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Ectoparasites and age-dependent survival in a desert rodent

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Abstract Host age is one of the key factors in host–parasite relationships as it possibly affects infestation levels, parasite-induced mortality of a host, and parasite distribution among host individuals. We tested two alternative hypotheses about infestation pattern and survival under parasitism in relation to host age. The first hypothesis assumes that parasites are recruited faster than they die and, thus, suggests that adult hosts will show higher infestation levels than juveniles because the former have more time to accumulate parasites. The second hypothesis assumes that parasites die faster than they are recruited and, thus, suggests that adults will show lower infestation levels because of acquired immune response and/or the mortality of heavily infested juveniles and, thus, selection for less infested adults. As the negative effects of parasites on host are often intensity-dependent, we expected that the age-related differences in infestation may be translated to lower or higher survival under parasitism of adults, in the cases of the first and the second hypotheses, respectively. We manipulated ectoparasite numbers using insecticide and assessed the infestation pattern in adult and juvenile

gerbils (*Gerbillus andersoni*) in the Negev Desert. We found only a partial support for age-dependent parasitism. No age-related differences in infestation and distribution among host individuals were found after adjusting the ectoparasite numbers to the host's surface area. However, age-related differences in survival under parasitism were revealed. The survival probability of parasitized juveniles decreased in about 48% compared to unparasitized hosts while the survival probability of adults was not affected by ectoparasites. Our results suggest that the effect of host age on host–parasite dynamics may not explicitly be determined by age-dependent differences in ectoparasite recruitment or mortality processes but may also be affected by other host-related and parasite-related traits.

Keywords Field manipulation · Host age · Infestation · Parasite distribution

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Introduction

Host–parasite dynamics is a result of interplay of various host-related and parasite-related parameters (e.g. Anderson and May 1978; Grenfell and Dobson 1995). Many important parameters in host–parasite dynamics, such as infestation level of hosts, parasite-induced host mortality and the consequent parasite distribution among host individuals are often age-dependent (Anderson and Gordon 1982; Hudson and Dobson 1997). Thus, host age might be one of the key factors affecting this dynamics (Anderson and Gordon 1982). During its ontogenesis, an individual organism often passes through very significant changes in morphology, physiology, ecology, and behaviour (e.g. Alberts and Cramer 1988; Reinert 1993; Munn and Dawson 2003). Some of these changes can be translated into changes in the exposure to infective stages of parasites, resistant ability and susceptibility to parasites (Gregory et al. 1992).

The infestation level of hosts is a result of a balance between the rates of parasite recruitment and parasite

mortality processes operating on the parasite population in or on the host (Hudson and Dobson 1995). Both processes may be affected by host age as the former process is mainly influenced by host's exposure to the parasites and the latter process is largely affected by the level of host resistance and susceptibility to infestation (Hudson and Dobson 1997). When parasites are recruited faster than they die, infestation is expected to increase with host age because adults in their longer life may accumulate more parasites than juveniles (hereafter, parasite recruitment hypothesis; see examples for cestodes, trematodes, protozoan, bacterial, and viral infections in Fichet-Calvet et al. 2003, and references therein). In contrast, if parasites die faster than they are recruited, infestation level may decrease with host age (hereafter, parasite mortality hypothesis). The reasons for parasite mortality that may cause the latter pattern can be either parasite-induced host mortality (Henricson 1977; Knudsen et al. 2002), or acquired immunity against parasites (Quinnell 1992; Davies and Gavgani 1999), or both. In the former case, heavily infested juvenile host die, and thus the survivors to maturity have lower infestation levels (Sol et al. 2003), while in the case of acquired immunity, adult hosts are more resistant against parasites, resulting again in juvenile-biased parasitism. Finally, in a population composed of juvenile, adult and senescent hosts, both processes (parasite recruitment and parasite mortality) may be important, resulting in a convex age-infestation curve (e.g. Gregory et al. 1992; Sorci 1996).

The age-related differences in infestation may cause age-related differences in parasite-induced host mortality as the negative effects of parasites on host are often intensity-dependent (Anderson and May 1978). Higher infestation levels of adult compared to juvenile hosts may make adult hosts more prone to parasite-induced host mortality (Knudsen et al. 2002), whereas higher infestation levels of juvenile hosts may subject juveniles to a higher treat of mortality (Sol et al. 2003).

Most studies of age-biased parasitism to date have three main deficiencies. First, in spite of the tight relation between age-related differences in infestation and in parasite-induced host mortality, only a few studies explore simultaneously these two phenomena (see, e.g., Sol et al. 2003). Second, most of the evidence on age-biased infestation levels came from microparasites or endoparasitic helminths (Hudson and Dobson 1997), whereas less attention was directed to ectoparasite infestation that could involve other mechanisms (e.g. different types of immune response, other ways of parasite acquisition) and generate different patterns. Finally, studies directed for testing age-related differences in parasite-induced host mortality are (1) rare and (2) often descriptive rather than experimental (Hudson and Dobson 1995; Rousset et al. 1996).

It is important to overcome these deficiencies as host age is a significant component in epidemiological theory (Anderson and Gordon 1982; Hudson and Dobson 1995; Rousset et al. 1996). Furthermore, the age-dependence of

parasitism may have a number of important ecological and evolutionary consequences for host–parasite relationships (Anderson and Gordon 1982; Sol et al. 2003). For example, age-specific infestation pattern can cause seasonal variation in parasite abundance (Gregory et al. 1992), while an increase in juvenile mortality induced by parasites can favour the evolution of reduced clutch or litter size (Martin et al. 2001).

In the present study, we made an attempt to overcome the deficiencies of earlier studies. We studied age-related differences in infestation and survival under parasitism by haematophagous arthropods in a free-living population of a rodent *Gerbillus andersoni* (de Winton 1902), combining a manipulation of parasite abundance and assessment of the infestation pattern in adult and juvenile hosts. In this system, ectoparasites have been shown to negatively affect their rodent host (Lehmann 1992) and to be distributed among host individuals in dependence of their intraspecific densities and environment conditions (Hawlena et al. 2005).

We hypothesized that both ectoparasite infestation and host survival under parasitism will be age-dependent. In particular, we tested two alternative hypotheses, the recruitment and the mortality hypotheses about infestation pattern and survival under parasitism in relation to host age. The distribution of parasites among host individuals may be linked both to age-related differences in infestation and survival under parasitism (Gregory et al. 1992; Hudson and Dobson 1997) and, thus, we expected also to find age-related differences in parasite distribution.

Materials and methods

Study animals

Gerbillus andersoni is a common nocturnal granivore inhabiting sandy areas of the western Negev Desert, Israel (Harrison and Bates 1991). It has been a focus of many ecological (see review by Rosenzweig and Abramsky 1997) and physiological (e.g. Degen and Kam 1991) studies. It can be readily trapped, recaptured and sampled for parasites in the field. The ectoparasite fauna associated with *G. andersoni* is composed mainly of fleas (Siphonaptera) and mesostigmatid mites (Parasitiformes) (Theodor and Costa 1967). The flea *Synosternus cleopatrae* (Rothschild 1904) is a predominant ectoparasite of *G. andersoni* (Lehmann 1992).

We distinguished between two age-groups according to the gerbil body mass, which is considered as a good indicator in post-weaned individuals (Peters 1983). Animals weighing below 20 g were considered juveniles since they do not reproduce. These are individuals between 1 and 5 months old that already live independently of their mother (Abramsky 1984; Stenseth and Lidicker 1992 and references therein). Animals above 20 g are usually physiologically ready to reproduce and thus considered as adults (Abramsky 1984; Shenvrot,

personal communication). The two groups can also be distinguished by the appearance and density of their fur. As the average lifespan of an individual *G. andersoni* in nature is less than 1 year (Abramsky 1984), most of the adult population composed of individuals between 5 and 8 months old, while senescent individuals are rare in natural populations.

Study area and experimental design

We estimated natural ectoparasite infestation levels and distribution among juvenile and adult hosts in two 1-ha plots in Ashalim sand dunes (30°59'N, 34°41'E). No manipulation was conducted in these plots (hereafter, undisturbed plots).

To estimate age-dependent survival under parasitism, we manipulated ectoparasite numbers on gerbils from two other 1.5-ha plots (600 m apart) that were adjacent (150 m) to the undisturbed plots. In these two plots, both juvenile and adult gerbils were randomly assigned to two treatments, individuals from which ectoparasites were removed (by insecticide, see below) or untreated control individuals (see below). Hence, each gerbil represented a unit of replication. There was no significant difference in the abundance (number of ectoparasites per individual host) of fleas, mites, and ticks between untreated control gerbils at the experimental plots and gerbils at undisturbed plots (Mann–Whitney tests: for fleas, June–July: $P=0.58$; September: $P=0.16$; October–November: $P=0.25$; for mites, June–July: $P=0.26$; September: $P=0.33$; for ticks, June–July: $P=0.54$; September: $P=0.59$).

Trapping methods

Experimental plots were sampled twice a month during July–October 2001 (eight trapping sessions), whereas undisturbed plots were sampled once a month during April–June, September, and November 2001 (five trapping sessions). Each trapping session lasted three consecutive nights and was carried out using 40 Sherman live-traps placed uniformly in four columns and ten rows (with 25 m between columns and 10–15 m between rows in the undisturbed and experimental plots, respectively). Each captured gerbil was marked individually by toe clipping, sexed, weighed to the nearest 0.01 g, and aged. Reproductively active individuals were omitted from the analysis due to their low abundance (see Results). Although reproductive status of the host can affect infestation levels and susceptibility to parasites (Fuller and Blaustein 1996), a very small sample size did not allow us to test this effect.

Ectoparasite collection

Ectoparasites were collected from each individual at first capture during every trapping session. Fleas were

removed by holding the gerbil over a plastic can, blowing over its fur, and collecting the fleas with an aspirator, until no fleas were detected on the host body. Mites and ticks (Parasitiformes) were usually aggregated in specific locations on the body of a gerbil. Ticks were often attached to ears, mouth or nose and were aggregated around open injuries, whereas mites were usually found aggregated near the base of the outer sides of the hind legs. This aggregated pattern allowed us to count these parasites on a gerbil body by carefully scanning the target areas before collecting a few specimens for further identification.

All fleas belonged to a single species, *S. cleopatrae*. All ticks collected were nymphs of *Hyalomma impeltatum* (Ticks mainly exploit rodents at their larval and nymphal stage), whereas mites belonged to genus *Androlaelaps* (*A. hirsti*, *A. insculptus*, *A. centrocarpus*, *A. marshalli*) and were dominated by adult females. To estimate number of mites, we pooled species and developmental stages. This rough sorting of ectoparasites into fleas, mites and ticks is reasonable for quantifying infestation densities as the differences in life history traits (e.g. mobility, location on the host, blood sucking strategies) between these groups are far greater than within them (Marshall 1981). To estimate the number of ectoparasites in host burrows, we excavated 19 active burrows of *G. andersoni* in October 2001. We removed sand by a shovel until we reached the burrow level, and then exposed the burrow section by section. This method enabled us to collect ectoparasites with an aspirator after every exposure, without the burrow collapsing.

Ectoparasite removal

Ectoparasites were manually removed from the treated gerbils at the experimental plots beginning from the very first trapping session, and insecticide (0.15% Pyrethrin solution by volume) was applied to these gerbils. The active ingredient of this solution has a low toxicity to mammals (Schoenig 1995). We renewed the insecticide treatment for insecticide treated individuals during subsequent trapping sessions whereas fleas of untreated individuals were counted and placed back to their original host.

Data analysis: testing age-dependent infestation and distribution in the undisturbed plots

We avoided pseudo-replications while estimating infestation levels in the undisturbed plots by including in the analyses the ectoparasite densities (ED) found on each host only at its first capture. We used regression analysis to test for the effect of age-group (juveniles vs adults) (independent variable) on the ectoparasite infestation levels (dependent variable). Infestation levels can also be confounded by other host-related and parasite-related

factors, and, as such, host gender and abundance of competitor ectoparasites were included in the regression models, too.

Infestation levels were estimated in two ways. Following the common approach, we first referred to the number of ectoparasite per host individual (hereafter, ectoparasite abundance). Additionally, we estimated ED per unit of host body surface ($ED = \text{ectoparasites} / \text{BM}^{0.67}$, where BM is host body mass). This calculation implemented the exponent of the intraspecific allometric relationship between body surface and body mass (Heusner 1985) and, therefore, represented parasite abundance corrected for the differences in resources availability. Statistical analyses were performed after logarithmic transformation of the original data.

Aggregated pattern of parasite distribution among host individuals is well described empirically using the negative binomial frequency distribution (Anderson and May 1978). We compared the observed frequency distribution of fleas, mites, and ticks among hosts with the expected frequency generated by this model, separately for juvenile and adult hosts. The distribution was fitted by a maximum-likelihood method, and the parameter k , an inverse measure of aggregation, was estimated accordingly [k tends toward zero as aggregation increases, but at values of 8 or above the negative binomial converges with the Poisson series (Southwood 1978)]. We also compared between the frequency distribution of each ectoparasite group among juvenile versus adult hosts using Kolmogorov–Smirnov goodness-of-fit test for continuous data. All statistical analyses in this part were two-tailed. Data in tables are untransformed and presented as means \pm SE.

Data analysis: testing age-dependent survival under parasitism in the experimental plots

We tested the efficiency of the insecticide by comparing ectoparasite numbers on each host before the application of the first treatment and at the gerbil's last capture, using Wilcoxon matched pairs test. An efficient removal of ectoparasites by insecticide would be indicated by a significant reduction in ectoparasite numbers on insecticide treated individuals while no change in ectoparasite numbers is expected on the untreated hosts.

As age-dependent survival under parasitism may occur via reduction in body condition (Schall et al. 1982; Puchala 2004), we also tested the effect of parasites on body mass change in juvenile and adult hosts. Daily percent body mass change of an individual was calculated as the difference between final and initial body mass divided by number of experimental days and initial body mass. Changes in body mass of insecticide-treated and untreated gerbils were compared using ANOVA. Natural growth of juveniles was a principal cause of body mass change during July–August (Table 3). Consequently, we conducted separate analyses for that

period and for September–October, when the population consisted of adults only. Data on daily body mass changes were arcsin-transformed prior to analyses.

We applied a proportional hazards model (Cox 1972) to test the effect of parasite removal on survival of individual hosts. We used survival time (number of days between the first and the last captures) as a dependent variable. Gender, treatment and treatment–gender interaction were used as covariates. As the distribution of survival time is truncated at the end, we repeated the analysis excluding the data obtained during the last trapping session. This did not change the results since only few individuals were recruited during the last few sessions (see below).

We included 120 recorded individuals in the survival analysis (insecticide treated: 36 adults and 30 juveniles; untreated: 25 adults and 29 juveniles) whereas for the body mass change and insecticide efficiency analyses we included only 86 individuals that were recaptured at least once (insecticide treated: 26 adults and 25 juveniles; untreated: 20 adults and 15 juveniles). All statistical tests in this part of the study were one-tailed because we had a priori expectation for the negative effect of ectoparasitism on host body mass and survival. Data in tables are untransformed and presented as means \pm SE.

Results

General information

In total, we captured 147 gerbils. Only 27 of them (14 insecticide treated and 13 untreated gerbils) were reproductively active (pregnant or lactating females, males with developed testicles). Of the remaining 120 individuals, 59 and 61 individuals were captured initially as juveniles and as adults, respectively. Thirty juveniles and 36 adults were treated with the insecticide. Percentages of recaptures in each of the trapping sessions were high and increased with time, with 77% at the second session and 84–100% recaptures in the six following sessions.

Ectoparasite distribution among host individuals is age-independent

Mite and tick distributions among hosts fitted well to the negative binomial distribution (Kolmogorov–Smirnov test: $D = 0.02$ – 0.09 , $P > 0.90$, for all comparisons of mites and ticks on juveniles and adults), were highly aggregated ($k = 0.79$ and $k = 0.93$ for mites among juveniles and adults, respectively, and $k = 0.26$ and $k = 0.51$ for ticks among juveniles and adults, respectively) and did not significantly differ between the two age-groups (Kolmogorov–Smirnov test: $D = 0.25$, $N = 53$ for mites and $D = 0.26$, $n = 58$ for ticks, $P > 0.5$ for both; Fig. 1). In contrast, the distribution of fleas was dependent on host

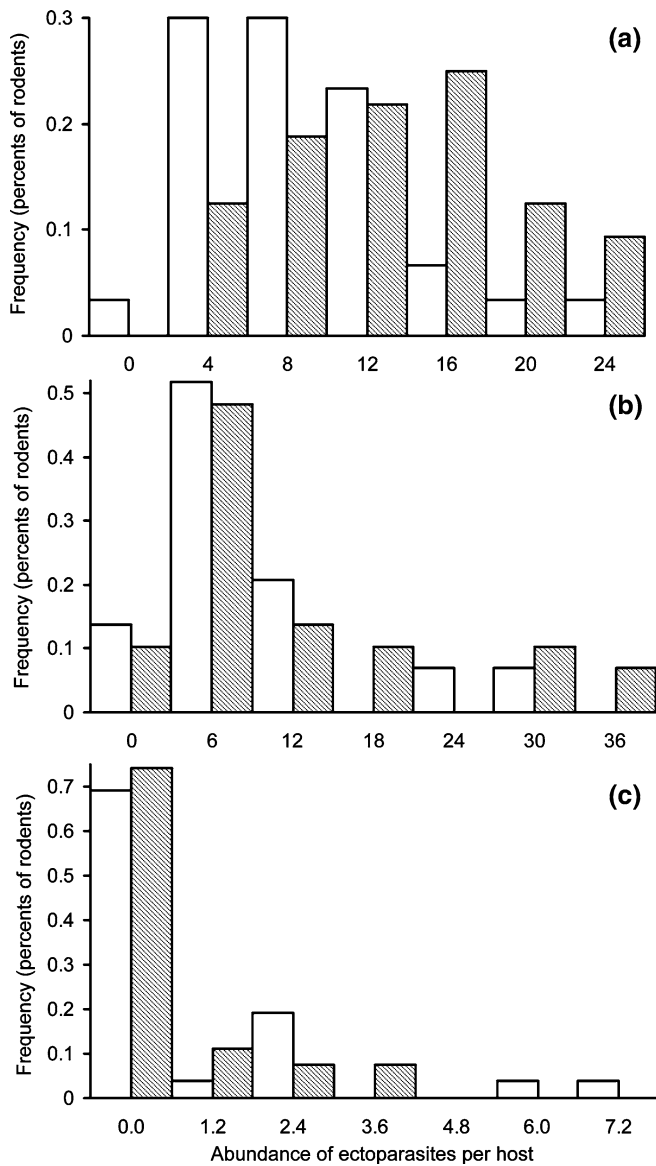


Fig. 1 Frequency distributions of flea (a), mite (b), and tick (c) abundances in adult (dashed bars) and juvenile (blank bars) gerbils (*Gerbillus andersoni*) in the undisturbed plots. The frequency was converted to percentages to allow easy comparison between the two age-groups

age-group (Kolmogorov–Smirnov test: $D=0.34$, $N=62$, $P<0.005$; Fig. 1), being more aggregated in juveniles ($k=2.91$), and less in adults ($k=6.58$). However, after adjusting the ectoparasite numbers to a host's surface area, no differences were found between frequency distributions of fleas, mites and ticks among juvenile and adult hosts (Kolmogorov–Smirnov test: $D=0.24$ – 0.26 , $P>0.20$ for all).

Ectoparasite infestation is age-independent

Ticks were the least abundant ectoparasites on *G. andersoni* both in terms of prevalence and intensity of

infestation. Fleas were the most abundant ectoparasites (Table 1).

The age-group of the host was the only significant variable included in the multiple regression model and it explained 11% of the variation in flea abundance ($r^2=0.12$, $df=51$, $P<0.01$). Intraspecific abundances as well as the host gender did not have a significant effect on flea abundance ($P_{\text{mites}}=0.48$, $P_{\text{ticks}}=0.42$, $P_{\text{gender}}=0.34$). Flea abundance was significantly lower in juveniles than adults (Table 2). However, after adjusting flea numbers to the host's surface area, the effect of host age-group disappeared (Table 2). No significant effect was found for the interaction between gender and the age-group and for separate effect of gender on flea abundance or flea densities (ANOVA: $F=0.14$ – 0.68 , $n=37$, $P>0.41$ for all).

We further tested if the absence of age-related differences in flea density is related to age-dependent host mortality by (1) comparing flea densities at the beginning of the study (June–July) on hosts that survived till the end of the study (after a decrease in host population size; September–October), and hosts that disappeared; and by (2) comparing flea densities on surviving hosts before and after a decrease in host population size. To control for seasonal effect on flea densities, we included in these two analyses only individuals that were captured at the end of June–beginning of July (20 gerbils from undisturbed plots and 45 untreated gerbils from experimental plots). No significant effect was found for the host groups (survived juvenile and adult hosts, disappeared juvenile and adult hosts) on flea density at the beginning of the study (ANOVA: $F=0.79$, $n=65$, $P=0.50$; Fig. 2). In addition, no effects of the interaction between host age-group and time (before and after a decrease in host population size) and no separate effects of time and age-group on flea densities of the survived hosts were found (repeated measures ANOVA, $n=37$, $F=0.020$, $P=0.89$ for interaction; $F=1.7$, $P=0.20$ for time, and $F=0.16$, $P=0.69$ for age-group; Fig. 2).

None of the host-related (age-group, gender) and parasite-related (interspecific densities) variables had a significant effect on mite and tick abundance (mites: $r^2=0.10$, $df=48$, $P=0.2$; ticks: $r^2=0.030$, $df=48$, $P=0.8$).

Survival under parasitism is age-dependent

Insecticide treatment reduced efficiently ectoparasite abundance (numbers per individual host) on insecticide-treated individuals between the first and the last capture events. Mean abundance of fleas, mites and ticks were significantly lower on the insecticide-treated gerbils at the last capture (Wilcoxon matched pairs tests: $n=51$; $Z=5.0$ for fleas; $Z=3.6$ for mites, and $Z=1.8$ for ticks, $P<0.05$ for all; Fig. 3). No significant differences in ectoparasite infestation between the first and the last capture events were found for untreated gerbils (Wilcoxon matched pairs

Table 1 Incidence and abundance of fleas (*Synosternus cleopatrae*), mites (*Androlaelaps centropus*, *A. insculptus*, *A. hirsti*, *A. marshalli* and *A. androgynus*), and ticks (*Hyalomma impeltatum*) collected from bodies (on undisturbed plots) and burrows of gerbils (*G. andersoni*) during April–November

| Parasite | Host age | Body | | | | Burrow | | | |
|--------------------------|----------|----------|----------|------------|----------|----------|----------|----------|----------|
| | | <i>n</i> | <i>P</i> | <i>I</i> | <i>R</i> | <i>n</i> | <i>P</i> | <i>I</i> | <i>R</i> |
| <i>S. c. pyramidis</i> | Adult | 32 | 100 | 12 ± 1.0 | 4–24 | 19 | 63 | 9 ± 2.6 | 0–31 |
| | Juvenile | 30 | 97 | 8.0 ± 0.96 | 0–22 | | | | |
| <i>Androlaelaps</i> spp. | Adult | 29 | 90 | 11 ± 2.0 | 0–35 | 19 | 68 | 13 ± 4.3 | 0–53 |
| | Juvenile | 29 | 86 | 7.9 ± 1.6 | 0–28 | | | | |
| <i>H. impeltatum</i> | Adult | 27 | 26 | 1.9 ± 0.3 | 0–3 | 19 | 0 | 0 | 0 |
| | Juvenile | 26 | 31 | 2.88 ± 0.7 | 0–7 | | | | |

n Numbers of sampled hosts or burrows, *P* prevalence of infestation (percentage of gerbils/burrows with ectoparasites), *I* intensity of infestation (mean ± SE of ectoparasites per infested gerbil/burrow), *R* abundance range

tests: $n = 35$; $Z = 0.44$ for fleas; $Z = 0.49$ for mites, and $Z = 1.1$ for ticks, $P > 0.13$ for all; Fig. 3).

Host age-group was the only factor that significantly affected daily percent body mass change of gerbils (ANOVA: $F = 4.8$ for July–August and $F = 4.6$ for September–October, $P < 0.05$ for both). Juveniles grew faster both over the period of increasing daily body mass and during the period of slower body mass change (Table 3). No significant effects were found for the interactions between gender-treatment and age-group-treatment on the percent daily body mass change either over the period of increasing daily body mass (July–August; ANOVA: $F = 0.60$, for gender-treatment and $F = 0.27$ for age-group-treatment, $P > 0.44$ for both) or during the period of slower body mass change (September–October; ANOVA: $F = 1.53$ for gender-treatment and $F = 0.0048$ for age-group-treatment, $P > 0.22$ for both). Also, no separate effects of either gender or treatment on the percent of daily body mass change were found either over the period of increasing daily body mass (ANOVA: $F = 0.26$ for gender and $F = 0.58$ for treatment, $P > 0.29$ for both) or during the period of slower body mass change (ANOVA: $F = 2.6$ for gender and $F = 0.22$ for treatment, $P > 0.11$ for both).

As most mortality occurred at the first 21 experimental days, when juvenile gerbils were less than 75 days old (Fig. 4), we conducted the survival analysis twice, for only the first 21 experimental days, and for the whole period of the study. A significant interaction between host age-group and treatment was found, but only at the first 21 days of experiment (Cox regression test: Wald

statistic = 1.9, $P = 0.085$ for the whole study period, and Wald statistic = 4.4, $P < 0.05$ for the first 21 days; Fig. 4). Average survival time of insecticide-treated juveniles was twice higher than that of untreated juveniles (61.40 ± 7.04 days, $n = 30$ vs 32.31 ± 7.12 days, $n = 29$, respectively). In contrast, average survival time of insecticide-treated and untreated adults was similar (51.17 ± 7.00 days, $n = 36$ vs 54.68 ± 7.56 days, $n = 25$, respectively). To ensure that the results do not depend on the 20-g threshold for host age-group division, we repeated the analysis for juveniles below 18 g and adults above 20 g. In spite of the decrease in sample size, the interaction between host age-group and treatment at the first 21 days remained significant (Cox regression test: Wald statistic = 2.9, $P < 0.05$).

No significant effect was found for the interaction between gender and treatment and for the effect of gender alone (Cox regression: Wald statistic = 0.27 for interaction and Wald statistic = 0.080 for gender, $P > 0.60$ for both).

Discussion

Our hypothesis about age-specific parasitism was only partly supported. Parasite-free juveniles survived significantly longer than parasitized juveniles while no such differences were detected for adult hosts. Therefore, this study provided the first direct evidence for age-related differences in parasite-induced host mortality in a wild host population. However, patterns in infestation and

Table 2 Abundance (mean ± SE) and densities (per unit of gerbil's body surface; mean ± SE) of fleas, mites, and ticks during April–November on undisturbed plots

| Host | Fleas | | | | Mites | | | | Ticks | | | |
|-----------|----------|-------------|----------|----------|----------|-------------|----------|----------|----------|---------------|----------|----------|
| | <i>n</i> | Abundance | <i>F</i> | <i>P</i> | <i>n</i> | Abundance | <i>F</i> | <i>P</i> | <i>n</i> | Abundance | <i>F</i> | <i>P</i> |
| Juveniles | 30 | 7.70 ± 0.96 | 6.55 | < 0.05 | 29 | 6.79 ± 1.49 | 3.22 | 0.078 | 26 | 0.88 ± 0.34 | 0.52 | 0.48 |
| Adults | 32 | 11.72 ± 1.0 | | | 29 | 9.79 ± 1.92 | | | 27 | 0.48 ± 0.18 | | |
| Age | <i>n</i> | Density | <i>F</i> | <i>P</i> | <i>n</i> | Density | <i>F</i> | <i>P</i> | <i>n</i> | Density | <i>F</i> | <i>P</i> |
| | <i>n</i> | Density | <i>F</i> | <i>P</i> | <i>n</i> | Density | <i>F</i> | <i>P</i> | <i>n</i> | Density | <i>F</i> | <i>P</i> |
| Juveniles | 30 | 1.29 ± 0.17 | 0.98 | 0.33 | 29 | 1.10 ± 0.24 | 0.67 | 0.42 | 26 | 0.14 ± 0.052 | 1.89 | 0.17 |
| Adults | 32 | 1.47 ± 0.12 | | | 29 | 1.23 ± 0.24 | | | 27 | 0.060 ± 0.023 | | |

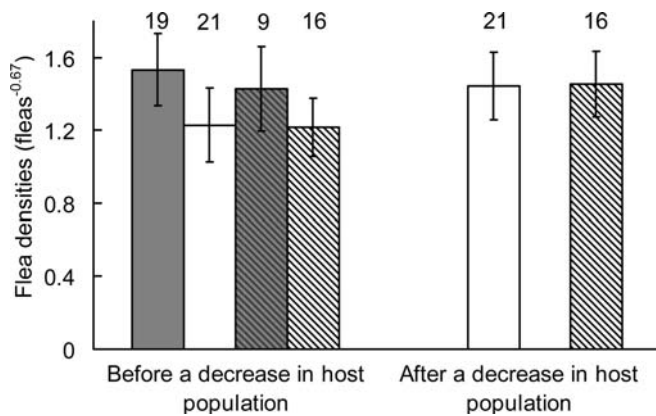


Fig. 2 Flea densities (\pm SE) on juvenile (bars without lines with either white or black background) and adult (lined bars with either dark or white background) untreated gerbils that disappeared (bars with a dark background) or survived (bars with a white background) till the end of the study, before (end June–July) and after decrease in host population size (September–October) in experimental and undisturbed plots. Numbers above bars represent the number of hosts that were sampled in each group

distribution of ectoparasites among host individuals were only in partial agreement with the hypothesis of age-dependent parasitism. We found higher flea infestation rates and lower aggregation levels in adult than in juvenile hosts. However, no age-related differences in infestation and distribution among host individuals were found after adjusting the flea numbers to the host's surface area. In addition, no age-related differences were found for mites and ticks. Thus, the patterns found in this study suggest that the effect of host age-group on host–parasite dynamics may involve different host-related and parasite-related processes and may depend on the natural history of the parasite. As a result, different age-specific patterns could be generated not only for ectoparasites in comparison with endoparasites, but also among different ectoparasite taxa.

Age-related differences in infestation levels and distribution among host individuals

The higher flea abundance on an adult compared to juvenile individuals combined with the lower aggregation of fleas among adults (before the size-correction) suggest that most flea individuals are forced to cope with high fur density, with the body temperature, resistant behaviour and other adult-typical traits. There are other reports on adult-biased flea infestation (e.g. Smit 1962), but these evidence are not unequivocal. First, there are also studies that either did not detect any effect of host age on flea abundance (e.g. Ulmanen and Myllymaki 1971) or even found an opposite trend (e.g. Brinck-Lindroth 1968). Second, all evidence on age-specific flea infestation were related to flea abundance per individual host rather than to flea densities (number of fleas per unit of host's surface area) and the former may be less relevant to the parasite

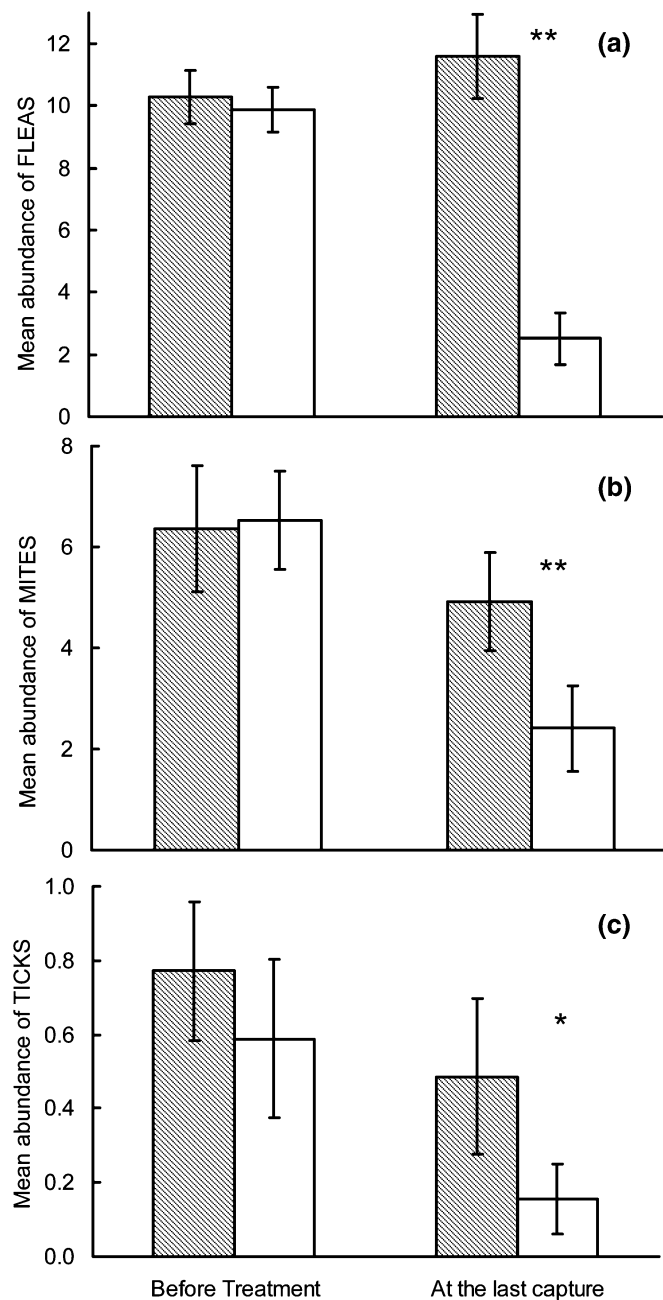


Fig. 3 Mean abundance (ectoparasite number per individual host) (\pm SE) of fleas (a), mites (b), and ticks (c) on 51 insecticide-treated gerbils (blank bars), and on 35 untreated gerbils (dashed bars) from experimental plots at first (before treatment) and last captures. Asterisks indicates significant differences between columns (* $P < 0.05$; ** $P < 0.001$)

recruitment and parasite mortality processes that generate age-specific patterns. The reasons for this, at least for fleas, can be that the parasite recruitment and parasite mortality, may strongly depend on the host's surface area because (1) flea–host immune interaction occur at the cutaneous interface (Wikel 1996), (2) the host's fur is used as a refuge from host grooming, and (3) fleas feed from capillaries near the surface of the skin. Consequently, adult-biased infestation in flea abundance but not in flea

Table 3 Daily percent of body mass change (mean \pm SE) of gerbils in experimental plots during periods of either increasing body mass (July–August) and slower body mass change (September–October)

| Host age | Treatment | July–August | | September–October | |
|----------|-------------|------------------|----------|--------------------|----------|
| | | Mean \pm SE | <i>n</i> | Mean \pm SE | <i>n</i> |
| Juvenile | Insecticide | 0.56 \pm 0.14 | 22 | 0.066 \pm 0.049 | 16 |
| | Untreated | 0.78 \pm 0.25 | 13 | 0.057 \pm 0.12 | 6 |
| Adult | Insecticide | 0.36 \pm 0.075 | 19 | −0.081 \pm 0.058 | 18 |
| | Untreated | 0.28 \pm 0.056 | 16 | −0.008 \pm 0.081 | 13 |

densities may not support the ‘parasite recruitment’ hypothesis (adult, long-lived hosts acquire more fleas than juveniles), but rather indicate that adult hosts, with the higher surface area, may support more fleas than juvenile hosts. For mites and ticks, that are usually aggregated on specific locations on the host body (Sonenshine 1985), the surface area should be less relevant and, indeed, adult hosts did not support higher numbers of mites and ticks than juvenile hosts.

Our failure to find explicit evidence for age-biased infestation for ectoparasites in terms of their densities may suggest that both ectoparasite recruitment and ectoparasite mortality are not affected by host age-group. There is some evidence that rodents develop acquired immunity against ectoparasites (Khokhlova et al. 2004), but the higher infestation levels of adult compared to juvenile hosts rule out the importance of this resistant mechanism. It appears also that parasite-induced host mortality does not significantly affect infestation levels as the level of infestation did not change after some juveniles and adults were lost from the host population (a comparison between infestation levels on juvenile and adults that survived till the end of the study and on the individuals that disappeared during the study; Fig. 2). Finally, there is no strong evidence that parasites accumulate on adult hosts.

Alternatively, it is possible that the processes of ectoparasite recruitment and ectoparasite mortality depend on host age but operate in opposite directions and, thus, the two processes cancel each other (Anderson and

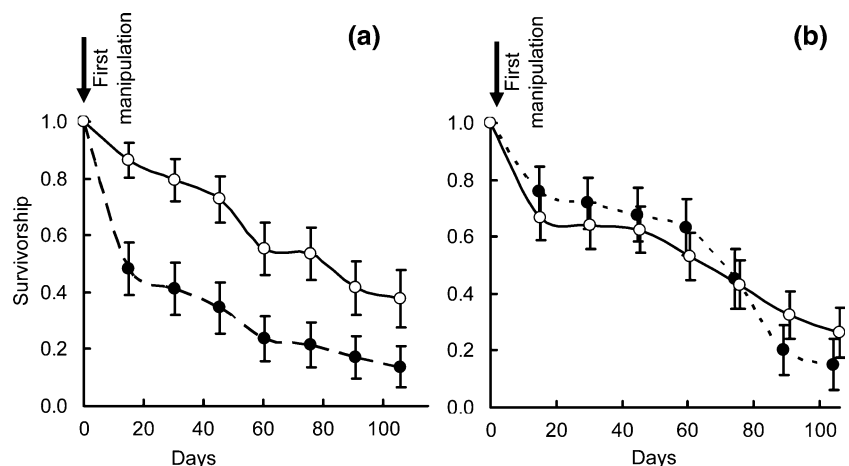
Gordon 1982). For example, the tendency of adult wood mice (*Apodemus sylvaticus*) to accumulate more nematodes *Heligmosomoides polygyrus* than juvenile wood mice counter the better ability of adults to mount an immune response (Quinnell 1992). Furthermore, the processes of ectoparasite recruitment and ectoparasite mortality may be influenced by factors other than the level of host exposure, immune response, and parasite-induced host mortality. For instance, in a larger-scale survey, it was shown that age-biased flea parasitism might change from juvenile-biased toward adult-biased as a function of soil temperature and ED (Hawlena et al. 2005).

Age-dependent survival under parasitism

The results of our field manipulation are in agreement with the results of Lehmann (1992), who found indications for negative effects of ectoparasites on survival and red blood cell indices of *G. andersoni*. We further pointed on juvenile hosts as the most susceptible host group responsible for these negative effects. We also found that the juvenile hosts are most likely to die under parasitism before approaching 75 days old (approximate age for the juveniles at the first 21 days of experiment; Fig. 4). As parasites or pathogens that could potentially be transferred to host via ectoparasites are rarely found in the gerbil blood (M. Spinu, unpublished data), these results combined with other evidence on negative effects of ectoparasites on the body condition, survival and reproduction of the host individual (Moller et al. 1990; Richner 1998; Lehmann 1992; Neuhaus 2003; Mooring et al. 2004; Puchala 2004) suggest that ectoparasites may directly affect the host fitness beside serving as disease agents.

We predicted that higher parasite-induced mortality of juveniles compared to adults would occur if juveniles will be more infested than adults. Although ED per unit surface were similar in adult and juvenile hosts, it is likely that the latter group with a larger ratio of body surface to body mass could not afford these densities. Additional energy requirements of juveniles for somatic

Fig. 4 Survival curves of insecticide treated (white circles, solid line) and untreated (black circles, dashed line) juvenile (a) and adult (b) gerbils from experimental plots over 4 months. Survivorship is the probability that a gerbil survive until day *t*. Vertical lines represent standard errors of the life table estimation



growth and maturation may make them more energetically constrained and thus more susceptible to infestation than adults. Nevertheless, our data on body mass change of the insecticide-treated and untreated gerbils do not support the energy-budget explanation as both juvenile and adults did not lose body mass due to infestation (Table 3). However, our failure to detect differences in body mass due to parasitism may be a result of the high individual variation in the rate of food consumption and energy expenditure in the field (Table 3). In contrast, in a laboratory experience parasitised juveniles of *G. andersoni* grew slower compared to control, clean gerbils, while no effect of flea parasitism on body mass was found in adult hosts (H. Hawlena et al., unpublished data). The absence of parasite effect on host body mass in the field may be also due to food compensation by foraging for longer periods. In this case, the lower survival of parasitised juvenile may be a result of a higher exposure to predators. For example, Murray et al. (1997) suggested that infested hares (*Lepus americanus*) foraged for longer periods and therefore were more vulnerable to predators compared with non-parasitised hares. Alternatively, it may be speculated that the age-dependent differences in survival are a consequence of other parasites that were transferred via ectoparasites to the hosts and caused higher pathology in the less immunized juvenile hosts. However, the very low blood infections found in this host species (M. Spinu, unpublished data) do not support this hypothesis.

The parasite-induced juvenile mortality may have ecological consequences for the host population. Significant decrease in survival of juvenile *G. andersoni* due to infestation may cause a decrease in population growth rate. We converted survival time of juvenile gerbils to survival probability by taking the ratio of mean survival time to total number of experimental days as 0.58 (61.4/106) and 0.30 (32.3/106) for insecticide-treated and untreated individuals, respectively. Since the average lifespan of an individual *G. andersoni* is less than 1 year (Abramsky 1984), a 48% reduction in survival probability $[(0.58-0.30)/0.58 \times 100]$ may have a significant influence on the number of reproductive adults of the following year. We defined survival time as number of days between the first and the last captures, assuming that missing animals died. This assumption was partly supported by the fact that none of the individuals that disappeared from the experimental plots were captured in any of the adjacent undisturbed plots. However, since our analysis cannot explicitly distinguish between death and dispersal, it is also possible that infested juveniles did not die but rather increased their dispersal rates, possibly as a strategy to avoid ectoparasites. The effect of parasites on dispersal decisions of hosts has been investigated in number of host–parasite systems (reviewed by Boulinier et al. 2001). Almost all of these studies involved ectoparasites and showed either no effect or an increase in dispersal rates under parasitism (Boulinier et al. 2001). Nevertheless, migration is very

costly in terms of time and energy and may decrease the survival probability (Byrom and Krebs 1999), and thus whether parasites affect juvenile survival directly or indirectly by increasing their dispersal rates, this effect seems to have an important influence on the population growth rates and densities.

A significant part of the reports on parasite-induced mortality in different vertebrate hosts deals with juveniles (Moller et al. 1990; Atkinson and Van Riper III 1991; Goater et al. 1993; Lehmann 1993; Van Vuren 1996; Kuperman et al. 2002), providing an indirect evidence that higher mortality of juveniles compared with adults due to parasitism may be the common rule in nature. If indeed experiments in other host–parasite systems will support this hypothesis, the next stage will be to incorporate age-related differences in parasite-induced host mortality into population dynamical models and to evaluate the role of these differences in stabilising host–parasite interactions. Attempts have been made to incorporate age-specific effects into these models, e.g. modelling of schistosomiasis in human populations (Gurarie and King 2005), but a more general framework is still needed.

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