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Host specificity and foraging efficiency in blood-sucking parasite: feeding patterns of the flea *Parapulex chephrenis* on two species of desert rodents

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Abstract Parasite species can adapt to ecological, behavioral, physiological and biochemical traits of a particular host species. The flea *Parapulex chephrenis* occurs on the spiny mouse *Acomys cahirinus*, but does not occur on a co-existing gerbil, *Gerbillus dasyurus*. To test the hypothesis that the host species affects feeding parameters of a host-specific flea, we studied the feeding rate, rate of blood digestion and resistance to starvation of *P. chephrenis* when feeding on *A. cahirinus* and *G. dasyurus*. We predicted that *P. chephrenis* would: (1) fill its gut with blood faster, (2) digest blood for a shorter time, and (3) survive longer when starved while feeding on its specific host, *A. cahirinus*, than on a non-specific host, *G. dasyurus*. These three responses were observed when *P. chephrenis* fed on the different hosts and, consequently, our predictions were supported. Twenty percent of fleas filled their midgut after feeding for 10 min on *A. cahirinus* but this occurred only after 25 min on *G. dasyurus*. The middle stage of blood digestion was significantly shorter in all fleas feeding on *A. cahirinus* than in fleas feeding on *G. dasyurus*. Flea survival was shorter when feeding on *G. dasyurus* than when feeding on *A. cahirinus* at 25°C, but no difference in survival time was found at 15 or 20°C. Both *A. cahirinus*, the specific host, and *G. dasyurus*, the non-specific host, coexist in rocky habitats, yet *P. chephrenis* occurs on one rodent and not the other. The absence of *P. chephrenis* on *G. dasyurus* in nature and the decreased foraging efficiency when feeding on this species in the laboratory suggests that some physiological and biochemical differences between hosts can lead to sharp ecological differences in host-parasite relationships.

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Introduction

Parasites should make the same decisions that every animal has to make regarding resource acquisition and fitness reward (Sukhdeo and Sukhdeo 1994). They can maximize their foraging efficiency and, consequently, reproductive success by selection of appropriate hosts. Appropriateness of a host is determined, in turn, by the degree of opening or closing of host-encounter and host-compatibility filters (Euzet and Combes 1980; Combes 1991, 2001). An encounter filter excludes all potential hosts that a parasite cannot meet for behavioural or ecological reasons, whereas a compatibility filter excludes species in which a parasite cannot survive and develop due to morphological, physiological or immunological constraints. These filters are, therefore, responsible for the formation of host ranges. The breadth of the host range, or the degree of host specificity, varies between and within parasite taxa (Combes 2001). Furthermore, the level of host specificity may reflect the co-evolutionary history of the relationship between a particular host species and a particular parasite species. In highly specific parasites, a species can become adapted to the ecological, behavioral, physiological and biochemical traits of a particular host species or group of species (Ward 1992; Poulin 1998).

Fleas (Siphonaptera) are parasites of higher vertebrates, being most abundant and diverse on small mammals. They usually alternate between periods when they occur on the body of their hosts and periods when they occur in the hosts' burrows or nests. In most cases, egg, larval and pupal development take place entirely

off-host. The larvae are usually not parasitic and feed on organic debris in the burrow and/or nest of the host. The degree of association between a particular flea species and a particular host species varies from highly host-specific to host-opportunistic fleas (Marshall 1981).

The physical and chemical properties of blood are known to be important characteristics of a host to which a host-specific flea is adapted (Marshall 1981). However, studies of the effect of feeding fleas on different host species are scarce and indirect (e.g., Seal and Bhattacharji 1961; Prasad 1969). Moreover, in most laboratory studies of the rate of blood digestion, fleas were fed on laboratory animals rather than on their natural hosts. For example, wild rodents were used as hosts in only 8 of 27 studies cited by Vatschenok (1988), while the others used mainly laboratory mice, rats, hamsters and guinea pigs.

In the flea assemblages of rodents in southern Israel, the occurrence of some flea species was dependent on both host species and habitat type, while other fleas were strictly host-dependent even though their hosts occurred in close contact with other potential hosts (Krasnov et al. 1997, 1998). Such an example of host-flea relations included *Parapulex chephrenis*. This flea was found on two spiny mouse species (*Acomys cahirinus* and *Acomys russatus*), which occur mainly in rocky habitats, but was absent on *Gerbillus dasyurus* and *Sekeetamys calurus*, gerbils that co-exist with the spiny mice. When *A. cahirinus* was occasionally recorded in other habitats, it was also parasitized by *P. chephrenis*. Moreover, *P. chephrenis* was able to discriminate between different host species, selecting *A. cahirinus* over *G. dasyurus* in host-choice experiments (Krasnov et al. 2002a).

We hypothesized that the host species affects feeding parameters of a host-specific flea. To test this hypothesis, we studied the feeding rate, rate of blood digestion and resistance to starvation after a single blood meal when *P. chephrenis* fed on either *A. cahirinus* or *G. dasyurus*. We predicted that *P. chephrenis* will engorge faster, digest blood for a shorter time and survive longer if starved when feeding on *A. cahirinus* than on *G. dasyurus*.

Materials and methods

The parasite

Fleas were obtained from our laboratory colonies started in 1999 using field-collected specimens from *A. cahirinus*. An individual rodent host was placed in a glass cage (60×50×40 cm) that contained a steel nest box with a screen floor and a pan containing a mixture of sand and dried bovine blood (larvae nutrient medium) on the bottom. We infested a host with 6–8 newly emerged fleas (initially, with field collected fleas). Gravid female fleas left the host and deposited eggs in the substrate and bedding material in the nest box. Once in 2 weeks, we collected all substrate and bedding material from the nest box and transferred it into an incubator (FOC225E, Velp Scientifica, Milan, Italy) where flea development and emergence took place at 25°C and 75% relative humidity. To assess the welfare of our flea colonies, we randomly collected ten fleas once a month and examined their body condition (egg formation in female oviducts, development of fat tissue in the abdomen cavity, engorgement of the midgut with blood) under a light microscope. No adverse signs were found. Colonies of fleas were maintained at 25°C and 75% RH with a photoperiod of 12:12 h (light:dark). We used both newly emerged and adult fleas. Newly emerged fleas did not feed from emergence until the experimental treatments. Adult fleas were on *A. cahirinus* once, 24 h after emergence, and then were fed only during the experiments.

The host

We used 20 adult male *A. cahirinus* from our laboratory colony. Progenitors of the colony were captured at the Ramon erosion cirque, Negev Highlands, Israel (30°35′N, 34°45′E). The rodents were maintained in glass cages (60×50×40 cm) at 25°C with a 12:12 photoperiod, with dried grass as bedding material. They were offered millet seed and alfalfa (*Medicago* sp.) ad libitum, and commercial cat chow or meal worms once a week. No water was available as the alfalfa supplied enough for the rodents' needs.

The level of infestation by fleas of rodents in our colonies was approximately 75% of the natural level of flea infestation (Krasnov et al. 1997). No adverse effects (e.g., on body mass and food intake) on infested rodents were observed. The experimental design was found to meet the requirements of the 1994 Law for the Prevention of Cruelty to Animals (Experiments on Animals) of State of Israel by the Ben-Gurion University Committee for the Ethical Care and Use Animals in Experiments (License IL-19-04-2001).

Feeding rate experiments

The rate of gut engorgement of *P. chephrenis* was determined when feeding on *A. cahirinus* and *G. dasyurus*. Measurements were done at 25°C and a relative humidity of 70%. The rodents were placed in wire mesh (5×5 mm) tubes (10 cm long and 2 cm diameter) that limited movement and did not allow self-grooming. These tubes were placed in individual white plastic pans and ten fleas, which had been starved for 1–2 days, were placed on each rodent. We then collected the fleas after they had been on their host for 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55 or 60 min. The fur of the rodent was brushed several times using a tooth-brush until all ten fleas were recovered. We assessed the level of flea midgut engorgement by examination of each flea under a light microscope (without dissection) and using the following classification: (1) low, less than 30% of the midgut filled with blood; (2) medium, 30–70% of the midgut filled with blood; and (3) high, more than 70% of the midgut filled with blood. Treatments, therefore, differed in terms of the host species (*A. cahirinus* or *G. dasyurus*), flea sex (male or female), flea age (newly emerged or adult) and the time the fleas were permitted to stay on a host. Each treatment was replicated 3 times, totaling 2 hosts × 2 sexes x 2 ages × 12 time periods× 3 replicates = 288 experiments. The order of treatment was selected randomly. Feeding rate was evaluated as a percentage of fleas with a highly engorged midgut after a timed period of feeding.

Digestion rate experiments

Newly emerged and adult fleas fed on *A. cahirinus* or *G. dasyurus* for 2 h. After consuming blood, the fleas were placed individually into 20 ml glass vials, each covered by a 5×5 cm nylon screen, which were then placed into refrigerated incubators (FOC225E, Velp Scientifica, Milan, Italy) maintained at 25°C and 92% relative humidity. Relative humidity was controlled using a saturated solution of potassium nitrate (Winston and Bates 1960). Temperature and humidity were monitored using a Fisherbrand Traceable Humidity/Temperature Pen with Memory (Fisher Scientific International, N.J., USA).

We examined the flea midguts under light microscopy every hour and estimated blood digestion status following the modified

classification of Ioff (1949) used in our previous studies (Krasnov et al. 2002b), namely: (1) early: midgut stretched and fully filled with light scarlet or dark red blood; (2) middle: the contour of the midgut is jagged and the content is dark brown or black; and (3) late: midgut contains only remnants of digested blood or is empty. We measured the duration of each stage. In total, we examined blood digestion in 145 newly emerged and 84 adult fleas.

Survival when starved

Newly emerged and adult male and female fleas (separately) fed on *A. cahirinus* and *G. dasyurus* for 1 h. We selected only fleas whose midgut was engorged with blood, which was confirmed by examining them using light microscopy. The fleas were placed individually into 20 ml glass vials, each covered with a 5×5 cm nylon screen, and assigned randomly to one of three temperature regimes (15, 20 and 25°C) and 92% relative humidity. There were 24 experimental treatments (2 host species× 2 flea sexes × 2 flea ages × 3 air temperatures) replicated 10 times each. Vials were checked twice a day (at 0800 and at 2000 hours) and the death of each flea was confirmed by examination using light microscopy.

Data analysis

Arcsine transformation of the percentage of fleas with an engorged midgut yielded a distribution that did not deviate significantly from normality (Shapiro-Wilks tests, NS). Therefore, we used parametric statistics. We analyzed this parameter using a 4-way ANOVA with host species, flea sex, flea age and feeding time as independent variables.

Digestion rate was measured as the time between consecutive digestion stages. The distribution of time variables demonstrated a significant deviation from normality (Shapiro-Wilks $W = 0.75–0.94$, $P < 0.01$). Log- and square-root transformations of these variables did not lead to a normal distribution (Shapiro-Wilks $W = 0.87–0.97$, $P < 0.01$). Consequently, we applied non-parametric statistics, namely Mann-Whitney tests for paired comparisons (within digestion stage between host species, flea sex and flea age) and Friedman ANOVA for multiple comparisons (among duration stages within host species, flea sex and flea age).

Survival of fleas did not deviated from normality (Shapiro-Wilks tests, NS) and was analyzed using 4-way ANOVAs with host species, flea sex, flea age and ambient temperature as independent variables. When parametric statistics were used, Tukey's honest significant difference (HSD) test was applied for all multiple comparisons, and a *t*-test was applied for paired comparisons. Because we examined the correlations of two-host species, both sexes and two ages as well as three air temperatures (in resistance to survival experiments) to a single dependent variable, we avoided an inflated type I error by Bonferroni adjustments of α. Significance is recorded at the adjusted level. Data are presented as means ± SE. Figures represent non-transformed data.

Results

Feeding rate

Host species and feeding time affected the rate of midgut engorgement similarly in both male and female, newly emerged and adult fleas (ANOVA, $F_{1,192} = 9.6$, $P = 0.002$ for host species effect; $F_{11,192} = 35.2$, $P < 0.0001$ for feeding time effect; $F_{1,192} = 4.5$, NS for sex effect and $F_{1,192} = 6.2$, NS for age effect). The interactions of all independent variables were not significant, except for the interaction between host species and feeding time (ANOVA, $F_{1,192} = 8.5$, $P = 0.002$).

The percentage of fleas with an engorged midgut did not differ significantly between those fed on different hosts after 5 and >20 min feeding (Tukey's HSD tests, NS). However, the percentage of fleas with an engorged midgut was significantly higher when feeding on *A. cahirinus* than on *G. dasyurus* after 10, 15 and 20 min of feeding (Tukey's HSD tests, $P < 0.0001$). Furthermore, the mean proportion of fleas with an engorged midgut attained 20% after 10 min of feeding on *A. cahirinus* and then steadily increased (Fig. 1). In contrast, an average of 20% of fleas with an engorged midgut was attained after 25 min feeding on *G. dasyurus* (Fig. 1) and only then was a steady increase observed.

Digestion rate

In newly emerged and adult fleas feeding on *A. cahirinus*, the early stage of blood digestion was shortest, and the middle stage was shorter than the late stage (Friedman ANOVA $\chi^2_2 = 17.55–40.58$, $P < 0.001$; Table 1). The early stage was also the shortest in both newly emerged and adult fleas feeding on *G. dasyurus* (Friedman ANOVA $\chi^2_2 = 12.80–23.44$, $P < 0.001$; Table 1), although no difference in the duration of middle and late stages of blood digestion was found in these fleas (Friedman ANOVA $\chi^2_2 = 3.90–4.33$, NS).

The age difference in the rate of blood digestion occurred for the early stage in both males and females feeding on either *A. cahirinus* or *G. dasyurus*, with the shorter duration of digestion in adult fleas (Mann-Whitney tests, $Z = 2.83–4.08$, $P < 0.001$; Table 1). No significant age difference in the duration of middle and late stages of blood digestion was found in any treatment. Sex difference in the rate of blood digestion was

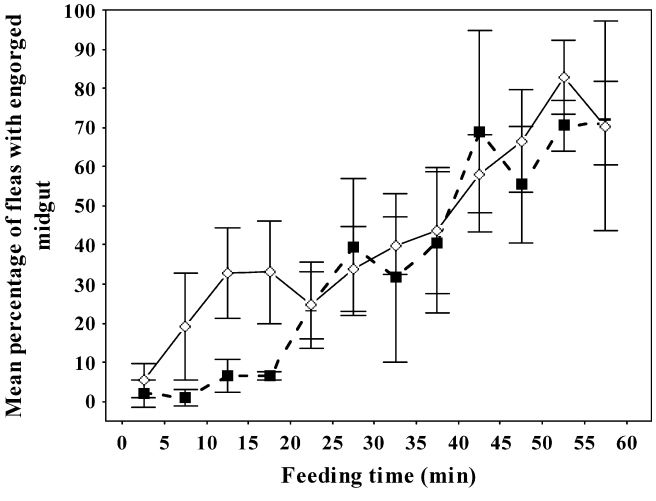

Fig. 1 The percentage of fleas with an engorged midgut after different periods of feeding on *Acomys cahirinus* (*solid line*) or *Gerbillus dasyurus* (*dashed line*)

Table 1 Mean duration (±SE) of early, middle and late stages of blood digestion in *Parapulex chephrenis* feeding on *Acomys cahirinus* or *Gerbillus dasyurus*

Host species	Flea age	Stage	Duration (h)
Acomys cahirinus	Newly emerged	Early	7.59 ± 0.24
		Middle	9.86 ± 0.39
		Late	14.06 ± 0.82
	Adult	Early	5.53 ± 0.53
		Middle	9.17 ± 0.59
		Late	13.88 ± 2.20
Gerbillus dasyurus	Newly emerged	Early	8.58 ± 0.63
		Middle	12.38 ± 0.64
		Late	10.67 ± 0.61
	Adult	Early	4.69 ± 0.75
		Middle	15.37 ± 0.91
		Late	17.40 ± 2.65

found only in newly emerged fleas feeding on *A. cahirinus*. The middle, but not early and late, stage of blood digestion was significantly shorter in males than in females (8.15 ± 0.77 h versus 10.60 ± 0.40 h, respectively, Mann-Whitney test, $Z = 2.68$, $P < 0.01$). Adult males and females, independently of host species, as well as newly emerged males and females feeding on *G. dasyurus*, digested blood at the same rate, all else being equal (Mann-Whitney tests, $Z = -1.93$–0.91, NS).

The effect of host species on the rate of blood digestion was significant only for the middle stage of blood digestion. This stage was shorter in all fleas feeding on *A. cahirinus* than that on *G. dasyurus* (Mann-Whitney tests, $Z = 2.34$–3.72, $P < 0.001$; Fig. 2). The duration of both early and late stages of blood digestion did not differ significantly in relation to host species, all else being equal (Mann-Whitney tests, $Z = -2.07$–1.44, NS).

Resistance to starvation

Flea sex, host species and air temperature affected the duration of flea survival (Table 2). Furthermore, three 2-way interactions were significant (Table 2). No difference in time of survival when starved was found between newly emerged and adult fleas (ANOVA, $F_{1,216} = 1.13$, $P = 0.3$).

In general, females survived longer than males at all temperatures and when feeding on both host species (Tukey's HSD tests, $P < 0.001$), except for the fleas feeding on *A. cahirinus* maintained at 25°C. In this case, no between-sex difference in survival time was found (Tukey's HSD test, $P = 0.9$). Within sex, survival time during starvation did not differ between 15 and 20°C (Tukey's HSD tests, $P = 0.4$–0.9), but was significantly lower at 25°C (Tukey's HSD tests, $P < 0.001$). This was true for all treatments except for males feeding on *A. cahirinus* whose time of survival did not differ at any air temperature (Tukey's HSD tests, $P = 0.7$–0.9).

The effect of host species on the time of survival when starved was significant at 25°C only. Both males and females survived longer when feeding on *A. cahirinus* than on *G. dasyurus* ($t = 5.31$, $df = 38$, $P < 0.0001$ for males, and $t = 2.81$, $df = 38$, $P < 0.001$ for females, Fig. 3).

Discussion

P. chephrenis engorged quicker, digested blood faster and survived longer when feeding on *A. cahirinus*, a specific host, than on *G. dasyurus*, a non-specific host. Consequently, our predictions were supported.

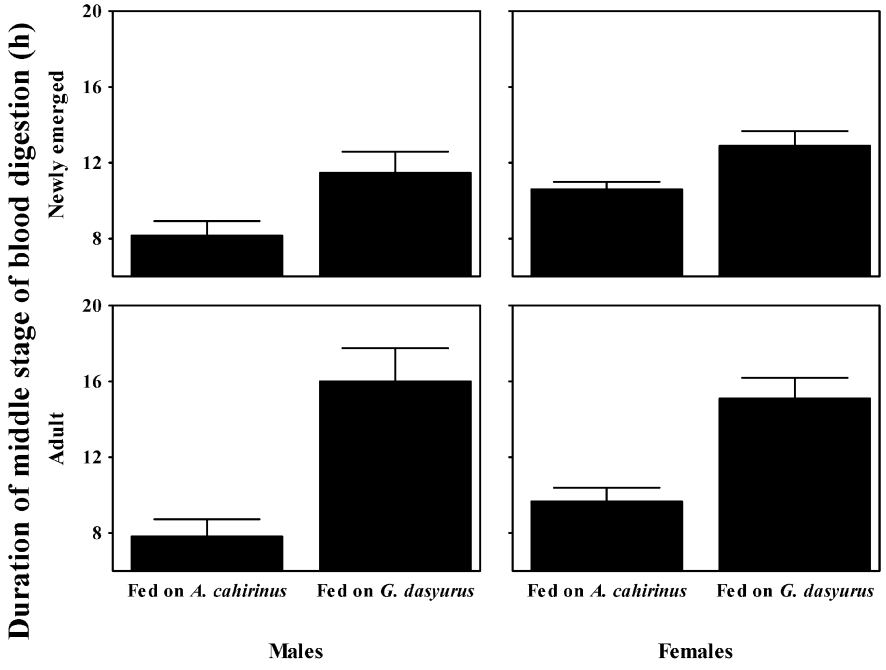

Fig. 2 The duration of the middle stage of blood digestion in newly emerged and adult *Parapulex chephrenis* feeding on *A. cahirinus* or *G. dasyurus*

Table 2 Summary of significant effects ($P < 0.001$) in 4-way ANOVA of the duration of survival in newly emerged and adult males and females of *P. chephrenis* at different air temperatures and feeding on *A. cahirinus* or *G. dasyurus*

	Df effect	SS effect	MS effect	*F*
Sex	1	160.07	160.07	48.23
Temperature	2	353.76	176.90	53.30
Host species	1	28.02	28.02	8.44
Temperature×Host species	2	32.56	16.28	4.91
Temperature×Age	2	258.07	129.04	38.88
Temperature×Sex	2	75.91	37.95	11.44
Error	216	716.80	3.32	

Feeding rate

In general, most flea species in previous studies were not strictly specific in relation to host blood (Vatschenok 1988). Some flea species, even with a relatively narrow host range in nature, fed on hosts of different taxonomic affinities in the laboratory. For example, mammalian fleas were able to consume mammalian, avian and even reptilian blood (Sgonina 1935, Fox et al. 1966, Vatschenok et al. 1976), although their fecundity was affected by the host species. However, this is not the case for other fleas. For example, *Ceratophyllus styx*, a flea of the sand martin *Riparia riparia*, did not consume the blood of non-specific hosts (Faasch 1935). The difference in the feeding rate of a flea on different hosts could be a result of the morphology of the mouthparts that can penetrate the skin of some hosts but not others (Marshall 1981; Vatchenok 1988). In addition, the feeding rate in fleas can vary with host behaviour: the feeding rate of *Echidnophaga gallinacea* increased when the domestic chicken, its host, became excited and its peripheral blood supply increased (Suter 1964). The above examples demonstrate the effect of host species on flea foraging, although most cited studies lack quantitative data.

The time from contact with the host to the beginning of feeding, which can be considered as the latency in foraging decision, was less in *P. chephrenis* feeding on its specific host than on its non-specific host. This supported our previous findings that *P. chephrenis* was able to distinguish between *A. cahirinus* and *G. dasyurus* when it selected *A. cahirinus* over *G. dasyurus* in host-choice studies (Krasnov et al. 2002a). Nonetheless, starving fleas began their blood meal even from a non-specific host, albeit it took longer to make this decision. *P. chephrenis* has been shown to prefer a host attacking strategy resembling that of a sit-and-wait predator rather than actively searching for a host (Krasnov et al. 2002a). This strategy can be profitable when parasitizing a social host such as *A. cahirinus* (Dasrkaya and Besedina 1961; Krasnov et al. 2002a). Such a behaviour may explain why *P. chephrenis*, when forced to feed on *G. dasyurus*, began feeding after an "uncertainty" period rather than jump off the non-specific host and search for a more suitable host.

Nevertheless, the time taken by most fleas to reach the fully fed stage was the same. This means that fleas feeding on gerbils started slowly but were then able to feed faster than on spiny mice so that after 20 min they had caught up with their conspecifics on the other host species. However, in our experiments fleas fed in the absence of host grooming. We suggest that the short latency of feeding is crucial for a flea as the latency of a host grooming effort aimed at removing fleas seems to be short (e.g., Eckstein and Hart 2000). In other words, a flea that begins to feed sooner would be less likely to be removed from a host by grooming before feeding completion.

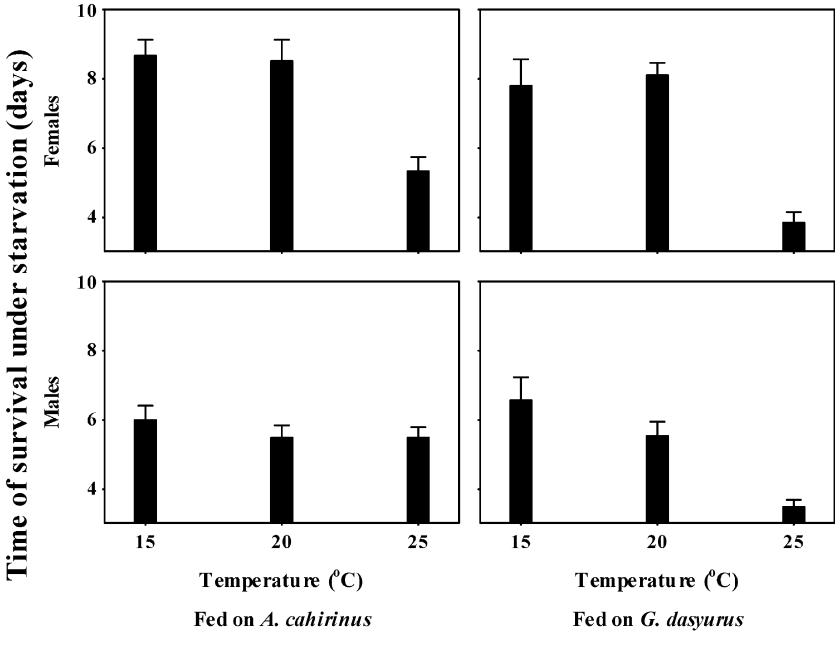

Fig. 3 The survival time when starved of newly emerged and adult *P. chephrenis* after feeding on *A. cahirinus* or *G. dasyurus* at three different air temperatures

Blood digestion

The rate of blood digestion by fleas is affected by host species. For example, *Xenopsylla skrjabini* took longer to digest the blood of laboratory guinea pigs and house sparrows (*Passer domesticus*) than the blood of its natural host, the great gerbil *Rhombomys opimus* (Vatschenok 1988). This between-host difference in digestion time could be due to between-host variability in the resistance of blood cells (both red and white) to the hemolytic activity of the flea digestive system (Vatschenok 1988). However, overall digestion time of blood from a natural host can be longer than that from laboratory animals because of different responses of digestion at different digestion stages (e.g., in *Xenopsylla cheopis* and *Nosopsyllus fasciatus*; Vatschenok et al. 1976). For example, the time taken for the hemolysis of hamster blood in the midgut of *X. cheopis* was shorter than that of mouse blood, however, blood hemolysis was only a part of the digestive process, and the overall digestion time for hamster blood was longer than that of mouse blood.

In this study, the difference between the digestion of blood from *A. cahirinus* and *G. dasyurus* occurred at the middle stage, which includes the hemolysis and digestion of blood to hematin, the final product of blood digestion (Vatschenok 1988). The duration of the early and late stages of digestion did not differ between hosts. Two later stages reflected mechanical rather than biochemical processes (midgut filling and release of the undigested remnants and final products, respectively). The increase in time of the middle stage of blood digestion when feeding on *G. dasyurus* may indicate that the digestive system of *P. chephrenis* is less adapted to this host than to *A. cahirinus*.

A sex-related difference in digestion rate has only been reported for *X. cheopis* (Vatschenok et al. 1976), with males requiring more time than females. We failed to confirm this finding. The duration of the middle stage of digestion in *P. chephrenis* was shorter in males than in females. Furthermore, sex differences in digestion rate occurred only in newly emerged fleas. Age differences in the rate of digestion found in this study supported previous findings, as a shorter duration of digestion in adult fleas was reported for *Pulex irritans*, *Xenopsylla conformis*, *Citellophylus tesquorum*, *Leptopsylla segnis*, *Neopsylla setosa*, *Ctenophthalmus golovi*, *Nosopsyllus laeviceps* (Brukhanova et al. 1978; Vatschenok 1988).

Survival when starved

Resistance to starvation in response to different environmental factors has been studied in many flea species, but the effect of host species has not been examined (Marshall 1981; Krasnov et al. 2002c, 2002d). In general, fleas survive longer with lower air temperatures and higher relative humidities (e.g., Silverman et al. 1981; Cooke 1999). Furthermore, newly emerged fleas are more resistant to starvation than adult fleas and females are more resistant than males (e.g., Edney 1945). Our results agreed with these findings except that we did not find an age effect on the time of survival when starved.

Higher resistance to starvation at a lower temperature can explain why we did not find between-host differences in time of survival at 15 and 20°C. The metabolic processes of fleas slow down at lower temperatures and, consequently, the response to feeding on a non-specific host is less expressed. At higher air temperatures, fleas feeding on a specific host survived longer, demonstrating that *A. cahirinus* is a more suitable host for *P. chephrenis* than *G. dasyurus*.

Foraging efficiency, fitness consequences and host specificity

The results of this study showed that foraging by *P. chephrenis* was more efficient on the specific than non-specific host in that the feeding rate was higher and resistance to starvation was greater when the flea was on *A. cahirinus* than on *G. dasyurus*. If the host is considered as a habitat for a flea, higher foraging efficiency can be one of the factors that determine the selection of the appropriate habitat/host. However, the evolutionary test for the appropriateness of a particular habitat/host is the fitness reward for the selection of that habitat/host. That is, the selection of the most appropriate host should provide the best fitness output in terms of life-time fecundity (Rosenzweig 1981; Lomnicki 1988). In previous studies, the egg production of female *P. chephrenis* was higher when feeding on *A. cahirinus* than on *G. dasyurus* (Krasnov et al. 2002a). A decline in the reproductive rate in fleas feeding on non-preferred hosts has been reported for other flea species. For example, the rat fleas *X. cheopis* and *Xenopsylla astia* failed to reproduce when fed on humans (Seal and Bhattacharji 1961). Fecundity and egg hatchability in *X. cheopis* were higher when the fleas fed on *Rattus rattus* than on *Bandicota bengalensis* (Prasad 1969).

The results of this study support the hypothesis of the coevolution of rodents and their fleas (Traub 1985). Higher feeding rate, shorter duration of digestion and greater resistance to starvation in *P. chephrenis* after feeding on a specific host in comparison with a non-specific host are consequences of this coevolution. Other parasitic arthropods also show evidence of coevolution. For example, the longevity of the bed-bug *Cimex lectularius* and the louse *Pediculus humanus* (both parasitic on humans) was shorter when they fed on laboratory mice or guinea pigs than on their usual host (Johnson 1940; Krynski et al. 1952).

In conclusion, the increase in feeding rate, digestion rate and resistance to starvation in *P. chephrenis* when feeding on a specific host in comparison with a non-specific host demonstrated the operation of a compatibility filter. This filter symbolizes gene or gene combinations implied in the compatibility of a specific

host-parasite system and the degree of its opening is determined by the genomes of both the parasite and the host (Combes 2000). Although *P. chephrenis* was able to consume the blood of *G. dasyurus*, the decrease in feeding rate, digestion rate and resistance to starvation suggest that the opening of the compatibility filter for the *P. chephrenis*-*G. dasyurus* relationship is smaller than that for the *P. chephrenis*-*A. cahirinus* relationship. However, the encounter filter for both of these relationships is opened because both host species occupy the same rocky habitats. The absence of *P. chephrenis* on *G. dasyurus* in nature and the decreased foraging efficiency when feeding on this species in the laboratory suggests that even subtle differences in the degree of opening of the compatibility filter on the physiological scale can lead to sharp differences in host-parasite relationships at an ecological level.

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