9.5 (5.86-14.81)	0.9 (0.14-3.67)
2012	69.7 (61.64-76.83)	62.7 (54.43-70.27)	55.6 (47.37-63.56)	14.1 (9.19-20.78)	26.8 (20.01-34.59)	11.3(6.87-17.58)
Site						
El Arbaein	56.3 (48.89-63.35)	55.4 (48.00-62.45)	50.9 (43.53-58.27)	9.8 (6.16-15.05)	12.5 (8.33-18.13)	0.9 (0.15-3.66)
Gebal	57.7 (45.43-69.26)	48.7 (36.41-61.02)	1.3 (0.11-7.91)	48.7 (36.41-61.02)	19.2 (11.21-30.70)	1.3 (0.11-7.91)
Gharaba	87.5 (81.87-91.67)	79.5 (72.93-84.89)	79.5 (72.93-84.89)	3.6 (1.58-7.38)	22.30 (16.73-28.99)	10.7 (6.80-16.14)
Tlah	72.9 (65.35-79.34)	70.5 (62.88-77.24)	62.8 (54.93-70.06)	17.1 (11.79-23.86)	14.7 (9.89-21.16)	3.1 (1.23-7.11)
Sex						
Males	68.57 (64.25-72.60)	63.3 (58.88-67.59)	49.0 (44.56-53.53)	20.0 (16.62-23.86)	14.8 (11.82-18.21)	4.8 (3.16-7.04)
Females	70.59 (66.23-74.62)	66.5 (62.04-70.73)	56.6 (51.99-61.03)	14.9 (11.92-18.47)	19.0 (15.66-22.86)	3.6 (2.22-5.72)
Age						
Class 1	40.1 (31.82-48.83)	34.4 (26.60-43.08)	30.6 (23.08-39.14)	4.5 (1.91-9.55)	6.4 (3.24-11.94)	1.3 (0.22-5.08)
Class 2	86.5 (82.65-89.62)	82.5 (78.28-86.06)	65.7 (60.74-70.35)	24.8 (20.73-29.41)	23.0 (18.99-27.51)	5.8 (3.86-8.70)

See text for detailed statistical analysis. Here all significant main effects are in bold.

Table 7. Abundance (mean \pm standad error) of spirurid nematodes, individually and in specific combinations by year, site, sex and age class

	All spiruroids	<i>P.muricola</i> + <i>M. muris</i>	<i>P. muricola</i>	<i>M. muris</i>	<i>S. kuntzi</i>	<i>G.aegypti</i>
Year						
2000	10.6 \pm 2.95	10.5 \pm 2.94	9.9 \pm 2.97	0.60 \pm 0.184	0.10 \pm 0.043	0 \pm 0
2004	11.1 \pm 2.52	10.6 \pm 2.51	10.0 \pm 2.53	0.62 \pm 0.164	0.41 \pm 0.122	0.038 \pm 0.0377
2008	12.6 \pm 2.02	12.3 \pm 2.02	11.2 \pm 2.04	1.11 \pm 0.313	0.25 \pm 0.099	0.009 \pm 0.0086
2012	12.2 \pm 2.01	11.0 \pm 1.96	10.6 \pm 1.95	0.39 \pm 0.107	1.02 \pm 0.288	0.183 \pm 0.0562
Site						
El Arbaein	8.7 \pm 1.80	8.4 \pm 1.78	8.2 \pm 1.79	0.23 \pm 0.083	0.27 \pm 0.103	0.009 \pm 0.0089
Gebal	3.0 \pm 0.49	2.6 \pm 0.48	0.04 \pm 0.038	2.51 \pm 0.476	0.40 \pm 0.123	0.026 \pm 0.0256
Gharaba	25.1 \pm 3.39	23.8 \pm 3.37	23.8 \pm 3.38	0.04 \pm 0.018	1.05 \pm 0.360	0.170 \pm 0.0551
Tlah	8.2 \pm 1.38	7.8 \pm 1.37	7.3 \pm 1.35	0.50 \pm 0.120	0.35 \pm 0.094	0.070 \pm 0.0482
Sex						
Males	7.3 \pm 0.84	6.7 \pm 0.77	6.1 \pm 0.78	0.61 \pm 0.107	0.55 \pm 0.190	0.095 \pm 0.0382
Females	16.0 \pm 2.06	15.4 \pm 2.06	14.7 \pm 2.07	0.74 \pm 0.177	0.49 \pm 0.095	0.050 \pm 0.0195
Age						
Class 1	4.2 \pm 0.94	3.8 \pm 0.83	3.7 \pm 0.83	0.15 \pm 0.060	0.36 \pm 0.233	0.019 \pm 0.0142
Class 2	16.1 \pm 1.67	15.4 \pm 1.67	14.4 \pm 1.69	0.98 \pm 0.158	0.61 \pm 0.096	0.102 \pm 0.0321

See text for detailed statistical analysis. Here all significant main effects are in bold.

Table 8. Prevalence (\pm 95% confidence limits) of oxyuroid nematodes, cestodes and acanthocephala.

	<i>Oxyuroid nematodes</i>	<i>S. minuta</i>	<i>A. africana</i>	<i>D. kuntzi</i>	<i>R. negevi</i>	<i>M. acomysi</i>
Year						
2000	62.7 (51.33-72.91)	25.4 (16.74-36.34)	17.9 (10.64-28.17)	46.3 (35.39-57.67)	4.5 (1.43-11.87)	4.5 (1.43-11.87)
2004	75.5 (68.83-81.14)	37.7 (31.06-44.91)	33.0 (26.60-40.18)	52.8 (45.65-60.00)	5.7 (3.12-9.89)	4.7 (2.42-8.72)
2008	52.6 (45.10-60.03)	16.4 (11.47-22.62)	13.8 (9.31-19.70)	39.7 (32.55-47.13)	12.1 (7.93-17.71)	2.6 (0.99-6.21)
2012	56.3(48.07-64.27)	28.9 (21.99-36.93)	21.1 (15.05-28.51)	28.2 (21.35-36.11)	14.8 (9.73-21.59)	9.2 (5.34-15.11)
Site						
El Arbaein	50.9 (43.53-58.27)	16.1 (11.30-22.12)	18.8 (13.55-25.22)	34.8 (28.09-42.16)	8.9 (5.50-14.13)	4.5 (2.18-8.53)
Gebal	60.3(48.01-71.72)	37.2 (26.22-49.42)	11.5 (5.65-21.62)	41.0 (29.43-53.28)	15.4 (8.14-26.27)	0.0 (0.00-5.84)
Gharaba	58.9 (51.58-66.03)	24.1 (18.31-30.93)	17.0 (11.97-23.26)	34.8 (28.09-42.16)	0.0 (0.00-2.10)	16.1 (11.30-22.12)
Tlah	72.1 (64.56-78.60)	33.3 (26.37-41.18)	34.1 (27.09-41.96)	48.8 (40.96-56.72)	17.1 (11.79-23.86)	0.8 (0.11-3.74)
Sex						
Males	62.4 (57.90-66.67)	25.2 (21.54-29.32)	21.0 (17.47-24.81)	40.5 (36.12-44.95)	4.8 (3.16-7.04)	4.3 (2.78-6.47)
Females	59.7 (55.16-64.16)	29.0 (24.95-33.31)	22.2 (18.55-26.22)	39.8 (35.41-44.39)	15.2 (12.32-18.96)	6.8 (4.77-9.46)
Age						
Class 1	72.6 (64.31-79.74)	21.0 (14.67-28.79)	26.8 (19.66-35.00)	59.2 (50.53-67.59)	3.2 (1.14-7.78)	3.2 (1.14-7.78)
Class 2	54.4 (49.34-59.40)	30.7 (26.22-35.47)	18.6 (14.97-22.89)	29.2 (24.79-34.01)	14.2 (11.02-18.13)	6.9 (4.74-9.95)

See text for detailed statistical analysis. Here all significant main effects are in bold.

Table 9 . Abundance (mean \pm standard error) of oxyuroid nematodes, cestodes and acanthocephalans by year, site, sex and age class

	<i>Oxyuroid nematodes</i>	<i>S. minuta</i>	<i>A. africana</i>	<i>D. kuntzi</i>	<i>R. negevi</i>	<i>M. acomysi</i>
Year						
2000	7.6 \pm 2.02	5.0 \pm 1.83	0.43 \pm 0.165	2.1 \pm 0.47	0.06 \pm 0.036	0.60 \pm 0.456
2004	49.0 \pm 26.64	45.1 \pm 26.66	1.40 \pm 0.378	2.6 \pm 0.37	0.06 \pm 0.023	1.36 \pm 1.311
2008	8.7 \pm 3.13	6.3 \pm 3.10	0.57 \pm 0.183	1.9 \pm 0.42	0.60 \pm 0.228	0.16 \pm 0.138
2012	19.8 \pm 6.58	18.0 \pm 6.51	0.71 \pm 0.179	1.1 \pm 0.23	0.37 \pm 0.112	1.30 \pm 0.721
Site						
El Arbaein	9.0 \pm 3.44	7.0 \pm 3.42	0.60 \pm 0.167	1.4 \pm 0.26	0.27 \pm 0.132	0.36 \pm 0.265
Gebal	7.7 \pm 1.72	5.7 \pm 1.68	0.28 \pm 0.128	1.7 \pm 0.37	0.47 \pm 0.251	0 \pm 0
Gharaba	9.1 \pm 3.21	6.8 \pm 3.16	0.55 \pm 0.175	1.7 \pm 0.43	0 \pm 0	3.09 \pm 1.533
Tlah	53.5 \pm 22.76	49.7 \pm 22.76	1.50 \pm 0.343	2.4 \pm 0.35	0.51 \pm 0.149	0.01 \pm 0.008
Sex						
Males	12.8 \pm 2.99	10.3 \pm 2.96	0.71 \pm 0.143	1.7 \pm 0.22	0.08 \pm 0.028	0.59 \pm 0.467
Females	31.0 \pm 13.30	28.2 \pm 13.29	0.88 \pm 0.200	1.9 \pm 0.29	0.53 \pm 0.138	1.20 \pm 0.661
Age						
Class 1	13.1 \pm 3.11	9.1 \pm 3.02	1.32 \pm 0.298	2.7 \pm 0.30	0.11 \pm 0.066	0.19 \pm 0.106
Class 2	27.3 \pm 10.83	25.4 \pm 10.82	0.50 \pm 0.091	1.4 \pm 0.22	0.42 \pm 0.107	1.30 \pm 0.638

See text for detailed statistical analysis. Here all significant main effects are in bold.

Legends to Figs

Fig. 1. Spatiotemporal dynamics in prevalence at the four study sites (A, C, and E) and abundance (B, D and F) of all helminths (A and B), all nematodes (C and D), and of all cestodes (E and F). Key to symbols used in B, C, D, E and F, as in A.

Fig. 2. Host sex, age, year and site-related changes in abundance of helminth taxa. A, combined helminths by site of study and sex; B, combined spiruroid nematodes by host age and sex; C, combined spiruroid nematodes by site, year and age class; D, *Protospirura muricola* by site, year and age class.

Fig. 3. Spatiotemporal dynamics at the four study sites in helminth species richness (A), diversity (B) and abundance of combined spiruroid nematodes (C), *Protospirura muricola* (D), *Mastophorus muris* (E) and *Streptopharagus* spp. (F). Key to symbols used, as shown in panel A.

Fig. 4. Variation in prevalence of spiruroid nematodes by year and study site. A, combined spiruroid nematodes; B, prevalence of *Protospirura muricola* and *Mastophorus muris* combined; C, *Protospirura muricola*; D, *Mastophorus muris*; E, *Streptopharagus* spp. F, *Gongylonema aegypti*. Key to symbols used in panel in A.

Fig. 5. Variation in prevalence of oxyuroid nematode, cestode and acanthocephalan helminths by year and study site. A, combined oxyuroid nematodes; B, *Syphacia minuta*; C, *Aspicularis africana*; D, *Dentostomella kuntzi*; E, *Rodentolepis negevi*. F, *Moniliformis acomysi*. Key to symbols used in panel A.

Fig. 6. Variation in abundance of oxyuroid nematode, cestode and acanthocephalan helminths by year and study site. A, combined oxyuroid nematodes; B, *Syphacia minuta*; C, *Aspicularis africana*; D, *Dentostomella kuntzi*; E, *Rodentolepis negevi*. F, *Moniliformis acomysi*. Key to symbols used in panel in A.

Fig. 7. Host age-related variation in prevalence and abundance of oxyuroid nematodes. A, prevalence of *S. minuta* by host sex and age; B, prevalence of *D. kuntzi* by host sex and age; C prevalence of *D. kuntzi* by study site and host age; D, abundance of *D. kuntzi* by study site and host age. Key to columns in panel in A.

Fig. 8. Scatter plots (A,B,C,D) and a plot of the centroids of functions 1 and 2 derived from Canonical Discriminant Function Analysis for 15 species of helminths in spiny mice grouped by site and year (E). A, Wadi El Arbaein; B, Wadi Gebal; C, Wadi Gharaba; D, Wadi Tlah. Key for coloured symbols representing the four surveys in different years are the same for A, B, C and D and are given in the legend in A.

Fig. 8E shows the centroids \pm S.E.M., each site represented by a different symbol, and each year by a different colour, as explained in the legend in E.

Fig.1

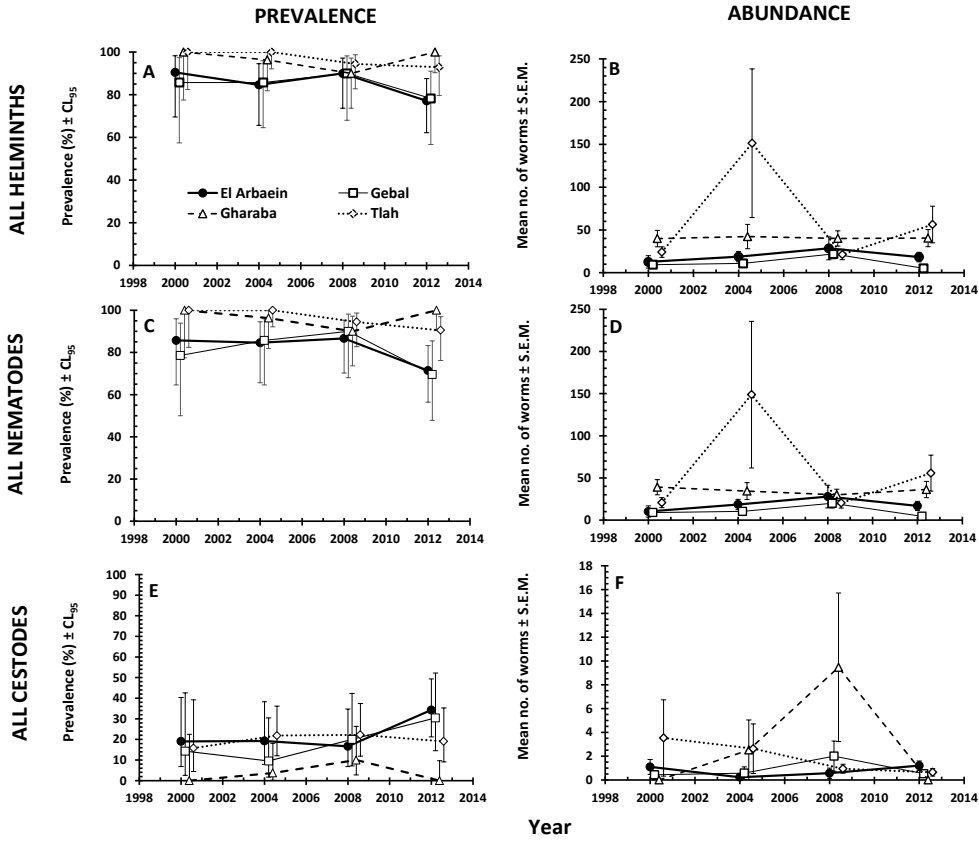


Fig. 2

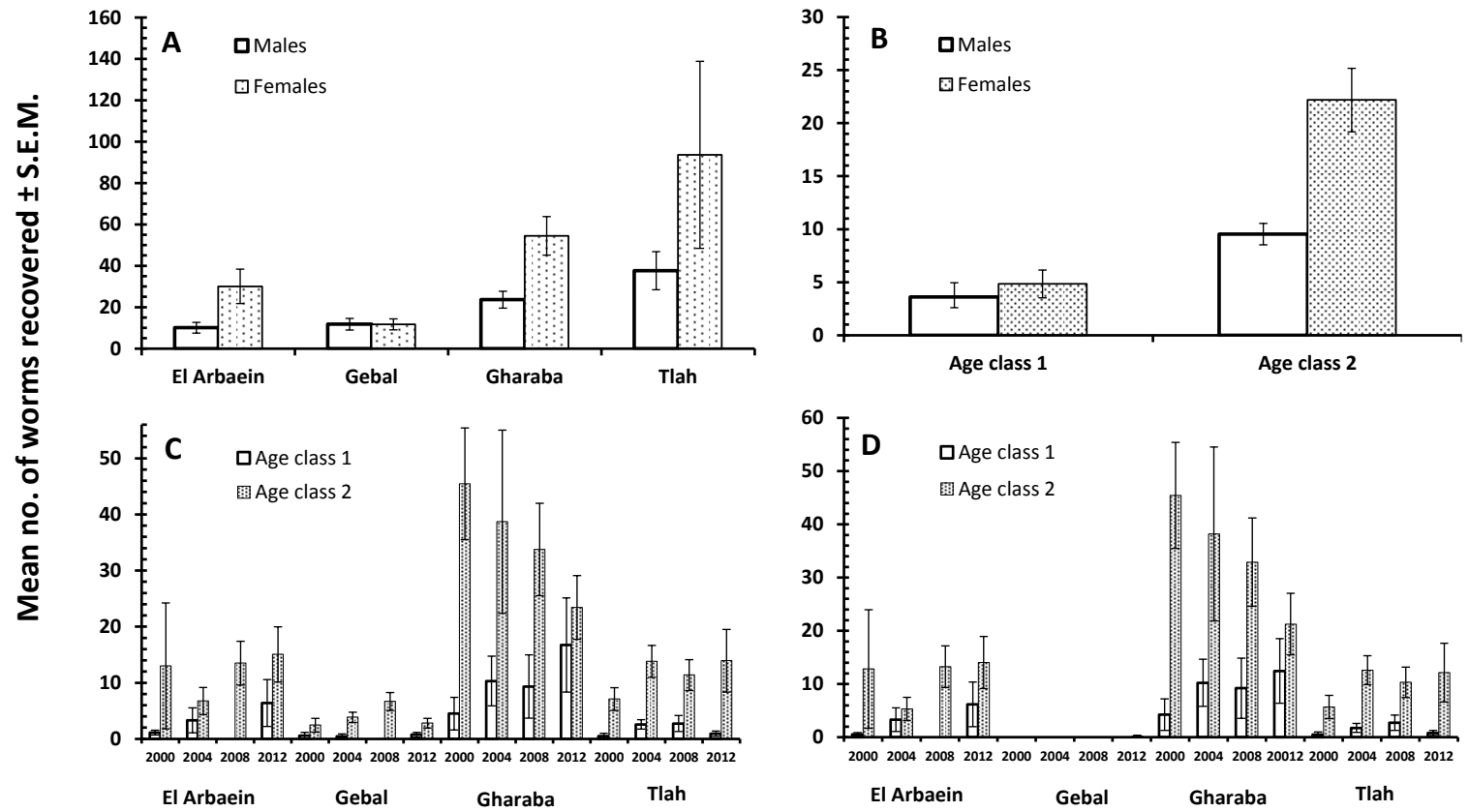


Fig. 3

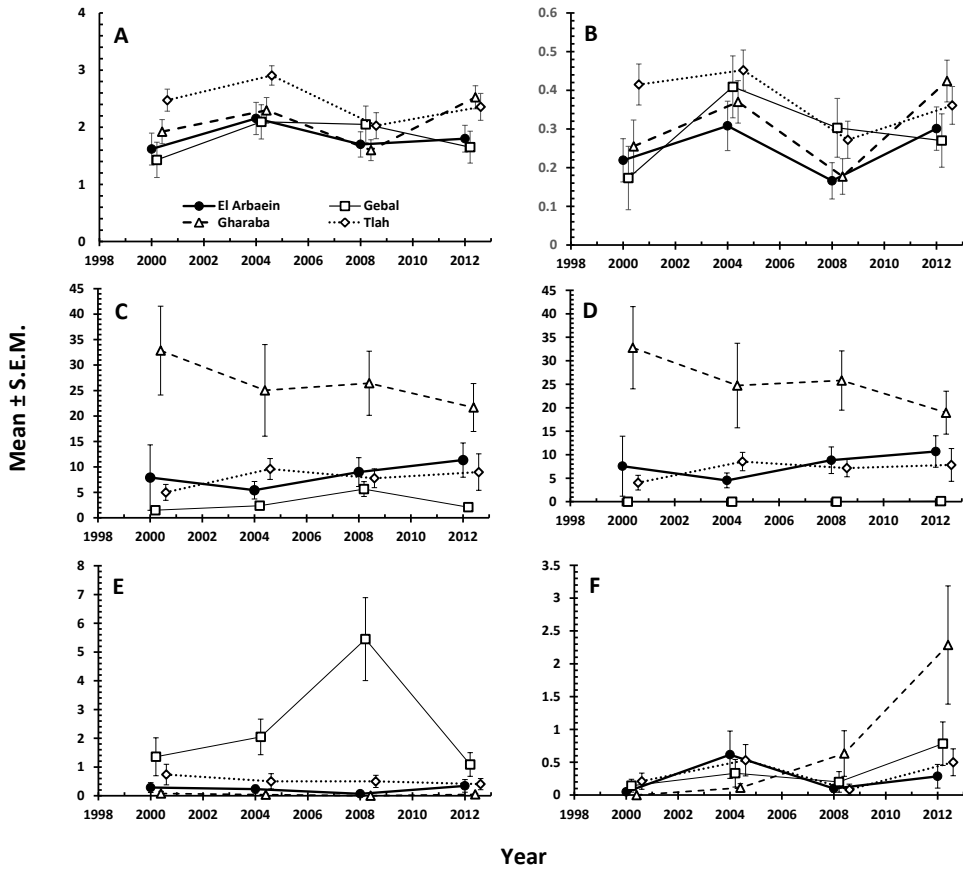


Fig. 4

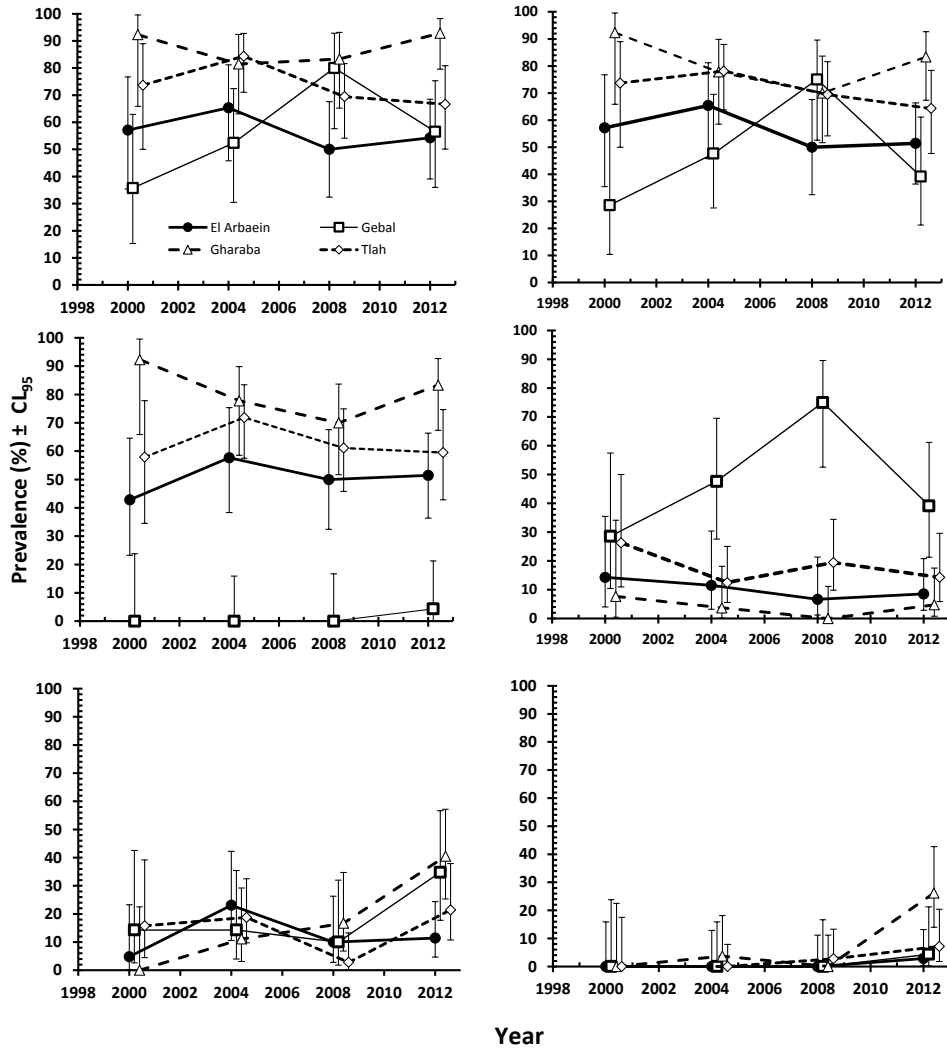


Fig. 5

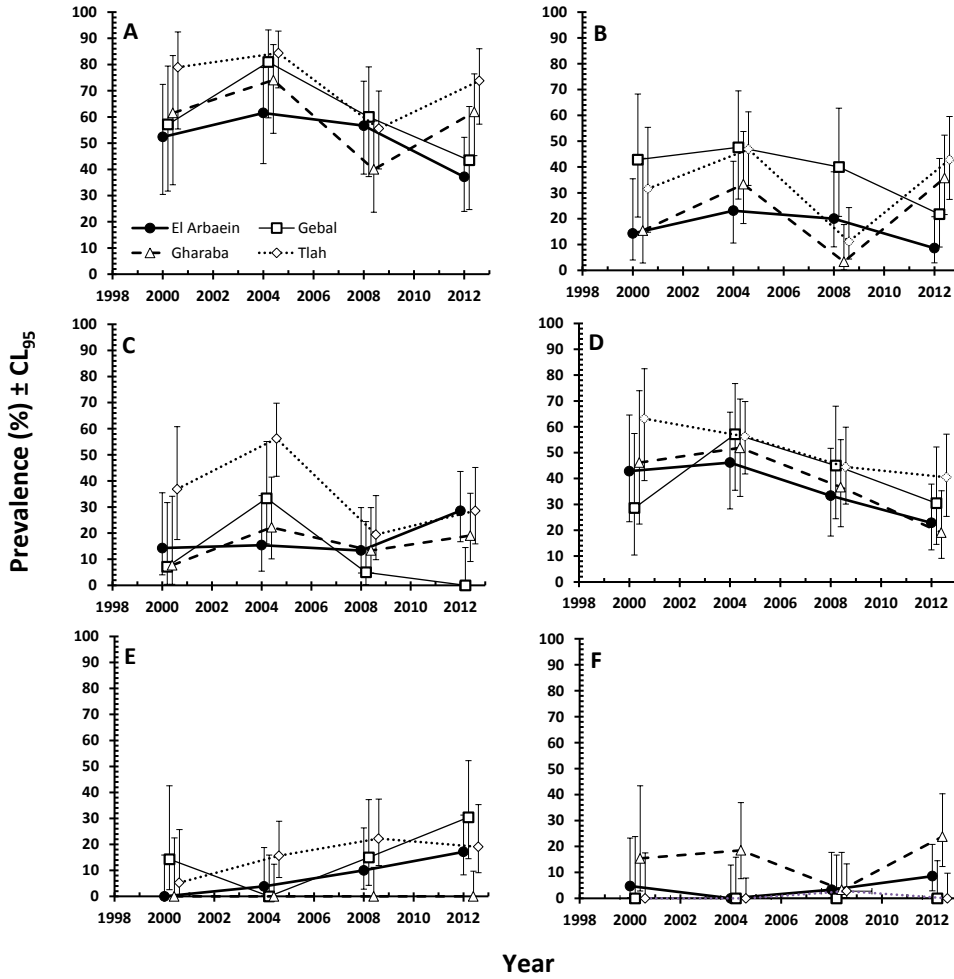


Fig. 6

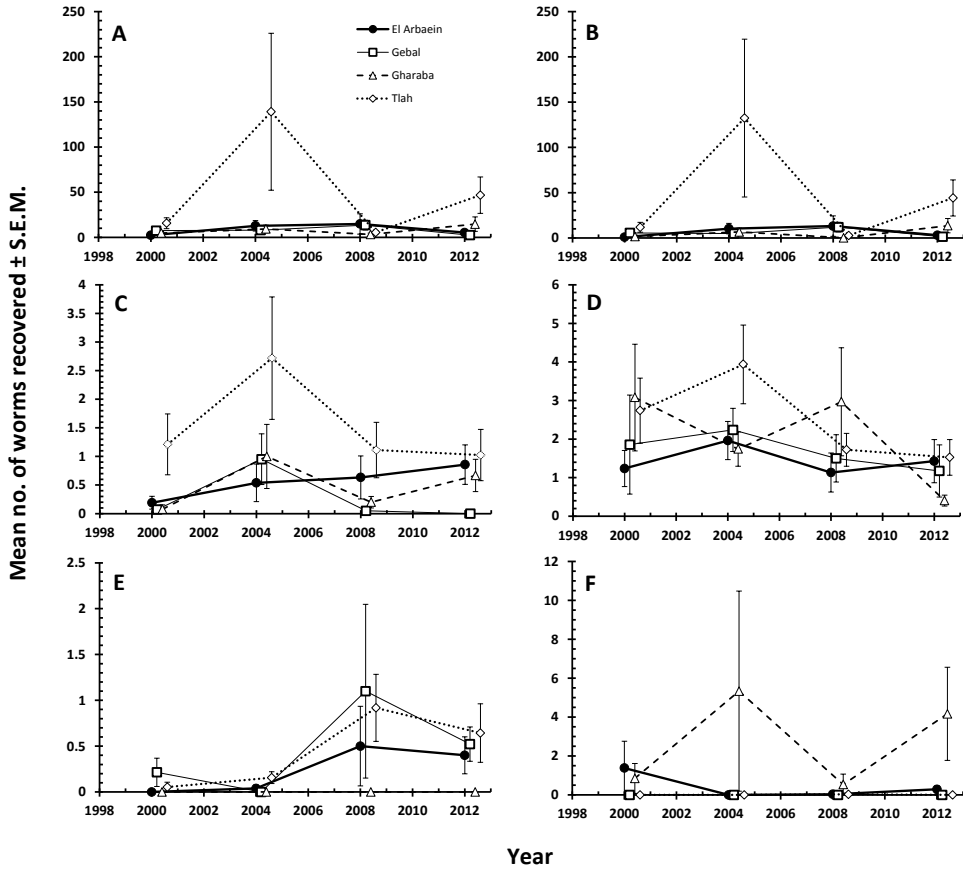


Fig. 7

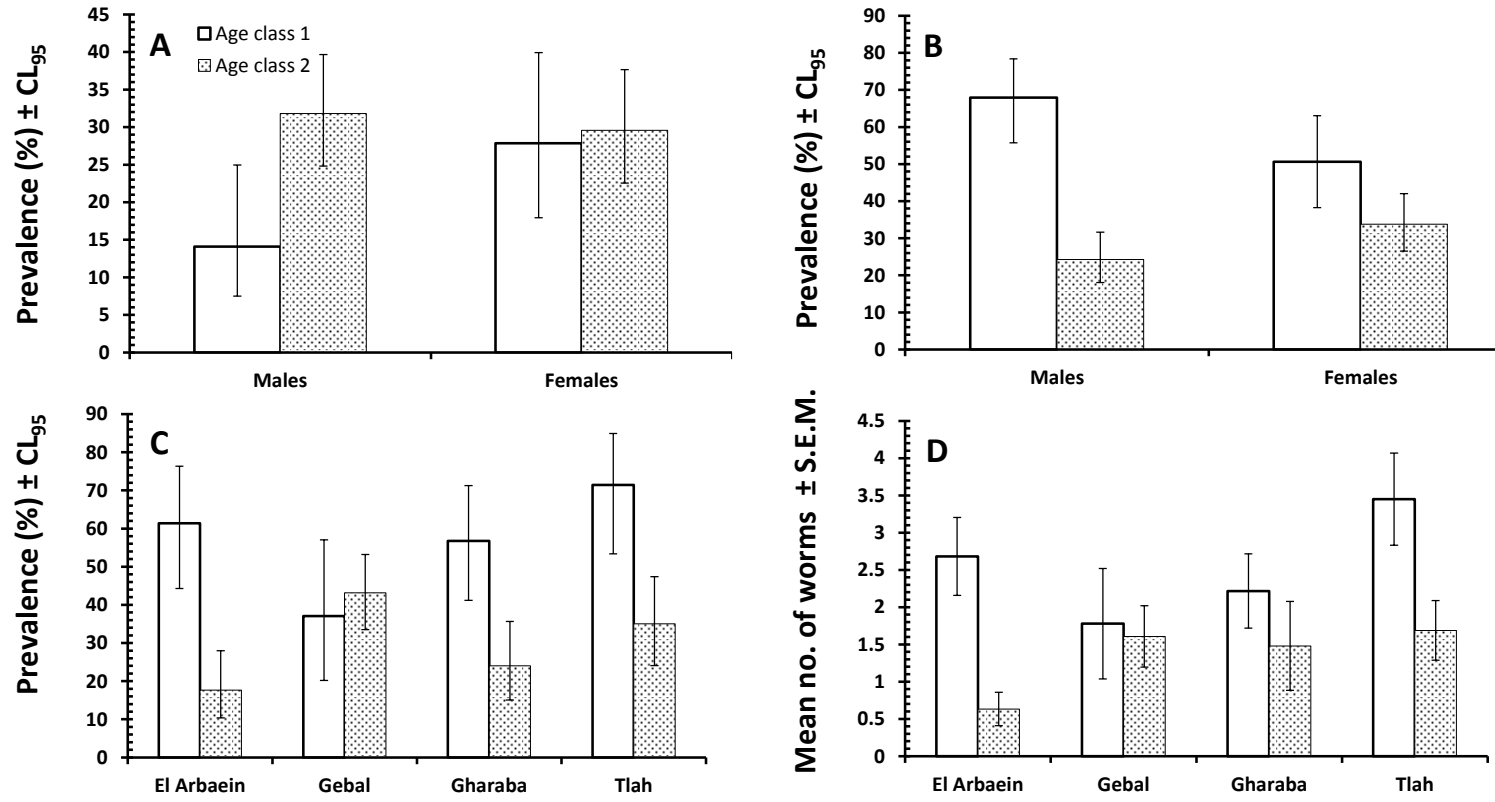
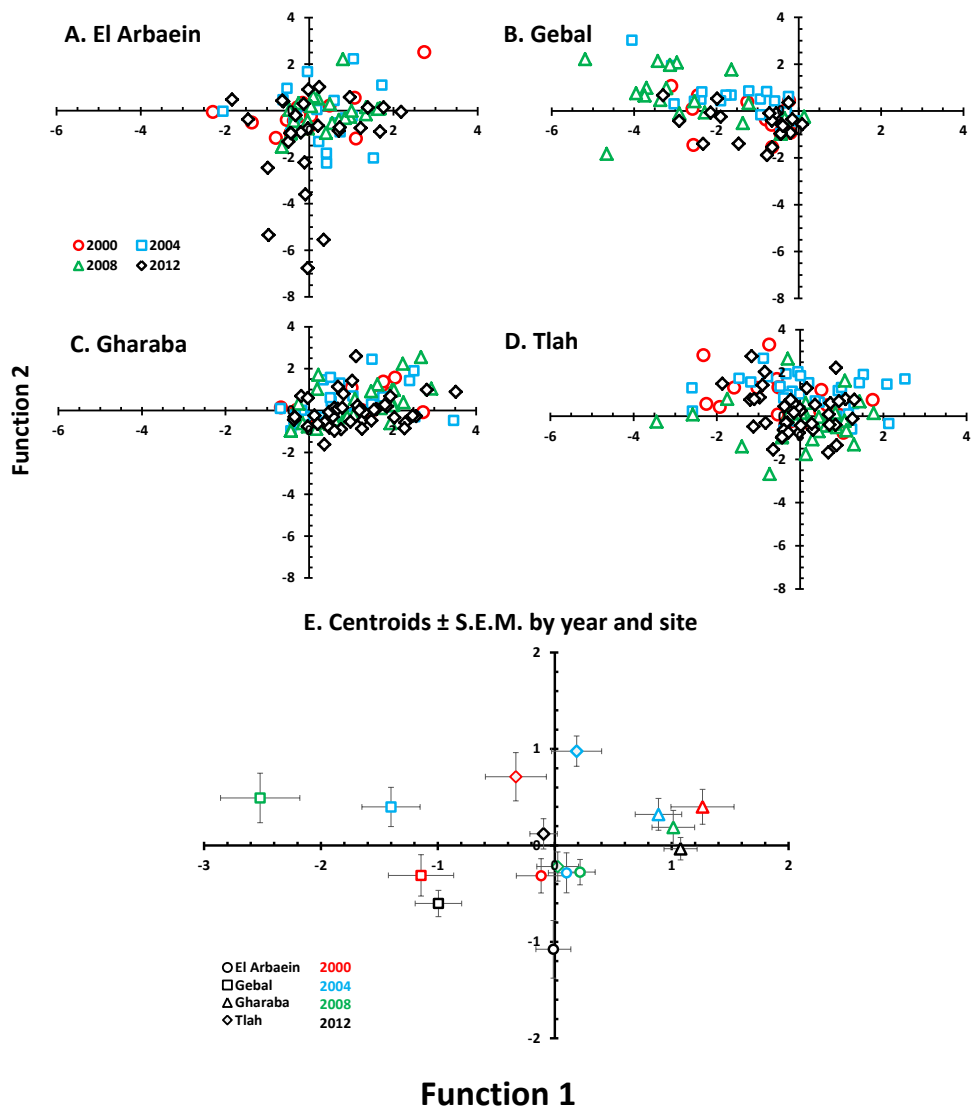


Fig. 8



SUPPLEMENTARY INFORMATION

Table 1. Measures of aggregation for individual species of nematodes by site and overall

Species	Wadi El Arbaein			Wadi Gebal			Wadi Gharaba			Wadi Tlah		
	k^1 (\pm SEM ⁴)	ρ^2	D^3	k^1 (\pm SEM ⁴)	ρ^2	D^3	k^1 (\pm SEM ⁴)	ρ^2	D^3	k^1 (\pm SEM ⁴)	ρ^2	D^3
All helminths combined	0.404 ⁶ , (0.0025)	109.7	0.739	0.636 ⁶ (0.0111)	24.3	0.611	0.670 ⁶ (0.0065)	87.9	0.614	0.489 ^{7,8} (0.0028)	1037.3	0.726
All nematodes combined	0.367 ⁶ (0.0022)	113.1	0.753	0.586 ^{7,8} (0.0098)	24.4	0.619	0.696 ⁶ (0.007)	73.4	0.609	0.469 ^{7,8} (0.0026)	1063.6	0.737
All spirurid nematodes Combined	0.222 ^{7,8} (0.0011)	41.7	0.788	0.456 ^{7,10} (0.0102)	6.4	0.661	0.547 ⁶ (0.0049)	51.4	0.621	0.452 ^{7,8} (0.0038)	30.1	0.669
<i>Protospirura muricola</i>	0.186 ^{7,8} (0.0008)	43.7	0.808	0.019 ¹¹	3.0	0.975	0.417 ^{7,8} (0.0030)	53.7	0.647	0.321 ^{7,8} (0.0021)	32.5	0.719
<i>Mastophorus muris</i>	0.073 ¹¹ (0.0009)	3.3	0.926	0.328 ^{7,10} (0.0057) (0.012)	7.0	0.714	nd ¹¹	1.0	0.956	0.112 ¹¹ (0.0011) (0.021)	3.7	0.882
<i>Streptopharagus spp.</i>	0.102 ¹¹ (0.0015)	4.4	0.922	0.189 ¹¹ (0.0063)	3.0	0.866	0.105 ^{7,10} (0.0007)	13.8	0.889	0.116 ^{7,10} (0.0015)	3.3	0.899
<i>Gongylonema aegypti</i>	nd ¹¹	1	0.982	0.010 ¹¹	2.0	0.975	0.150 ¹¹ (0.0063)	2.0	0.914	0.022 ¹¹ (0.0001)	4.3	0.974
All oxyuroid nematodes Combined	0.165 ^{7,8} (0.0006)	147.5	0.875	0.278 ^{7,8} (0.0025)	30.0	0.751	0.216 ^{7,8} (0.0010)	126.7	0.840	0.226 ^{7,8} (0.0007)	1247.9	0.835

<i>Dentostomella kuntzi</i>	0.223 ⁶ (0.0025)	5.4	0.783	0.272 ⁶ (0.0046)	6.4	0.773	0.188 ⁶ (0.0016)	12.1	0.817	0.330 ⁶ (0.0035)	6.6	0.731
<i>Aspicularis africana</i>	0.112 ⁶ (0.0011)	5.2	0.890	0.081 ¹¹ (0.0013)	4.5	0.924	0.098 ⁶ (0.0008)	6.2	0.903	0.192 ⁶ (0.0015)	10.1	0.826
<i>Syphacia minuta</i>	0.033 ⁶ (<0.0001)	188.2	0.949	0.120 ⁶ (0.0006)	38.4	0.849	0.057 ^{8, 12, 13, 14} (0.0001)	163.4	0.932	0.067 ^{7, 8} (0.0001)	1345.2	0.891
All cestodes combined	0.137 ⁶ (0.0013)	6.2	0.875	0.087 ¹⁴ (0.0007)	11.6	0.907	0.028 ^{8, 12, 13} (Nd ¹⁵)	114.9	0.966	0.068 ^{13, 16} (0.0002)	39.6	0.933
<i>Rodentolepis negevi</i>	0.050 ¹¹ (0.0003)	7.3	0.949	0.089 ^{13, 16} (0.0011)	10.3	0.914	Nd ¹⁷			0.104 ⁶ (0.0009)	5.6	0.904
<i>Moniliformis acomysi</i>	0.014 ^{13, 16} (<0.0001)	21.9	0.973	Nd ¹⁷			0.040 ^{8, 12, 13} (0.0001)	85.2	0.947	ND ^{11, 15}	1.0	0.985

Table 1. Continued

Species	Combined		
	k^1 (\pm SEM ⁴)	I^2	D^3
All helminths combined	0.475 ^{8, 9} (0.0009)	591.4	0.715
All nematodes combined	0.456 ^{8, 9} (0.0008)	626.0	0.722
All spirurid nematodes Combined	0.327 ⁶ (0.0005)	48.4	0.739
<i>Protospirura muricola</i>	0.192 ⁶ (0.0002)	53.6	0.796
<i>Mastophorus muris</i>	0.091 ⁶ (0.0002)	7.0	0.901
<i>Streptopharagus</i> spp.	0.102 ⁶ (0.0002)	9.1	0.912

<i>Gongylonema aegypti</i>	0.044 ¹¹ (0.0002)	2.7	0.970
All oxyuroid nematodes Combined	0.195 ^{8,9} (0.0002)	949.2	0.863
<i>Dentostomella kuntzi</i>	0.248 ⁵ (0.0007)	7.7	0.782
<i>Aspicularis africana</i>	0.119 ⁶ (0.0003)	8.3	0.890
<i>Syphacia minuta</i>	0.058 ^{7,8} (<0.0001)	1075.0	0.930
All cestodes combined	0.049 ⁵ (<0.0001)	69.6	0.957
<i>Rodentolepis negevi</i>	0.058 ⁶ (0.0001)	7.4	0.948
<i>Moniliformis acomysi</i>	0.014 ⁶ (<0.0001)	79.8	0.983

1. Negative binomial exponent.

3. Index of discrepancy (Poulin 1993).

2. Index of dispersion = Variance to mean ratio.

4. Standard error of the mean estimate.

5. Significantly different from Poisson, binomial, Gaussian and negative binomial distribution

6. Not significantly different from the negative binomial distribution but significantly different from Poisson, Gaussian and binomial distributions

7. Not significantly different from the negative binomial distribution but significantly different from Poisson and binomial distributions

8. Insufficient degrees of freedom for test of Gaussian distribution

9. Significantly different from Poisson, binomial, and negative binomial distribution

10. Not significantly different from the Gaussian distribution

11. Insufficient degrees of freedom to test any distribution

12. Significantly different from Poisson and binomial distributions

13. Insufficient degrees of freedom for test of negative binomial distribution

14. Significantly different from Gaussian distribution, insufficient degrees of freedom for test of other distributions

15. Cannot be calculated

16. Significantly different from Poisson, binomial and Gaussian distributions

17. Not done. No worms of this species recovered