

# Is a starving host tastier? Reproduction in fleas parasitizing food-limited rodents

B. R. KRASNOV,\*† I. S. KHOKHLOVA,‡ M. S. ARAKELYAN\*§ and  
A. A. DEGEN‡

\*Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Mizpe Ramon, Israel, ‡The Wyler Department of Dryland Agriculture, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Israel, and §Department of Zoology, Yerevan State University, Yerevan, Armenia

## Summary

1. We hypothesized that food availability, and therefore body condition, of a rodent host, *Meriones crassus*, affects egg production and survival, and development time of preimago and adults of the first generation of the flea *Xenopsylla ramesis*.
2. Egg production was significantly higher in fleas parasitizing underfed than control animals.
3. Food availability for hosts affected survival of eggs and larvae produced by fleas on these rodents, but did not affect survival of pupae. More than twice the number of eggs from fleas on food-limited hosts survived than those from fleas on control rodents. Highest larval survival was recorded in fleas on rodents with 30% of maintenance energy intake.
4. Survival of new generation imagos was lowest in fleas from parents on hosts with the highest food limitation. By contrast, survival of parent fleas was highest on hosts offered 30% of maintenance energy intake.
5. Time of egg and larval development was longest on hosts consuming 30% of energy requirements for maintenance. By contrast, there was no difference in time to emergence in pupae from flea females on rodents from different treatments. Survival time under starvation of imago of the first generation was shortest in offspring of fleas that parasitized *M. crassus* offered the minimal amount of food. The opposite was true for parent fleas.
6. The results suggest nutritional and/or energetic cost of host resistance, measured as host-mediated parasite fitness loss, as well as possible adaptive stress-induced immunosuppression.

*Key-words:* Egg production, flea, food limitation, rodent host, survival

*Functional Ecology* (2005) **19**, 625–631

doi: 10.1111/j.1365-2435.2005.01015.x

## Introduction

Distribution of parasite individuals across a host population is characterized by their aggregation. Most individuals of the parasite occur on a few host individuals, while most host individuals have only a few, if any, parasites (Anderson & May 1978). The general cause of the heterogeneous distribution of parasites is due to host heterogeneity of the rate of gain or loss of parasites (Poulin 1998). In other words, if some hosts have more parasites than would be predicted by chance, it suggests

that they offer the parasites a better quality habitat. In particular, intraspecific host variation in suitability for a parasite can be caused by the variation in the pattern of resource acquisition by a parasite such as intrahost variation in defences.

Hosts defend themselves against parasites using specific behavioural, physiological and/or immunological mechanisms that can result in loss of fitness in the parasites. This host-mediated loss of fitness in a parasite is considered to be host resistance (Poulin 1998). The defence against parasites can be costly for a host. For example, activation of an immune response and even maintenance of a competent immune system is an energetically demanding process that requires trade-off decisions among competing energy demands for growth,

reproduction, thermoregulation, work and immunity (Sheldon & Verhulst 1996). Empirical evidence suggests that such costs can be high (e.g. Moret & Schmid-Hempel 2000).

The trade-off between the advantage of resistance and its cost should be most critical for hosts that face energy limitations. Therefore, energy-deprived hosts might be less resistant and, thus, represent better patches for parasites. Intraspecific host variation in energy reserves can arise due to a variety of reasons (Kam & Degen 1993; Cumming & Bernard 1997). As a result, in many non-tropical vertebrate animals, disease prevalence is increased during periods of food shortage compared with periods when food is readily available (Lochmiller, Vestey & McMurray 1994). However, resources that parasites extract from their hosts (e.g. blood) can be of a lower quality in energy-deprived hosts (De Pedro *et al.* 2003). Thus, hosts in good condition can be a better food source than hosts in poor condition (Dawson & Bortolotti 1997). Consequently, parasites face a trade-off between the choice to attack less defended but lower-quality, vs more defended but higher-quality, hosts. From the evolutionary perspective, the strategy of parasitizing either energy deprived or energy-rich hosts would depend on relative fitness rewards from exploiting these hosts. This reasoning leads to two alternative predictions regarding the effect of host energy deprivation on reproductive patterns of a parasite. Reproductive output of a parasite will be higher when exploiting energy deprived hosts if the fitness increment due to reduced host defences is higher than the fitness decline due to lower quality of resources extracted from a host. Alternatively, this reproductive output will be lower when exploiting energy deprived hosts if the fitness increment due to reduced host defences is lower than the fitness decline due to lower quality of extracted resources.

The effect of body condition of hosts on their resistance to parasites has been studied in a variety of animals by manipulating the body condition of hosts (Oppliger, Christe & Richner 1996; Brown, Loosli & Schmid-Hempel 2000; Jokela *et al.* 2005). However, all of these studies have investigated this phenomenon from the host perspective, whereas the effect of host condition on parasite parameters (apart for abundance) has largely been neglected.

Here, we studied the effect of host energy intake on parasite fitness. We hypothesized that food limitation of a rodent host, *Meriones crassus*, affects reproductive potential (in terms of egg production) and quality of offspring (in terms of survival and development time of preimaginal stages and adults of the first generation) of its characteristic flea parasite *Xenopsylla ramesis*. Fleas (Siphonaptera) are parasites of higher vertebrates, being most abundant and diverse on small mammals. In most cases, preimaginal development is entirely off-host. Larvae of almost all flea species are not parasitic and feed on organic debris in the burrow and/or nest of the host.

## Materials and methods

### MAINTENANCE OF FLEAS AND RODENTS

Fleas and rodents (27 adult males) were obtained from our laboratory colonies started from field-collected individuals. Details on the flea and rodent-rearing procedures can be found elsewhere (Krasnov *et al.* 2001a,b, 2004). In this study we used only newly emerged fleas, 2 days of age, which did not feed from emergence until experimental treatments. The study was conducted under permits from the Israel Nature and National Parks Protection Authority and Ben-Gurion University Committee for the Ethical Care and Use of Animals in Experiments.

### FOOD LIMITATION TREATMENTS

Prior to experimental trials with fleas, the rodents were placed in individual plastic cages ( $20 \times 40 \times 15$  cm<sup>3</sup> with 3 mm clean sand as a substrate) and divided randomly into three groups (nine individuals per group). One group (control group, C) was offered millet seeds equivalent to approximately 100% of maintenance energy requirements, whereas the two other groups were offered 60% (group T1) and 30% (group T2), respectively, of maintenance requirements. In addition, rodents were offered 3 g fresh alfalfa leaves, which provided their water needs but with minimal additional energy (I. Khokhlova, unpublished data). Energy requirements for maintenance of *M. crassus* were taken as  $8.3 \text{ kJ } m_b^{-0.54} \text{ day}^{-1}$  (Khokhlova, Degen & Kam 1995) and calculated for each animal based on its body mass ( $m_b$ ). Animals were weighed daily at 09.00 h to 0.01 g (Ohaus CT200-S electronic balance, Ohaus Corporation, Pine Brook, NJ, USA). Food offered was weighed to 0.0001 g (Mettler-Toledo AB, Dietikon, Switzerland). Animals from the control group and animals from the T1 treatment maintained their body mass throughout the experimental period; their body mass after the first week was  $98.9 \pm 2.1\%$  and  $97.3 \pm 1.7\%$ , respectively, of initial body mass. However, body mass of rodents from the T2 group decreased after the first week to  $81.1 \pm 1.8\%$  of initial body mass.

### MANIPULATIONS WITH FLEAS

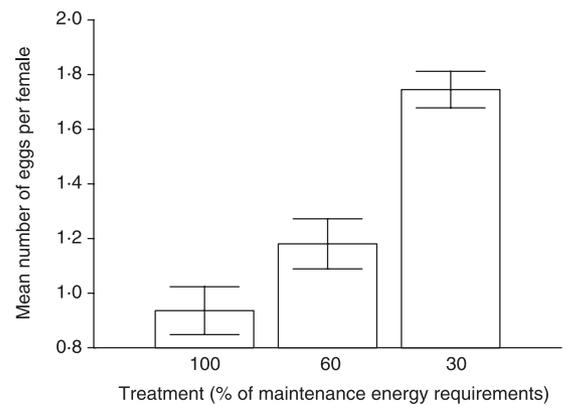
We selected 945 newly emerged female and 270 newly emerged male *X. ramesis* and assigned them randomly to the three experimental treatments that differed in food availability to a rodent host. We placed 35 female and 10 male fleas on each rodent a week after the beginning of experiments. Four days after the fleas were in the rodent cage, we collected the fleas by brushing the hair of the rodent with a toothbrush and sieving the cage substrate until no fleas could be recovered during 10 min of either brushing or sieving. No behavioural difference during manipulations was recorded among rodents of the three experimental groups. In total, we

recovered 804 female and 156 male fleas. Each female flea was examined under a light microscope, and the degree of egg development (early, middle or late stage) was determined visually (see Krasnov *et al.* 2002 for details). Fleas with egg development of middle and late stages (729 fleas) were placed individually in glass vials (200 ml) that contained a thin layer of sand and small pieces of filter paper, assigned an individual number and transferred into an incubator and maintained at 25 °C air temperature and 90% r.h. (see Krasnov *et al.* 2001a for details). Vials were checked twice a day during three consecutive days. After oviposition, we counted eggs and placed them individually into new vials. Vials with eggs were checked twice a day until all larvae hatched. Because death of an egg cannot be readily identified, an egg was considered dead if no larva hatched after 7 days (maximal hatching time of *X. ramesis* at 25 °C air temperature and 90% r.h.; Krasnov *et al.* 2001b), but these eggs were further monitored for 20 days. After eggs hatched, each larva was transferred to another vial with clean sand and dry bovine blood. Vials with larvae were checked twice a day until a larva pupated or died. Vials with cocoons were checked twice a day and were shaken slightly during checking to stimulate flea emergence. Because death of a cocooned pupa cannot be readily identified as in the case of eggs, a pupa was considered dead if no imago emerged after 15 days (maximal emergence time of *X. ramesis* at 25 °C air temperature and 90% r.h.; Krasnov *et al.* 2001b). However, these cocoons were monitored for another 20 days. Vials with newly emerged imagos were checked twice a day and the death of a flea was confirmed by examining it under light microscopy. In addition, we identified the sex of each newly emerged imago by examining its genitalia under light microscopy. Duration of developmental time of each stage, as well as survival time under starvation of parent females and newly emerged fleas, were recorded. In total, 729 females produced 1150 eggs, from which 973 larvae hatched. Of these larvae, 766 pupated and 730 fleas of the new generation emerged.

#### DATA ANALYSIS

To adjust for deviations from normality, we applied a log-transformation on the duration of developmental time of each stage and survival time of imago. These parameters were analysed using one- or two-way ANOVAS with treatment of hosts and sex of newly emerged fleas (where appropriate) as independent variables. Duncan's test was used for multiple comparisons. We analysed the differences in survival within preimaginal stage among rodents from different treatments using the Cox 'proportional hazards' regression. The individual number of a rodent host was treated as a block effect in the survival analysis.

The difference in preimaginal flea survival was tested among treatments within each developmental stage using a  $\chi^2$ -test.  $\chi^2$  values were based on the sums (for each



**Fig. 1.** Mean ( $\pm$  SE) number of eggs produced by the female flea *X. ramesis* when feeding on *M. crassus* offered different energy levels. See text for details of different treatments.

treatment) of the score assigned to each survival time using Mantel's procedure (Statsoft 2004), as well as pairwise between treatments using the Cox–Mantel test. In addition, we calculated odds ratio of survival of imago and each preimaginal stage for different treatments and tested the odds ratio for a departure from the null case of 1.0 using the  $\chi^2$ -test of independence for  $2 \times 2$  tables.

Male and female fleas (both preimago and imago) differ in their sensitivity to various factors (Krasnov *et al.* 2001a,b). In particular, this difference is manifested in differential survival rate during preimaginal development. To test the effect of host food availability on sex ratio of newly emerged adults, we analysed  $2 \times 2$  contingency tables of emerged males and females using  $\chi^2$ -tests. We searched for deviation of sex ratio of newly emerged adults from 1:1 and compared this sex ratio between host treatments.

#### Results

Egg production by flea females differed significantly when they fed on rodents from different treatments ( $F_{2,726} = 28.8$ ,  $P < 0.0001$ ; Fig. 1). Fleas that parasitized control animals produced significantly fewer eggs than those that parasitized underfed animals (Duncan's test,  $P < 0.04$  for both comparisons). Furthermore, egg production of fleas fed on rodents with 60% of maintenance energy intake was significantly lower than that of fleas fed on rodents with 30% of maintenance energy intake (Duncan's test,  $P < 0.00001$ ).

Survival analysis indicated that food availability of rodent hosts affected survival probability of eggs and larvae produced by fleas fed on these rodents (Tables 1 and 2). This probability was significantly different among treatments ( $\chi^2 = 13.5$  and  $\chi^2 = 55.5$ , respectively,  $P < 0.0001$  for both). More than twice the number of eggs from fleas on food-limited rodents survived than those on control rodents (Cox–Mantel test statistic =  $-2.69-3.69$ ,  $U = -10.7-15.7$ ,  $P < 0.007$  for both; Table 2). However, no difference in egg survival was found between fleas on rodents from the two treatment groups (Cox–

**Table 1.** Survival analysis of preimaginal and imago *X. ramesis*. Parent fleas were fed on 27 individuals of *M. crassus* on three treatments of energy intake (a categorical block effect, HI)

Stage	Effect	df	$\beta$ (SE)	<i>t</i> -value	Wald statistics	<i>P</i>
Egg	Treatment	2	-0.27 (0.09)	-2.95	8.71	0.003
	HI	26	0.01 (0.04)	0.27	0.07	0.78
Larva	Treatment	2	-0.35 (0.09)	-3.69	13.63	0.0002
	HI	26	0.04 (0.03)	1.27	1.62	0.20
Pupa	Treatment	2	0.28 (0.25)	1.13	1.29	0.25
	HI	26	-0.02 (0.09)	1.15	1.32	0.24
Imago	Treatment	2	0.09 (0.05)	1.37	1.90	0.10
	HI	26	-0.09 (0.02)	0.02	0.22	0.60
Parent imago	Treatment	2	-0.41 (0.04)	-9.01	81.2	0.0001
	HI	26	-0.004 (0.01)	-0.34	0.12	0.73

**Table 2.** Odds ratio of survival ( $\chi^2$ ) and mean ( $\pm$  SE) duration of either development (for eggs, larvae and pupae) or survival under starvation (for imago) of *X. ramesis* from *M. crassus* hosts with different levels of energy intake. All odds ratios are significant ( $P < 0.001$ ). C: 100% of maintenance energy requirements; T1: 60% of maintenance energy requirements, T2: 30% of maintenance energy requirements

Stage	Treatment	Odds ratio of survival	$\chi^2$	Development or lifetime (days)
Egg	C	3.09	25.1	5.2 $\pm$ 0.03
	T1	6.02	74.1	5.2 $\pm$ 0.03
	T2	6.39	221.4	5.9 $\pm$ 0.01
Larva	C	3.06	31.8	13.9 $\pm$ 0.2
	T1	3.09	30.3	13.9 $\pm$ 0.1
	T2	4.84	116.9	15.0 $\pm$ 0.1
Pupa	C	21.4	58.6	14.8 $\pm$ 0.3
	T1	22.8	88.96	14.7 $\pm$ 0.2
	T2	19.3	248.2	15.2 $\pm$ 0.1
Imago	C	-	-	26.3 $\pm$ 0.7
	T1	-	-	27.1 $\pm$ 0.7
	T2	-	-	24.5 $\pm$ 0.4
Parent female	C	-	-	10.4 $\pm$ 0.6
	T1	-	-	11.8 $\pm$ 0.6
	T2	-	-	16.8 $\pm$ 0.4

Mantel test statistic = 0.28,  $U = 1.3$ ,  $P > 0.8$ ). The highest survival of larvae was recorded in fleas fed on rodents with only 30% of maintenance energy intake (treatment 2) (Cox–Mantel test statistic = -2.59–28.61,  $U = -9.7$ –28.6,  $P < 0.03$  for both comparisons; Table 2), whereas no difference in survival was found between larvae of fleas fed on control rodents and rodents with 60% of maintenance energy intake (Cox–Mantel test statistic = 1.81,  $U = 7.3$ ,  $P > 0.07$ ). By contrast, survival of pupae did not differ among host treatments ( $\chi^2 = 3.2$ , Cox–Mantel test statistic = -0.92–1.75,  $U = -1.3$ –4.2,  $P > 0.07$  for all).

Sex ratio of newly emerged imagos did not differ significantly from 1:1 in any treatment ( $\chi^2 = 0.12$ –1.25,  $P > 0.3$  for all). Survival of imago fleas of the new generation differed among hosts on which their parents had fed ( $\chi^2 = 12.9$ ,  $P < 0.001$ ). The lowest survival was found in fleas from parents feeding on hosts with the

highest food limitation (Cox–Mantel test statistic = -2.55–2.62,  $U = 16.4$ –28.7,  $P > 0.05$  for both comparisons), but not in fleas from parents feeding on rodents from the two other treatments (Cox–Mantel test statistic = -0.43,  $U = -3.2$ ,  $P > 0.6$ ). Survival of parent fleas also depended on the level of food available for their hosts ( $\chi^2 = 106.7$ ,  $P < 0.0001$ ), being the highest for those offered 30% of maintenance energy intake (Cox–Mantel test statistic = -7.00–9.11,  $U = -61.4$ –71.8,  $P > 0.0001$  for both comparisons). In addition, survival of parent fleas did not differ between those feeding on control hosts and hosts with 30% of maintenance energy intake (Cox–Mantel test statistic = 1.42,  $U = 11.7$ ,  $P > 0.1$ ).

#### DEVELOPMENTAL TIME OF PREIMAGO AND SURVIVAL TIME UNDER STARVATION OF IMAGO

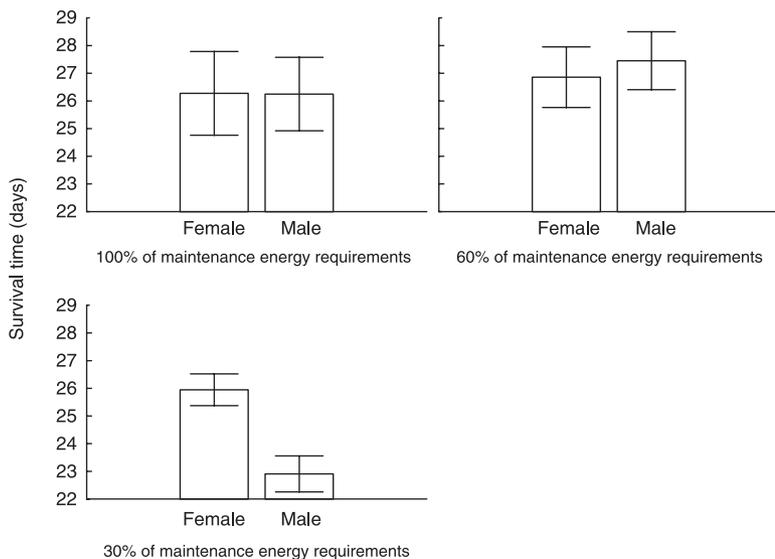
Time to hatching differed significantly among eggs produced by females feeding on rodents with different levels of food limitation (ANOVA,  $F_{2,970} = 327.6$ ,  $P < 0.0001$ ), being longest if the host diet provided 30% of energy requirements for maintenance (Table 2, Duncan's test,  $P < 0.00001$ ). The same was true for the time to pupation of larvae (ANOVA,  $F_{2,765} = 15.0$ ,  $P < 0.0001$ ). Larvae produced by females on control rodents or rodents with 60% of maintenance energy intake developed significantly faster than those produced by fleas on hosts limited to 30% of maintenance energy intake (Table 2, Duncan's test,  $P < 0.0001$ ). By contrast, no difference in time to emergence was found among pupae from females on rodents from different treatments (ANOVA,  $F_{2,727} = 2.4$ ,  $P > 0.05$ ; Table 2).

Time of survival under starvation of imago of the first generation was significantly shorter in offspring of fleas that parasitized *M. crassus* offered the minimal amount of food (ANOVA,  $F_{2,727} = 3.97$ , Duncan's test;  $P < 0.01$  for both analyses). Although the effect of flea sex on this time appeared not to be significant in general (ANOVA,  $F_{1,727} = 0.96$ ,  $P > 0.3$ ), significance of the interaction term (sex  $\times$  treatment;  $F_{2,727} = 3.13$ ,  $P < 0.04$ ) demonstrated that this effect was manifested differently among treatments. Indeed, newly emerged females survived significantly longer than newly emerged males if the rodent on which a parent flea fed was limited to 30% of maintenance energy intake, whereas no sex difference in survival time was found in the other two treatments (Fig. 2).

Energy intake of the host also affected the longevity of the starving parent female fleas (ANOVA,  $F_{2,726} = 58.4$ ,  $P < 0.0001$ ). However, in contrast to the case with the fleas of the first generation, flea survival was longer on hosts with lower energy intake (Duncan's test;  $P < 0.01$ ).

#### Discussion

Our hypothesis that food limitation of a host affects reproductive potential and quality of the offspring of an ectoparasite was confirmed. Moreover, each of



**Fig. 2.** Mean ( $\pm$  SE) survival time under starvation of newly emerged male and female *X. ramesis* in different treatments.

two alternative predictions was partly supported. Reproductive output of a flea was higher when exploiting underfed hosts than well-fed hosts in that egg production and survival of at least two of the preimaginal stages (eggs and larvae) were higher in underfed hosts. However, the quality of flea offspring in terms of development time of eggs and larvae was lower when a flea exploited malnourished hosts.

Both higher egg production and higher survival of eggs and larvae can be related to a decline in the immune responses in hosts with limited food intake. Immunosuppression may be a result of two mechanisms, namely resource reallocation to other metabolic needs (Sheldon & Verhulst 1996) and/or avoidance of immunopathology caused by food stress via neuroendocrine mechanisms (Råberg *et al.* 1999). The immunity has been shown to be an energetically and/or nutritionally demanding process (Sheldon & Verhulst 1996; but see Klasing 1998). Furthermore, relationships between parasitism, immunity and reproduction observed in wild birds and mammals strongly suggest a high energy cost of the immune system (Oppliger *et al.* 1996; Demas & Nelson 1998; Ilmonen *et al.* 2003). Indeed, flea egg production increased when their hosts maintained body mass, in spite of food limitation. It is possible that body composition of the rodents changed and body energy was reduced, although the body mass itself did not decrease (Kam, Khokhlova & Degen 1997). This confirms that host resistance against parasites which, in our case, is related to the immune defence system and is measured via parasite fitness, is not only nutritionally, but also energetically demanding (see review in Lochmiller & Deerenberg 2000).

From an ecological viewpoint, short-term suppression of the immune system may be advantageous for a host because it enables reallocation of resources to functions that support immediate survival during

periods of food limitation (Apanius 1998). However, if food limitation occurs in a predictable manner (e.g. seasonally), it can be advantageous to suppress other functions (e.g. reproduction) rather than immune function. Indeed, the 'winter immunoenhancement hypothesis' was suggested by Nelson & Demas (1996) to explain the increase in the immune parameters during winter reproduction break in small mammals from temperate environments (Lochmiller & Dabbert 1993; Lochmiller *et al.* 1994).

However, the immune system is potentially harmful to the host because a high immune responsiveness increases the risk of immunopathology (such as an autoimmune response). Furthermore, stress, such as food limitation, may activate the hypothalamic–pituitary–adrenal axis and increase plasma levels of glucocorticoid steroids (see Råberg *et al.* 1999 and references therein) which are largely immunosuppressive. Indeed, reduced food availability was shown to elevate corticosterone concentrations and suppress immune function (Demas & Nelson 1998). Råberg *et al.* (1999) argued that the immunosuppression via neuroendocrine mechanisms is adaptive because it allows the avoidance of hyperactivation and subsequent immunopathology during stressful situations.

Increased survival of eggs and larvae of fleas feeding on food-limited hosts suggests that a supposedly weakened immune function of underfed hosts affected parasite fitness in terms of both quantity and quality of offspring. In other words, the increment of flea fitness because of host food limitation was due to both a higher number of eggs produced and higher survival of eggs and of larvae hatched from these eggs. Furthermore, in many flea species, larvae feed not only on organic debris but also on dried blood of the host obtained through the faeces of adults. The host blood obtained by larvae may exert immunological activity against them. This possibility was excluded in our experiments since the larvae were fed by dried bovine blood, but it can be important in a natural situation. As a result, the larvae produced by females exploiting a malnourished immune-suppressed host may have better chances of survival than larvae from females feeding on a well-nourished host with a good body condition.

By contrast with eggs and larvae, survival and developmental time of flea pupae did not depend on the nutritional status of the host. In general, sensitivity of flea pupal stages to various factors is low because pupae are enclosed within the protective microenvironment of the cocoon. Nevertheless, pupal mortality and the rate of development depend mainly on the condition of the larvae, in particular, on their nutritional status (Linardi, DeMaria & Botelho 1997). This strong effect of larval condition can mask the effect of other factors, including those related to nutrition status of a host and on the survival and development of the pupae.

Nevertheless, eggs and larvae produced by females on underfed hosts developed for longer than those

produced by females on hosts with higher food availability. In addition, fleas of the new generation born from parents feeding on strongly food-limited hosts died from starvation earlier than those born from parents feeding on rodents consuming more food. This occurrence was more pronounced in male than in female fleas, confirming our previous findings on lower resistance to starvation in males (Krasnov *et al.* 2002). Longer development time and earlier death due to starvation of fleas whose parents parasitized underfed hosts suggest that although fleas can benefit by exploiting a weakened host in terms of quantity of offspring and one of their quality components (higher survival ability), they can also lose in terms of other quality components of offspring (longer development time). Field observations on the distribution of parasites among hosts differing in body condition indicate that the former option is usually chosen (but see Dawson & Bortolotti 1997), especially given that parasites seem to be able to select between hosts according to fitness considerations (e.g. Krasnov *et al.* 2004 for fleas). For example, higher abundances of parasites were found in hosts with poorer body condition (Whiteman & Parker 2004). However, it is difficult to distinguish between a cause and a consequence in observational studies of host body condition and parasite abundance. Indeed, manipulation of parasite numbers demonstrated that, at least in some host–parasite systems, it was parasitism that caused the decrease in host body condition rather than inferior host body condition that attracted parasites (Neuhaus 2003).

Finally, starving parent fleas survived for longer if their rodent host was underfed. This again can be explained by weakened immunoregulatory and effector responses of underfed rodents. Responses stimulated by ectoparasites involve various components (see Jones 1996). Supposedly lower titres of these components can favour resistance to starvation of an ectoparasite. This can be especially important to fleas for at least two reasons. First, fleas are exposed to strong and/or specific immune attacks because of their intimate association with host blood, the site of major immune defence systems, and skin associated lymphoid tissues (Wikel 1996). Second, digestion in fleas is intracellular and they lack a peritrophic membrane (Vatschenok 1988) which, in many arthropods, separates ingested food from the gut epithelium and, thus, may restrict penetration of ingested immune effector components (Eiseman & Binnengton 1994).

### Acknowledgements

This study was supported by the Israel Science Foundation (grant no. 249/04 for BRK, ISK and AAD). We thank two anonymous reviewers for helpful comments. This is publication no. 177 of the Ramon Science Center and no. 482 of the Mitrani Department of Desert Ecology.

### References

- Anderson, R.M. & May, R.M. (1978) Regulation and stability of host–parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology* **47**, 219–247.
- Apanius, V. (1998) Stress and immune defence. *Stress and Behavior. Advances in the Study of Behavior*, Vol. 27 (eds A.P. Møller, M. Millinski & P.J.B. Slater), pp. 133–153. Academic Press, New York.
- Brown, M.J.F., Loosli, R. & Schmid-Hempel, P. (2000) Condition-dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* **91**, 421–427.
- Cumming, G.S. & Bernard, R.T. (1997) Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**, 309–317.
- Dawson, R.D. & Bortolotti, G.R. (1997) Ecology of parasitism of nestling American kestrels by *Carnus hemapterus* (Diptera, Carnidae). *Canadian Journal of Zoology* **75**, 2021–2026.
- Demas, G.E. & Nelson, R.J. (1998) Photoperiod, ambient temperature, and food availability interact to affect reproductive and immune function in adult male deer mice (*Peromyscus maniculatus*). *Journal of Biological Rhythms* **13**, 253–262.
- De Pedro, N., Delgado, M.J., Gancedo, B. & Alonso-Bedate, M. (2003) Changes in glucose, glycogen, thyroid activity and hypothalamic catecholamines in tench by starvation and refeeding. *Journal of Comparative Physiology B* **173**, 475–481.
- Eiseman, C.H. & Binnengton, K.C. (1994) The peritrophic membrane – its formation, structure, chemical-composition and permeability in relation to vaccination against ectoparasitic arthropods. *International Journal for Parasitology* **24**, 15–26.
- Ilmonen, P., Hasselquist, D., Langefors, A. & Wiehn, J. (2003) Stress, immunocompetence and leucocyte profiles of pied flycatchers in relation to brood size manipulation. *Oecologia* **136**, 148–154.
- Jokela, J., Taskinen, J., Mutikainen, P. & Kopp, K. (2005) Virulence of parasites in hosts under environmental stress: experiments with anoxia and starvation. *Oikos* **108**, 156–164.
- Jones, C.J. (1996) Immune responses to fleas, bugs and sucking lice. *The Immunology of Host–ectoparasitic Arthropod Relationships* (ed. S.K. Wikel), pp. 150–174. CAB International, Wallingford.
- Kam, M. & Degen, A.A. (1993) Energetics of lactation and growth in the fat sand rat, *Psammomys obesus* – new perspectives of resource partitioning and the effect of litter size. *Journal of Theoretical Biology* **162**, 353–369.
- Kam, M., Khokhlova, I.S. & Degen, A.A. (1997) Granivory and plant selection by desert gerbils of different body size. *Ecology* **78**, 2218–2229.
- Khokhlova, I.S., Degen, A.A. & Kam, M. (1995) Body size, gender, seed husking and energy requirements in two species of desert gerbilline rodents, *Meriones crassus* and *Gerbillus henleyi*. *Functional Ecology* **9**, 720–724.
- Klasing, K.C. (1998) Nutritional modulation of resistance to infectious diseases. *Poultry Science* **77**, 1119–1125.
- Krasnov, B.R., Khokhlova, I.S., Fielden, L.J. & Burdelova, N.V. (2001a) The effect of temperature and humidity on the survival of pre-imaginal stages of two flea species (Siphonaptera: Pulicidae). *Journal of Medical Entomology* **38**, 629–637.
- Krasnov, B.R., Khokhlova, I.S., Fielden, L.J. & Burdelova, N.V. (2001b) Development rates of two *Xenopsylla* flea species in relation to air temperature and humidity. *Medical and Veterinary Entomology* **15**, 249–258.
- Krasnov, B.R., Burdelova, N.V., Shenbrot, G.I. & Khokhlova, I.S. (2002) Annual cycles of four flea species

- (Siphonaptera) in the central Negev desert. *Medical and Veterinary Entomology* **16**, 266–276.
- Krasnov, B.R., Khokhlova, I.S., Burdelova, N.V., Mirzoyan, N.S. & Degen, A.A. (2004) Fitness consequences of density-dependent host selection in ectoparasites: testing reproductive patterns predicted by isodar theory in fleas parasitizing rodents. *Journal of Animal Ecology* **73**, 815–820.
- Linardi, P.M., DeMaria, M. & Botelho, J.R. (1997) Effects of larval nutrition on the postembryonic development of *Ctenocephalides felis felis* (Siphonaptera: Pulicidae). *Journal of Medical Entomology* **34**, 494–497.
- Lochmiller, R.L. & Dabbert, C.B. (1993) Immunocompetence, environmental stress, and the regulation of animal populations. *Trends in Comparative Biochemistry and Physiology* **1**, 823–855.
- Lochmiller, R.L. & Deerenberg, C. (2000) Trade-offs in the evolutionary immunology: just what is the cost of immunity. *Oikos* **88**, 87–98.
- Lochmiller, R.L., Vestey, M.R. & McMurray, S.T. (1994) Temporal variation in humoral and cell-mediated immune response in a *Sigmodon hispidus* population. *Ecology* **75**, 236–245.
- Moret, R. & Schmid-Hempel, P. (2000) Survival for immunity: the price of immune system activation for bumblebee workers. *Science* **290**, 1166–1168.
- Nelson, R.J. & Demas, G.E. (1996) Seasonal changes in immune function. *Quarterly Review of Biology* **71**, 511–548.
- Neuhaus, P. (2003) Parasite removal and its impact on litter size and body condition in Columbian ground squirrels (*Spermophilus columbianus*). *Proceedings of the Royal Society of London B* **270**, S213–S215.
- Oppliger, A., Christe, P. & Richner, H. (1996) Clutch size and malaria resistance. *Nature* **381**, 565.
- Poulin, R. (1998) *Evolutionary Ecology of Parasites*. Chapman & Hall, London.
- Råberg, L., Grahn, M., Hasselquist, D. & Svensson, E. (1999) On the adaptive significance of stress-induced immunosuppression. *Proceedings of the Royal Society of London B* **265**, 1637–1641.
- Sheldon, B.C. & Verhulst, S. (1996) Ecological immunology: costly parasite defenses and trade offs in evolutionary ecology. *Trends in Ecology and Evolution* **11**, 317–321.
- Statsoft Inc. (2004) *STATISTICA (Data Analysis Software System), Version 7*. www.statsoft.com.
- Vatschenok, V.S. (1988) *Fleas – Vectors of Pathogens Causing Diseases in Humans and Animals*. Nauka Publishing House, Leningrad (in Russian).
- Whiteman, N.K. & Parker, P.G. (2004) Body condition and parasite load predict territory ownership in the Galapagos hawk. *Condor* **106**, 915–921.
- Wikel, S.K., ed. (1996) *The Immunology of Host–ectoparasitic Arthropod Relationships*. CAB International, Wallingford.

Received 6 January 2005; revised 9 March 2005; accepted 7 April 2005