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ARTHROPODS AND MEDICAL ENTOMOLOGY - ORIGINAL PAPER

Intraspecific variation of body size in fleas: effects of host sex and flea phenology

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Abstract
We investigated the effects of host sex and flea phenology (estimated as periods of high versus low abundance) on individual body size in four fleas of small mammals. *Amalaraeus penicilliger* and *Ctenophthalmus uncinatus* are ectoparasites of the bank vole *Myodes glareolus*, whereas *Doratopsylla dasycnema* and *Palaeopsylla soricis* are ectoparasites of the common shrew *Sorex araneus*. We found significant effects of host sex and phenology on the body size of all flea species, although there was no general trend in the directions of these effects. Larger *A. penicilliger* were found on female hosts, whereas larger *P. soricis* were found on male hosts. In the remaining species, larger fleas were collected from male hosts during periods of high abundance (male *C. uncinatus* and female *D. dasycnema*) and from female hosts during periods of low abundance (male *C. uncinatus*). Regarding phenology, larger fleas were recorded during periods of either high (*A. penicilliger*, *C. uncinatus*, *D. dasycnema*) or low (*C. uncinatus*, *P. soricis*) abundance, but this depended on flea and/or host sex. We conclude that the directions of the host sex and phenology effects varied between flea species. Furthermore, the direction of the host sex effect was mediated by the effect of phenology and vice versa.

Keywords Body size · Fleas · Host sex · Peak abundance · Flea phenology

Introduction

Body size is a fundamental species property, associated with a variety of physiological, behavioural, and ecological traits (see reviews in Peters 1983; Brown 1995). It is thus not surprising that numerous studies have dealt with the associations between body size and various traits. Body size variation in these studies was mostly considered at an interspecific rather than an intraspecific level. However, every species demonstrates individual variation in body size. It has recently been shown that intraspecific phenotypic variation, including variation in body size, may have a profound influence on a number of population and community processes (Bolnick et al. 2011; Xu 2016; Griffiths et al. 2018). One of the reasons for this is that the body size of an individual is strongly associated with its fecundity (Honěk 1993), longevity (Miller et al. 2002), and intra- or interspecific competitive abilities (Gribbin and Thompson 1990).

Intraspecific variation in body size can be caused by both intrinsic (e.g., genetic) and extrinsic (i.e., environmental) factors (e.g., Aragón and Fitze 2014). In holometabolous insects, many extrinsic factors influence the body size of imagoes indirectly via their direct effect on larvae. Among these factors, ambient temperature (Blanckenhorn 1997; Angilletta et al. 2004), diet quality and quantity (Nijhout 2003), and larval density (Schneider et al. 2000) are the strongest. These factors are interrelated because, for example, larval diet quantity is obviously negatively correlated with larval density. In addition, an insect's adult body size may be affected by maternal age (Najafpour et al. 2018) and maternal diet quality (Zirbel and Alto 2018).

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In ectoparasitic arthropods, an important factor affecting individual body size is the affinity of a maternal host (i.e., a host from which parent ectoparasites extract the resources and transform them into offspring) in terms of its species, sex, or age. This is because a host represents either maternal diet (e.g., for fleas) or larval diet (e.g., for chiggers) or both (e.g., for lice). Consequently, the body sizes of conspecific ectoparasites may differ between individuals produced by mothers that exploited hosts of different species, sexes, or ages. Several experimental studies have demonstrated that this indeed may be the case. For example, Khokhlova et al. (2014) reported the association between the offspring body size of fleas and the phylogenetic distance of the maternal rodent host from a flea's principal host, with new imagoes being larger if their maternal hosts were phylogenetically distant from the principal host. This was the result of the trade-off between the offspring's quantity and quality because the number of new imagoes demonstrated the opposite trend. Female fleas fed on male rodents produced larger offspring than those fed on female rodents, presumably due to the immunosuppressive effect of androgens (Folstad and Karter 1992), although this pattern was mainly found in male, but not female, offspring (Khokhlova et al. 2010a; Liberman et al. 2013). The effect of rodent host age on flea body size was manifested by the largest offspring produced by females fed on senescent hosts (having deteriorated immune systems; Pelletier et al. 2005) as compared with those fed on the juvenile or adult hosts (Liberman et al. 2013). All these patterns have been found in controlled laboratory experiments with laboratory colonies of fleas and rodents, whereas the effect of, for example, host sex can differ in the wild (Horne et al. 2017). To the best of our knowledge, however, no field study of individual variation in insect ectoparasite body size has been carried out.

The body size of conspecific arthropods occurring in the same region may vary seasonally (e.g., Laska et al. 2017). The reasons behind this may include the responses to variation in ambient temperature (Rodrigues and Moreira 2004), food availability to larval stages (Peat et al. 2005), and/or reproductive output (Khokhlova et al. 2014). However, identification of seasons according to calendar (i.e., summer, winter, etc.) lacks a biological component because, for example, the range of preferred temperatures triggering reproduction varies among species (e.g., Krasnov et al. 2002). Instead, from a biological perspective, identification of periods of circannual variation in species traits should be considered via phenology, i.e., the timing of life-history events, estimated as, for example, peak activity (i.e., periods of high abundance) (Gillespie et al. 2017).

Here, we investigated the effect of host sex and flea phenology on individual body size in four flea species parasitic on small mammals in north-western Russia. *Amalaraeus penicilliger* (Grube, 1851) and *Ctenophthalmus uncinatus* (Wagner, 1898) are common ectoparasites of the bank vole *Myodes glareolus* (Schreber, 1780), whereas *Doratopsylla dasycnema* (Rothschild, 1897) and *Palaeopsylla soricis* (Dale, 1878) are common ectoparasites of the common shrew *Sorex araneus* Linnaeus, 1758. Fleas are holometabolous insects that are strictly haematophagous at their imago stage and detritivorous at the larval stage. In a majority of flea species (including all species considered in this study), adults alternate time periods between residing on a host's body and inhabiting a host's burrow/nest, whereas pre-imaginal development takes place predominantly in the host's burrow/nest. Upon emergence, new imagoes usually wait for a host to visit its burrow and then attack (Krasnov 2008). Consequently, we assumed that fleas collected from an individual host were produced by the mother's exploitation of this host, and thus, their body size was mainly determined by the maternal diet quality (Khokhlova et al. 2014).

We predicted that the effect of host sex on flea body size would conform to the results obtained in the laboratory experiments (Khokhlova et al. 2010a). In other words, male fleas collected from male hosts would be larger than male fleas collected from female hosts, whereas the body size of female fleas would not differ in dependence on host sex. This is because (a) male hosts represent generally better food source for fleas due to presumably lower immunocompetence and (b) male fleas are more sensitive to host sex than female fleas (Khokhlova et al. 2010a). Regarding the effect of flea phenology, larger fleas collected during periods of high abundance would indicate better conditions of larval nutrition, whereas smaller fleas during these periods would indicate either the effect of larval intraspecific competition (Khokhlova et al. 2010b) or a trade-off between the number and size of the offspring (Lack 1947) or both.

Methods

Data collection and body size measurements

We measured fleas deposited in a flea collection of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg. These fleas were collected from *M. glareolus* and *S. araneus* sampled at 13 sites in the vicinity of the town of Oskuy (59.277709° N, 32.089136° E) situated in the northern part of the Ilmen-Volkhov Lowland (Novgorod region, Russia) from 1999 to 2002 (details can be found in Vashchonok and Tret'yakov 2003, 2004). Small mammals were sampled every month (except February, July, and October 2000) using snap-traps deposited in two to three lines of 50–100 traps per site for 3 to 5 days and checked twice a day. Sex and age (based on general appearance) but not reproductive state of each animal was recorded. Each animal was placed into an individual linen bag immediately after capture, transferred to a field laboratory, and thoroughly examined for ectoparasites under a light microscope or magnifying glass. Fleas were collected with forceps, while the mammal was brushed with a toothbrush, and were placed and stored in 70% ethanol. Detailed information on distribution of various flea species on various host species as well as on seasonal abundance of fleas can be found elsewhere (Balashov et al. 2002; Vashchonok and Tret'yakov 2003, 2004, 2005; Vashchonok 2006).

Prior to measurements, flea specimens were soaked in 10% sodium hydroxide until all muscles dissolved (visual examination under a light microscope). Then, fleas were transferred to Petri dishes filled with distilled water and kept there for 3 h, while the water was changed every hour. Finally, each specimen was partly desiccated by soaking it in 50% ethanol for 1 h. All fleas were measured by the same person (N.V.S.) using the light microscope Micromed 3 ver. 3-20M (CIT NELIAN, Moscow, Russia) with a 4×/0,11 lens and digital camera MC-HD2 (LOMO-Microsystems, Saint Petersburg, Russia). The measurements were done on-screen using the software "MC-View" V1.9_20180907 (LOMO-Microsystems, Saint Petersburg, Russia) (see Fig. S1 in Electronic Supplementary Material). We measured maximal body length to the nearest 0.001 mm. Each measurement was done twice with the image being rotated 180 degrees between each measurement to reduce error. Then, the two measurements of the same specimen were averaged. In total, we measured body size in 753 males and females of four flea species (from 157 to 225 individuals per species).

Data analyses

We used data on body size of fleas collected from adult hosts only. The body size variable distribution (within flea species and flea sex) did not differ from normality (Kolmogorov-Smirnov tests; $d = 0.06–0.13$ $p > 0.20$ for all). To test for the effects of host sex and phenology, as well as for the interaction between these factors, on the body size of an individual flea, we used generalized linear mixed-effects models (GLMM) implemented in the "nlme" package (Pinheiro et al. 2019) implemented in R (R Core Team 2019). We evaluated phenology via periods of high or low abundance (e.g., Gillespie et al. 2017). Consequently, an explanatory variable describing phenology was introduced into the models as a dichotomous nominal variable with two levels. For each flea species, periods of high abundance were determined based on the direct observations in the study area and published elsewhere (Vashchonok and Tret'yakov 2003, 2004). Periods of high abundance for fleas parasitic on *M. glareolus* were February–April for *A. penicilliger* (on average, 1.5–4 fleas per infested individual vs 0–0.2 fleas per infested individual in other months) and April for *C. uncinatus* (on average, 2–3 fleas per infested individual vs 0–0.5 fleas per infested individual in other months) (Vashchonok and Tret'yakov 2003). For fleas parasitic on *S. araneus*, periods of high abundance were April, June, and September–October for *D. dasycnema* (on average, 0.6 fleas per infested individual vs 0–0.1 fleas per infested individual in other months) and April and September–October for *P. soricis* (on average, 1.8–2 fleas per infested individual vs 0–0.4 fleas per infested individual in other months) (Vashchonok and Tret'yakov 2004).

GLMMs were run separately for each flea species and for male and female fleas because of strong female-biased sexual size dimorphism in these insects (e.g., Krasnov et al. 2003; Surkova et al. 2018). Because more than one flea of either species and/or sex was collected in a given year in a given sampling site and often from a given host individual, we included the individual host number nested within the sampling site nested within the sampling year as random effects in each linear mixed-effects model. Then, we used Tukey's tests for multiple comparisons, adjusted for mixed-effects models, to test for differences in body size between or within fleas exploiting male and female hosts between or within periods of high or low abundance using the R package "emmeans" (Lenth 2020).

Results

The results of the linear mixed-effects models of the effects of host sex and flea phenology (periods with high versus low abundance) and interaction between these factors on flea body size are presented in Table 1. A significant effect of host sex on body size was detected in male *A. penicilliger* and *C. uncinatus* (both parasitic on *M. glareolus*) and male and female *P. soricis* (parasitic on *S. araneus*), whereas a significant effect of flea phenology was found in female *A. penicilliger*, male *C. uncinatus*, and both male and female *D. dasycnema* (parasitic on *S. araneus*). Interaction between the two factors appeared to be significant for females of three of four flea species (*A. penicilliger*, *D. dasycnema*, and *P. soricis*) and male *C. uncinatus*.

Female *A. penicilliger* harboured by both male and female hosts during low abundance periods did not differ in size (Fig. 1; Table 2). They also did not differ from conspecifics collected from male hosts during high abundance periods (Table 2). However, female fleas exploiting female hosts during this period were significantly larger (Fig. 1; Table 2). In contrast, male *A. penicilliger* exploiting female hosts were larger than those exploiting male hosts during low, but not high, abundance periods (Fig. 1; Table 2).

No effect of either host sex or flea phenology on the body size of female *C. uncinatus* was found (Fig. 2; Table 2), whereas the body size of males of these species differed in dependence on both of these factors, as well as their interaction (Fig. 2; Table 1). Interestingly, in the periods of low abundance, fleas collected from male hosts were larger than those collected from

Table 1 Summary of the generalized linear mixed-effects models of the effects of host sex (HS) and phenology (Ph: periods of high versus low abundance) on the body size of female and male fleas of four species. Individual host number nested in sampling site nested in sampling year were introduced as random effects in each model. Reference levels for the fixed effects were female for host sex and period of high abundance for phenology. Coefficient estimates and *t* values are related to each fixed effect separately. Significance levels: *$p < 0.05$; **$p < 0.01$; ns: non-significant

Flea species	Flea sex	*N*	Fixed effect	Coefficient estimate ± SE	*t* value
A. penicilliger	Females	88	HS	0.005 ± 0.05	0.01ns
			Ph	0.29 ± 0.09	2.97**
			HS × Ph	−0.24 ± 0.11	−2.21*
	Males	69	HS	−0.15 ± 0.05	−2.78*
			Ph	−0.09 ± 0.06	−1.35ns
			HS × Ph	0.05 ± 0.08	0.57ns
C. uncinatus	Females	109	HS	−0.06 ± 0.06	−1.03ns
			Ph	−0.04 ± 0.09	−0.41ns
			HS × Ph	0.08 ± 0.10	0.46ns
	Males	59	HS	−0.14 ± 0.06	−2.20*
			Ph	−0.24 ± 0.09	−2.57*
			HS × Ph	0.33 ± 0.11	3.11**
D. dasycnema	Females	63	HS	−0.003 ± 0.05	−0.06ns
			Ph	−0.15 ± 0.06	−2.34*
			HS × Ph	0.21 ± 0.08	2.47*
	Males	140	HS	−0.01 ± 0.03	−0.35ns
			Ph	0.09 ± 0.03	2.64**
			HS × Ph	−0.01 ± 0.05	−0.28ns
P. soricis	Females	102	HS	0.22 ± 0.10	2.26*
			Ph	0.005 ± 0.04	0.10ns
			HS × Ph	−0.26 ± 0.11	−2.38*
	Males	123	HS	0.10 ± 0.04	2.37*
			Ph	−0.05 ± 0.03	−1.58ns
			HS × Ph	−0.06 ± 0.05	−1.26ns

female hosts, whereas the opposite was true for the periods of high flea abundance (Fig. 2; Table 2). Consequently, male *C. uncinatus* harboured by male hosts in high abundance periods were larger than those collected from male hosts in low abundance periods, whereas male fleas harboured by female hosts showed the reverse pattern (Fig. 2; Table 2).

Female *D. dasycnema* exploiting male hosts during periods of high abundance were significantly larger than those exploiting female hosts during this period, whereas there was no difference in body size between female fleas harboured by male and female hosts during the periods of low abundance (Fig. 3; Table 2). In addition, female fleas collected from male hosts during high abundance periods were significantly larger than their counterparts collected from hosts of either sex during low abundance periods (Fig. 3; Table 2). Male *D. dasycnema* were significantly larger during high rather than low abundance periods, but their body size did not differ between fleas harboured by male and female hosts in both periods (Fig. 3; Table 2).

The largest female *P. sociris* exploited male hosts during low abundance periods (Fig. 4; Table 2). The difference in body size between them and females (a) collected from male hosts during periods of low abundance and (b) collected from hosts of either sex during periods of high abundance (Table 2) resulted in a significance of the interaction between host sex and phenology factors (Table 1). During periods of low, but not high, abundance, male *P. soricis* exploiting male hosts were larger than those exploiting female hosts (Fig. 4; Table 2). They were also larger than male fleas collected from hosts of either sex during periods of high abundance (Fig. 4; Table 2).

Discussion

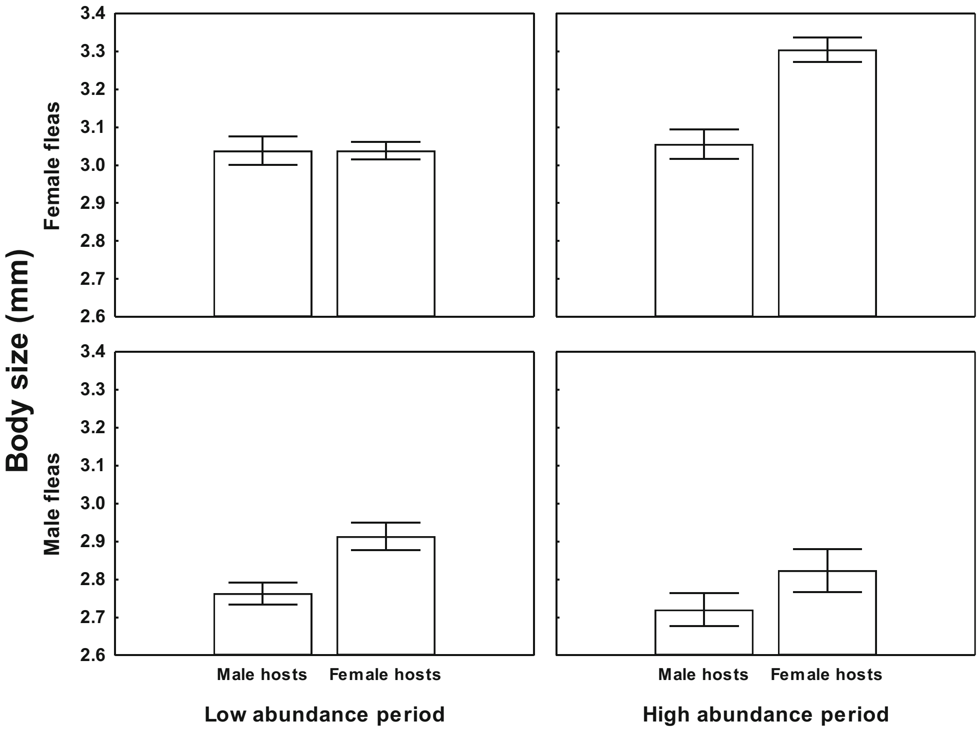
In general, our predictions were not supported. Despite strong effects of host sex and flea phenology on the body size of all four flea species, there was no general trend regarding the direction of these effects. In one species (*A. penicilliger*), larger fleas were found on female hosts, whereas in another species (*P. soricis*), larger fleas were found on male hosts. In the remaining two species, larger fleas were collected from male hosts during periods of high abundance (male *C. uncinatus* and female *D. dasycnema*) and from female hosts during periods of low abundance (male *C. uncinatus*). From the phenological perspective, larger fleas were recorded during periods of either high (*A. penicilliger*, *C. uncinatus*, *D. dasycnema*) or low (*C. uncinatus*, *P. soricis*) abundance, but this depended on flea and/or host sex.

Table 2 Results of multiple comparisons of the body sizes of male and female fleas of four species exploiting female versus male hosts (F and M, respectively) during periods of low versus high abundance (L and H, respectively)

Flea species	Flea sex	Period of abundance	Host sex	Contrast	*t* ratio	*p*
A. penicilliger	Females	L		M - F	0.11	0.92
		H		M - F	−2.68	0.02
			F	H - L	3.04	0.005
			M	H - L	0.84	0.35
	Males	L		M - F	−2.55	0.01
		H		M - F	−1.06	0.12
			F	H - L	−1.17	0.19
			M	H - L	−0.22	0.41
C. uncinatus	Females	L		M - F	−1.05	0.31
		H		M - F	0.29	0.87
			F	H - L	−0.41	0.68
			M	H - L	0.93	0.48
	Males	L		M - F	−2.19	0.03
		H		M - F	2.16	0.02
			F	H - L	−2.57	0.01
			M	H - L	2.15	0.05
D. dasycnema	Females	L		M - F	−0.06	0.95
		H		M - F	2.99	0.005
			F	H - L	−2.34	0.02
			M	H - L	1.02	0.31
	Males	L		M - F	−0.36	0.72
		H		M - F	−0.69	0.49
			F	H - L	2.65	0.01
			M	H - L	2.18	0.03
P. soricis	Females	L		M - F	2.27	0.03
		H		M - F	−0.88	0.38
			F	H - L	0.11	0.92
			M	H - L	−2.64	0.01
	Males	L		M - F	2.37	0.02
		H		M - F	1.10	0.27
			F	H - L	−1.59	0.11
			M	H - L	−2.99	0.004

Male-biased parasitism in higher vertebrates is a well-known phenomenon (see Krasnov et al. 2012 for review) that has been explained by two main, not mutually exclusive, hypotheses. One hypothesis suggested that the main reason for gender-biased parasitism is a gender difference in mobility, with male hosts being more mobile than female hosts; thus, the chances of males to be exposed to a larger variety and number of parasites are greater than those of females (Lang 1996). A second hypothesis connected male-biased parasitism to differences in immunocompetence between male and female hosts because of the immunosuppressive effect of androgens (Zuk and McKean 1996) or a higher investment of females in immune defence (Rolff 2002). Obviously, the body size of imago fleas is unlikely to be affected by the level of mobility of a host animal, whereas the results of laboratory experiments (e.g., Khokhlova et al. 2010a) strongly supported the effect of the weaker immunocompetence of male hosts on flea body size. However, the difference in immune defensibility between male and female hosts varied seasonally, being stronger during the reproductive period (usually from mid-spring to late summer in temperate zones). In fact, the level of immunosuppressive androgens in male rodents is usually elevated during the reproductive period (Bronson 1989). In addition, the immune function in males during this period may be depressed due to the trade-off between reproduction and self-maintenance (Kortet et al. 2003). As a result, male bias in ectoparasite infestation may occur during the reproductive period only (e.g., Krasnov et al. 2005). Consequently, larger fleas on male hosts could be expected mainly during the host reproductive period. This was indeed the case for both fleas parasitic on shrews, namely *P. soricis* (larger fleas on male rodents during periods when host reproduction took place, while flea abundance was low) and *D. dasycnema* (larger fleas on male rodents during periods when host reproduction took place, while flea abundance was high). To some extent, this may also be true for male *C. uncinatus*, with larger fleas collected from male hosts in April (period of high abundance) when the reproduction of hosts (voles) starts. However, larger individuals of male and female *A. penicilliger* and male *C. uncinatus* were found on female voles. This suggests that factors other than immunocompetence-related differences between host sexes may influence flea body size. For example, female *Myodes* voles spend a much longer time in their nests than males do (Gromov 2009). As a result, the amount of organic matter, including host

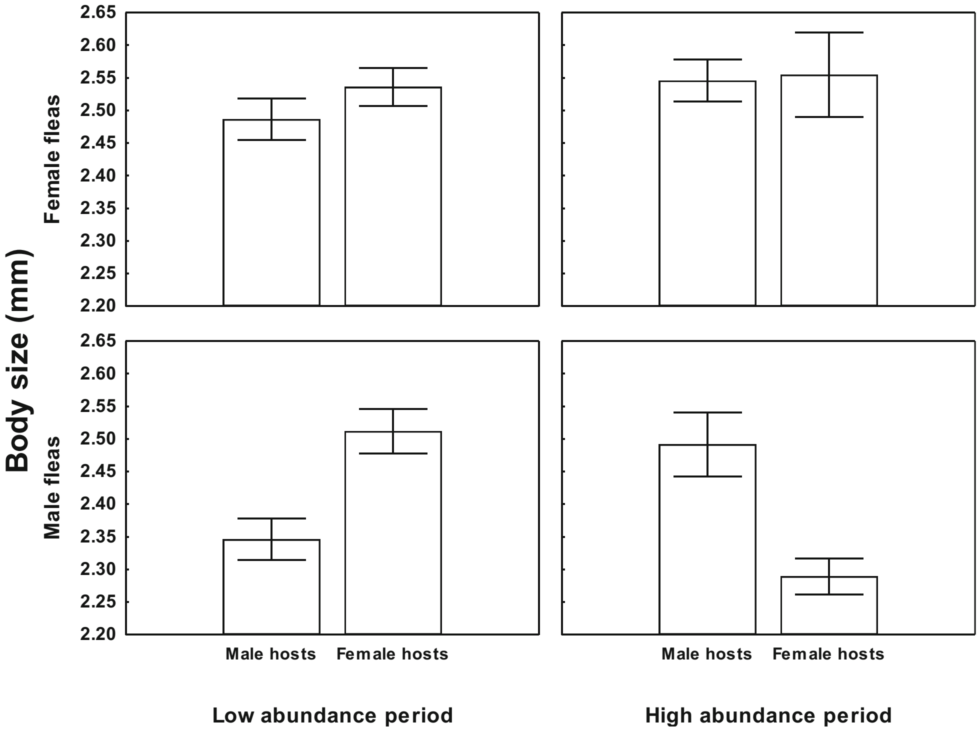
Fig. 1 Body size (mean ± SE) of male and female *Amalaraeus penicilliger* collected from male and female *Myodes glareolus* during high (February–April) and low (remainder of the year) abundance periods



faeces, is likely greater in female than in male nests. This may result in higher availability of food for larval fleas, decreased competition between larvae (Khokhlova et al. 2010b), and, thus, larger body sizes of fleas exploiting female hosts. We recognize, however, that this explanation is speculative and warrants further investigation.

Response to host sex in terms of body size was manifested in both male and female *A. penicilliger* (although only during period of high abundance for the latter) and *P. soricis*, but only in one sex of *C. uncinatus* (males) and *D. dasycnema* (females). This may have resulted from differential sensitivities of male and female fleas to host-related factors in some flea

Fig. 2 Body size (mean ± SE) of male and female *Ctenophthalmus uncinatus* collected from male and female *Myodes glareolus* during high (April) and low (remainder of the year) abundance periods



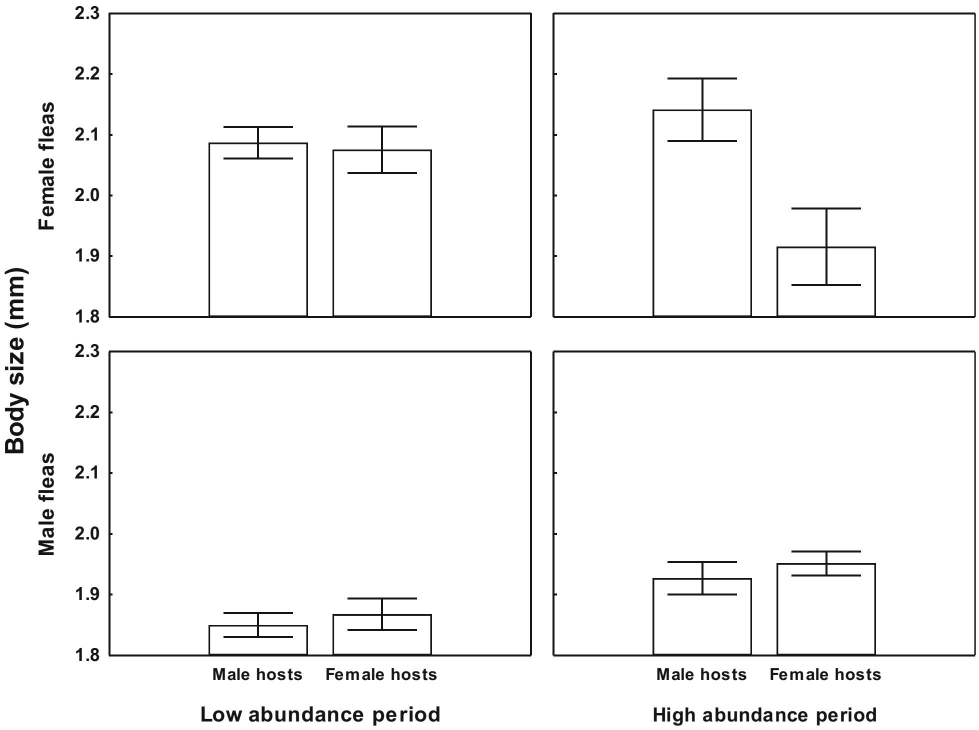


Fig. 3 Body size (mean ± SE) of male and female *Doratopsylla dasycnema* collected from male and female *Sorex araneus* during high (April, June, and September–October) and low (remainder of the year) abundance periods

species. For example, the effect of maternal host sex on body size in *Xenopsylla ramesis* (Siphonaptera: Pulicidae) was manifested in male, but not female, offspring (Khokhlova et al. 2010a). These differences in responses may somehow be associated with sex-related differences in flea physiology, which, in turn, are linked with differences in biological roles between males and females (see Krasnov 2008 for review). However, the exact mechanism behind sex-associated differential sensitivity to various factors is unknown.

We did not find any clear trend in the effect of flea phenology on flea body size. The explanation for this could be that the pure effect of flea phenology is masked by the complex

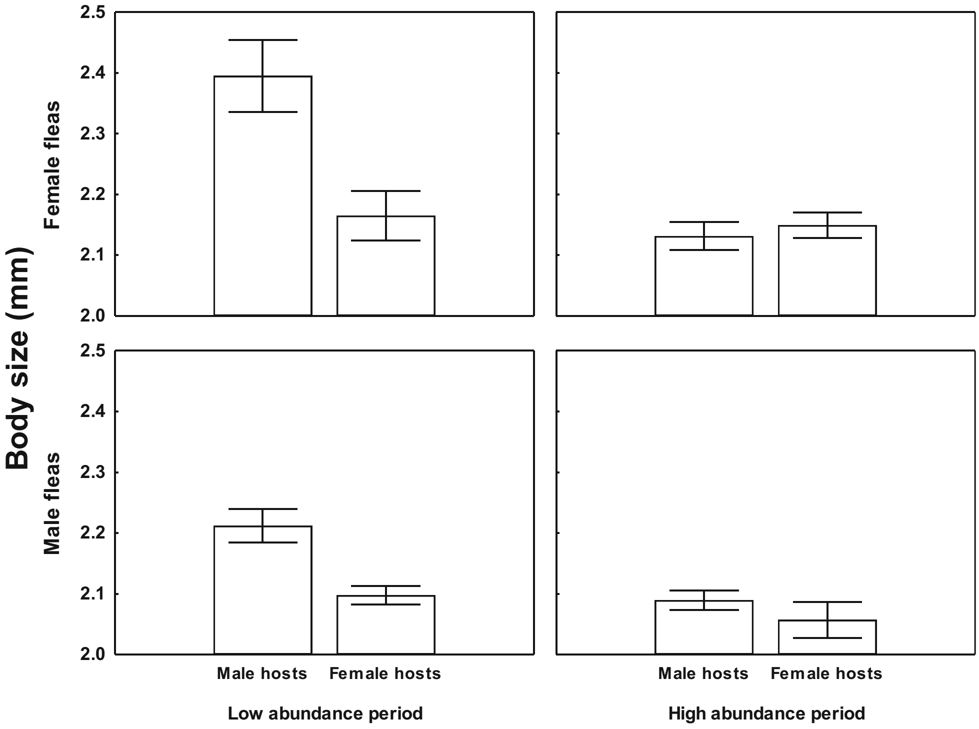


Fig. 4 Body size (mean ± SE) of male and female *Palaeopsylla soricis* collected from male and female *Sorex araneus* during high (April and September–October) and low (remainder of the year) abundance periods

interplay between (a) seasonal variation in external environmental factors, such as temperature and relative humidity; (b) the seasonal dynamics of flea reproduction and development; and (c) the seasonal dynamics of host abundance, age composition, and spatial behaviour. The strong effects of ambient temperature and relative humidity on flea development and body size of a new imago are well known (Krasnov 2008). However, these effects have mainly been studied in the laboratory (e.g., Krasnov et al. 2001), whereas pre-imaginal flea development occurs in the microclimatically stable conditions of host burrows. Thus, these effects in the natural populations of many fleas may be weakly pronounced. This is especially true for fleas such as *C. uncinatus* that stay on their hosts for a very short time and spend most of their life in hosts' burrows (Brinck-Lindroth and Smit 2007). Nevertheless, flea hosts, in our study, either dig shallow burrows or build their nests under stones, tree roots, and dense vegetation, so both adult and pre-imaginal fleas could be subjected to external temperature and humidity.

A flea's reproductive cycle pattern may confound the effect of flea phenology on body size. For example, *P. soricis* demonstrates two periods of peak emergence per year, periods of high abundance (mid-spring and early to middle fall) (Vashchonok and Tret'yakov 2004). The spring generation of this species is represented by individuals that supposedly overwinter as either diapausing imagoes or cocoons (Vashchonok and Tret'yakov 2004). Their smaller body size could be the result of presumably low food availability for larvae after the fall peak of emergence (e.g., because hosts have already stopped their reproduction). The smaller size of fleas that emerge in early fall could be caused by a shorter duration of larval growth under relatively high summer temperatures (Silverman et al. 1981; but see Kiefer et al. 2016). However, the annual cycle of *D. dasycnema* is similar to that of *P. soricis* (Vashchonok and Tret'yakov 2004), but *D. dasycnema* demonstrates an opposite trend to that of *P. soricis* in the relationships between phenology and body size. Perhaps, some other, still unknown, factors play a role in determining the phenological variation of body size in this species.

It is also possible that maternal fleas, since they are able to distinguish between male and female hosts (Khokhlova et al. 2011), adjust their host selection seasonally to ensure that female and male offspring are larger at critical periods. In other words, it could be more advantageous (offspring-wise) for mother fleas to exploit a male or a female host in dependence on phenological phase because of the reproductive consequences of body size. On the one hand, although no association between female flea size and its clutch size was found, larger females survived longer without feeding after oviposition (Kiefer et al. 2016). This suggests that a larger female may have more opportunities for future reproduction and, thus, higher life-time fecundity than a smaller female (Berger et al. 2008). In other words, large body size was not translated into immediate fitness benefits, but allowed a female to increase her fitness in the future. This also suggests that larger females invested more into future, rather than current, reproduction (Berger et al. 2012). Larger body size in male fleas may be positively correlated with mating success as is the case with other insects (e.g., Agosta 2010). The proximate mechanism behind this is the better locomotory abilities of larger individuals (Rothschild et al. 1975). In addition, copulation in some fleas is associated with courtship behaviour (Hsu and Wu 2001), so larger males have an advantage over smaller males in locating a female and successfully mating. On the other hand, larger fleas (both males and females) are likely subjected to more host grooming than their smaller conspecifics because they (a) are more conspicuous, (b) may inject a higher amount of allergen-containing saliva in the bite wound so that irritation caused by their bite is stronger (Lee et al. 1999), and (c) may be more easily removed by a host.

In conclusion, the directions of the effects of host sex and flea phenology on body size varied between flea species. Furthermore, the direction of the effect of host sex was mediated by the effect of flea phenology and vice versa.

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Compliance with ethical standards

This article relies on previously collected data deposited at the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia) and does not contain experiments with human participants or animals. For this type of study, formal consent is not required.

Conflict of interest The authors declare that they have no conflict of interest.

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