The effect of behavioural interactions on the transfer of fleas (Siphonaptera) between two rodent species

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ABSTRACT: The transfer of fleas between the house mouse, Mus musculus, and the midday jird, Meriones meridianus, through social contacts was studied by performing interspecific dyadic encounters on a neutral arena. M. meridianus and M. musculus exchanged parasites through social contacts. The intensity of this exchange was higher between mice and adult male and young jirds than between mice and adult female jirds. The pattern of behavioural interactions was the main determinant of the intensity of flea exchange. Adult female jirds were highly aggressive towards mice. In contrast, interactions between male and young jirds and mice were mainly cohesive and resulted in higher frequency of flea transfer. The proportion of fleas transferred was positively correlated with the number and cumulative duration of tactile contacts between opponents in dyads. Journal of Vector Ecology 26 (2): 181-190. 2001.

Keyword Index: Flea transfer, Nosopsyllus laeviceps, Nosopsyllus mokrzeckyi, Meriones meridianus, Mus musculus, behaviour.

INTRODUCTION

Most ectoparasitic insects are, to some extent, host-specific and the great majority of ectoparasite taxa are found upon one or a few closely related host species (Marshall 1981). In particular, this is true for fleas that are largely associated with species that possess distinctive shelters. The latter are necessary for the immature stages of most fleas. Only a few fleas that have a very high reproductive rate, coupled with a close attachment to the host (e.g., Tungidae, Vermipsyllidae), are associated with homeless mammals (Hopkins 1957). Nevertheless, the degree of host-specificity varies among fleas (Marshall 1976) and the host-restriction is true only partly for fleas.

A considerable amount of work has been done on host preferences of rodent fleas due to their importance in the epidemiology of plague (e.g., Haas 1965, Nazarova and Tikhvinskaya 1971, Ryckman 1971). It has been often shown that the majority of rodent fleas are pleioxenous (2 or more host genera in the same family) or polyxenous (2 or more host families). Nevertheless, the degree of association between a particular flea species and a particular host species varies. For example, a rodent species can be either a true or accidental host for a flea species. True principal and true exceptional hosts may be distinguished among true hosts for most species of rodent fleas, whereas preferred and normal hosts can be further distinguished among principal true hosts (Marshall 1981).

The transfer of fleas from one host species to another can be important in the epidemiology of a number of diseases as different rodent species have different ties with humans. This transfer generally occurs either through body contact or through visiting burrows of other species. For example, Rödl (1979) reported on the exchange of fleas between the vole Clethrionomys glareolus and the mouse Apodemus flavicollis that occurred largely through contact between individuals. Other authors also stated that behavioural interactions mediate flea interchange among small mammal hosts (Hartwell et al. 1958, Sviridov 1963, Buckle 1978). However, this has never been tested experimentally.

Midday jirds Meriones meridianus Pall. (mean adult body mass 45-50 g) and house mice Mus musculus L. (mean adult body mass 14-15 g) co-exist in grassland habitats in the semi-desert Northern Caspian lowlands (Kalmykia, southern Russia). The pattern of spatial distribution of the two species in habitats of co-occurrence was described by Krasnov (1984). Mice were
spatially associated mainly with adult male jirds as well as with young jirds but not with adult female jirds. Furthermore, removal experiments demonstrated that reproduction of mice was inhibited and their home ranges were restricted in the presence of jirds, whereas the number of mice increased and their home ranges expanded when jirds were removed (Krasnov 1984). Laboratory experiments showed that aggressive behavioural interactions were a possible mechanism of spatial distribution of the two species (Krasnov 1984). Moreover, odours mediate interactions between these two species (Krasnov and Khokhlova 1996). Mice avoided the jird odour, and this avoidance based on odour cue was shown to be a learned rather than innate phenomenon (Krasnov and Khokhlova 1996).

In the Northern Caspian lowlands, M. meridianus is a preferred host of the flea Nosopsyllus laeviceps (Wagn., 1916), whereas the main flea parasitizing the feral M. musculus is Nosopsyllus mokrzeckyi (Wagn., 1916). However, jirds are often parasitized by the “mouse” flea N. mokrzeckyi (Lavrovsky et al. 1983) and the “jird” flea N. laeviceps has been frequently recorded on mice (Suverneva et al. 1983). We hypothesized that these two rodent species can exchange their parasites through social contacts. We also hypothesized that the pattern of behavioural interactions is the main determinant of the intensity of flea exchange and, therefore, we predicted that the intensity of this exchange would be higher between mice and adult male and young jirds than between mice and adult female jirds. To test this prediction we compared the flea transfer between a mouse and a jird during dyadic encounters on a neutral arena.

MATERIALS AND METHODS

Experimental animals

Both mice and jirds were live-trapped in one location in the southern part of the Northern Caspian lowlands, about four kilometers W of former Chernozemelsk (now Achinery, 45°25'N, 45°35'E). Each animal was thoroughly examined for fleas when captured. The fur of the animal was combed, using a toothbrush, over a white plastic bath and fleas were carefully collected. The fur was brushed several times until no fleas were recovered. Animals were housed individually in a wire cage (40 by 50 by 40 cm) with wood shavings as bedding material and offered millet seed, carrots and water ad libitum. Animals were maintained under a natural light cycle at 25°C. Each individual was tested 24 h after capture. The use of animals followed the Guidelines for the Use of Animals in Research (published in each January issue of Animal Behaviour).

We used only adult male mice with scrotal testes and adult female mice out of estrus. To confirm the latter, vaginal smears of females were examined immediately prior to test. All mice were sexually experienced. The same was true for adult jirds. In addition, we used subadult jirds of both sexes. A jird was considered to be subadult if its body mass was less than 30 g and it was reproductively inactive. Each individual rodent was tested only once.

Because of uncertainties of M. musculus s. lato taxonomy, chromosomal and biochemical analyses were made of the mice. Mice proved to be M. musculus musculus (Frisman and Krasnov 1986, Yakimenko et al. 1986, Korobitsyna et al. 1993). Fleas N. laeviceps and N. mokrzeckyi were obtained from the laboratory stocks of the “Microb” Anti-Plague Institute (Saratov, Russia). Only male fleas were used.

Experimental procedure

Dyadic encounters were conducted in a glass arena (70 cm by 40 cm by 50 cm) located in a darkened room, with a dim red light shining into the arena from the front. A plywood partition, dividing the arena into two equal parts, kept animals separated prior to each encounter. Encounters were conducted after sunset. Four to five encounters were conducted per evening and night. After each series of encounters, the rodents were transported to the trapping site and released in their capture locations.

Opponents in dyads were rodents of different species. There were 16 encounter types in the experimental set: two flea-donor species, two sexes of mice, two sexes of jirds and two ages of jirds. Each encounter type was replicated 10 to 12 times and thus there were 167 encounters of 30 min each.

Only one participant in each dyad was infested with fleas, whereas the other was left clean. Twenty minutes prior to the encounter, we placed a flea-donor into a small glass “infestation chamber” (10 cm by 10 cm by 20 cm) and infested it with 10 individuals of the fed fleas of the respective species (N. laeviceps for jirds and N. mokrzeckyi for mice). Immediately before the encounter, the infestation chamber was thoroughly checked for fleas that jumped off the host.

At the onset of each encounter, each of two individuals to be encountered was placed on either side of the partition and allowed to become familiar with the arena. During this period, animals generally explored their surroundings for several minutes and then settled into a corner of the arena. After 20 min, the partition was removed, and interactions between animals were recorded continuously for 30 min. The quantity and duration of the intervals were empirically determined during a few preliminary encounters. Between the
encounters, we thoroughly wiped the arena with 70% ethanol and dried it. After 30 min of encounter, we examined each opponent for fleas by combing its fur using a toothbrush as described above. In addition, we examined the arena for fleas that had jumped off. We recorded if there was flea transfer and how many fleas transferred.

During the encounters, we recorded the following behaviours that were classified into three groups according to apparent motivational similarity: (1) cohesive behaviour (tactile contact), (2) agonistic offensive behaviour (attack) and (3) agonistic defensive behaviours (escape). Tactile contact was regarded as occurring when rodents have immediate body contact (not during lock fights) for more than 2 sec and if this contact was not followed by any agonistic behaviour. In addition, we measured the duration that opponents sat side by side with close tactile contact and calculated a cumulative time of direct body contact.

**Data processing**

Data from each encounter were expressed as the number of behaviours of a particular type per either an individual (attacks and escapes) or per experiment (tactile contact). Logarithmic transformation of all variables, except the proportion of fleas transferred, provided distributions that did not differ significantly from normal (Shapiro-Wilks tests, NS). The proportion of fleas transferred was adjusted to normality by arcsin-transformation (Shapiro-Wilks test, NS).

The effect of sex and age of the opponents on behavioural interactions was analysed by multivariate three-factor analysis of variance (3-way MANOVA). The independent factors in this analysis were sex of mouse opponent, sex of jird opponent and age of jird opponent. Tukey HSD test was applied for multiple comparisons. The frequency of flea transfer in dependence of a jird-mouse dyads was affected by sex and age of the jird but not by sex of the mouse (Table 1). Adult female jirds attacked mice more often than adult males and young jirds did (Tukey’s HSD tests, *p*<0.001, Figure 1). In addition, adult female jirds fled from mice significantly less than other jirds did (Tukey’s HSD tests, *p*<0.001), whereas the frequency of escapes of subadult female jirds during encounters was the highest (Tukey’s HSD tests, *p*<0.01). Mice attacked mainly subadult female jirds (Tukey’s HSD tests, *p*<0.001). Furthermore, the frequency of mouse attacks did not depend on the attacker’s sex (*F*=3.07, *df*=1,166, *p*<0.1). Escapes of a mouse were recorded mainly in dyads where a jird partner was an adult female (Tukey’s HSD tests, *p*<0.001, Figure 2).

Behavioural interactions

The number of occurrences of behaviour in the jird-mouse dyads was affected by sex and age of the jird but not by sex of the mouse (Table 1). Adult female jirds attacked mice more often than adult males and young jirds did (Tukey’s HSD tests, *p*<0.001, Figure 1). In addition, adult female jirds fled from mice significantly less than other jirds did (Tukey’s HSD tests, *p*<0.001), whereas the frequency of escapes of subadult female jirds during encounters was the highest (Tukey’s HSD tests, *p*<0.01). Mice attacked mainly subadult female jirds (Tukey’s HSD tests, *p*<0.001). Furthermore, the frequency of mouse attacks did not depend on the attacker’s sex (*F*=3.07, *df*=1,166, *p*<0.1). Escapes of a mouse were recorded mainly in dyads where a jird partner was an adult female (Tukey’s HSD tests, *p*<0.001, Figure 2).

Tactile contacts were recorded mainly in dyads where a jird was not an adult female (Tukey’s HSD tests, *p*<0.001, Figure 3). The number of tactile contacts and the cumulative duration of them were highly positively correlated (Pearson’s *r*=0.92, *p*<0.005) and, so, the cumulative time of body contacts was the lowest in the dyads with adult female jirds (Tukey’s HSD tests, *p*<0.001).

**Flea exchange**

Frequency of transfer of both flea species was the lowest in the dyads with female adult jirds (Figure 4). Results of the log-linear analysis of the table with frequencies of flea transfer in dependence on a flea species and sex and age of opponents and interactions of these factors demonstrated that the most appropriate model fitting the observed frequencies should include two two-way interactions (between transfer and sex of a jird and between transfer and age of a jird) and one three-way interaction (between transfer and sex and age of a jird) (Table 2). The overall model fitted the observed table (Maximum Likelihood *χ*²=11.22, *df*=24, *p*=0.99). In addition, separate examination of models with each of these interactions demonstrated the model with only three-way interaction of transfer with sex and age of a jird partner fitted the observed table (Maximum Likelihood *χ*²=46.04, *df*=28, *p*=0.01 for the transfer and sex of jird interaction and Maximum Likelihood *χ*²=46.04, *df*=28, *p*=0.01 for the transfer and age of jird interaction).
Table 1. Summary of multiple analysis of variance (MANOVA) of six behavioural parameters (jird attack and escape, mouse attack and escape, tactile contact, cumulative time of tactile contact) in dependence on sex of jird and sex and age of mouse.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Wilks’ Lambda</th>
<th>Rao’s $R$</th>
<th>df</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meriones sex</td>
<td>0.50</td>
<td>26.04</td>
<td>1, 155</td>
<td>0.00</td>
</tr>
<tr>
<td>Meriones age</td>
<td>0.32</td>
<td>55.05</td>
<td>1, 155</td>
<td>0.00</td>
</tr>
<tr>
<td>Mus sex</td>
<td>0.93</td>
<td>1.80</td>
<td>1, 155</td>
<td>0.10</td>
</tr>
<tr>
<td>Meriones sex x Meriones age</td>
<td>0.47</td>
<td>29.47</td>
<td>1, 155</td>
<td>0.00</td>
</tr>
<tr>
<td>Meriones sex x Mus sex</td>
<td>0.95</td>
<td>1.46</td>
<td>1, 155</td>
<td>0.19</td>
</tr>
<tr>
<td>Meriones age x Mus sex</td>
<td>0.94</td>
<td>1.58</td>
<td>1, 155</td>
<td>0.16</td>
</tr>
<tr>
<td>Meriones sex x Meriones age x Mus sex</td>
<td>0.94</td>
<td>1.65</td>
<td>1, 155</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Table 2. Significant partial (PA) and marginal (MA) association models of the table of frequency of flea transfer in dependence on a flea species and sex and age of opponents in the dyads.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>PA $\chi^2$</th>
<th>PA $p$</th>
<th>MA $\chi^2$</th>
<th>MA $p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transference x sex Meriones</td>
<td>1</td>
<td>21.68</td>
<td>0.001</td>
<td>18.60</td>
<td>0.001</td>
</tr>
<tr>
<td>Transference x age Meriones</td>
<td>1</td>
<td>20.48</td>
<td>0.001</td>
<td>16.89</td>
<td>0.001</td>
</tr>
<tr>
<td>Transference x sex Meriones x age</td>
<td>1</td>
<td>13.99</td>
<td>0.001</td>
<td>12.69</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Table 3. Summary of ANOVA of the percentage of flea transfer in dependence on flea-donor species and sex and age of opponents in the dyads.

<table>
<thead>
<tr>
<th>Effect</th>
<th>MS effect</th>
<th>MS error</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Donor species</td>
<td>0.00</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.02</td>
<td>0.89</td>
</tr>
<tr>
<td>Meriones sex</td>
<td>2.04</td>
<td>0.10</td>
<td>1, 152</td>
<td>20.67</td>
<td>0.00</td>
</tr>
<tr>
<td>Meriones age</td>
<td>2.31</td>
<td>0.10</td>
<td>1, 152</td>
<td>23.40</td>
<td>0.00</td>
</tr>
<tr>
<td>Mus sex</td>
<td>0.07</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.76</td>
<td>0.39</td>
</tr>
<tr>
<td>Donor species x Meriones sex</td>
<td>0.00</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.04</td>
<td>0.83</td>
</tr>
<tr>
<td>Donor species x Meriones age</td>
<td>0.01</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.06</td>
<td>0.81</td>
</tr>
<tr>
<td>Meriones sex x Meriones age</td>
<td>1.56</td>
<td>0.10</td>
<td>1, 152</td>
<td>15.77</td>
<td>0.00</td>
</tr>
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<td>Donor species x Mus sex</td>
<td>0.00</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.00</td>
<td>0.98</td>
</tr>
<tr>
<td>Meriones sex x Mus sex</td>
<td>0.00</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.02</td>
<td>0.89</td>
</tr>
<tr>
<td>Meriones age x Mus sex</td>
<td>0.01</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.13</td>
<td>0.72</td>
</tr>
<tr>
<td>Donor species x Meriones sex x Meriones age</td>
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<td>0.10</td>
<td>1, 152</td>
<td>0.07</td>
<td>0.79</td>
</tr>
<tr>
<td>Donor species x Meriones sex x Mus sex</td>
<td>0.01</td>
<td>0.10</td>
<td>1, 152</td>
<td>0.14</td>
<td>0.71</td>
</tr>
<tr>
<td>Donor species x Meriones age x Meriones age</td>
<td>0.26</td>
<td>0.10</td>
<td>1, 152</td>
<td>2.62</td>
<td>0.11</td>
</tr>
<tr>
<td>Meriones sex x Meriones age x Mus sex</td>
<td>0.16</td>
<td>0.10</td>
<td>1, 152</td>
<td>1.64</td>
<td>0.20</td>
</tr>
<tr>
<td>Donor species x Meriones sex x Meriones age x Mus sex</td>
<td>0.34</td>
<td>0.10</td>
<td>1, 152</td>
<td>3.45</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Figure 1. Log mean number (±S.E.) of attacks initiated by a jird during a 30 min encounter.

Figure 2. Log mean number (±S.E.) of escapes demonstrated by a mouse during a 30 min encounter.
Figure 3. Log mean number (±S.E.) of tactile contacts recorded during a 30 min encounter.

Figure 4. Frequency of *N. laeviceps* and *N. mokrzeckyi* transfer during a 30 min encounter of dyads differed by sex and age of a jird.
Proportion of fleas transferred was affected by age and sex of a jird as well as by interaction of these factors (Table 3). Proportion of fleas transferred was the lowest when a jird was an adult female (Tukey’s HSD tests, \( p < 0.001 \), Figure 5). Furthermore, this proportion was positively correlated with number and cumulative duration of tactile contacts between opponents in dyads (\( r^2 = 0.36, F = 93.34, \text{df} = 1.166, p < 0.001 \) and \( r^2 = 0.53, F = 182.54, \text{df} = 1.166, p < 0.001 \), respectively). Although these two regressions did not differ significantly (\( t = 0.23 \) for intercepts and \( t = 0.16 \) for slopes), the cumulative time of tactile contact seemed to be a better predictor of the proportion of fleas transferred than the number of tactile contacts (note higher \( r^2 \) values).

DISCUSSION

Our predictions appeared to be true in that *M. meridianus* and *M. musculus* exchanged their parasites through social contacts. The pattern of behavioural interactions was the main determinant of the intensity of flea exchange. The intensity of this exchange was higher between mice and adult male and young jirds than between mice and adult female jirds.

We attribute the higher aggression of adult female jirds towards mice in comparison with male and young jirds to differences in territorial behaviour between jirds of different sex and age. Female jirds guard their home ranges against intruding conspecifics, whereas male jirds do not (Verevkin 1985). Presumably, they also guard their home ranges from rodents of other genera as well. The absence of aggressive responses in young female jirds can be explained by the fact that jirds develop the stereotype of their territorial behaviour close to adulthood (see Goltsman et al. 1977 and references therein).

As mentioned above, transfer of fleas between hosts can occur either through occupation of the same habitat or through body contact, for example, between predator and prey (Marshall 1981). Flea interchange between species occurring in the same habitat has been demonstrated previously (Haas 1965, Ryckman 1971, Nazarova 1981), as well as flea exchange between predator and prey (Nazarova 1981). Our results support the hypothesis that inter-specific social contacts also play an important role in ectoparasite exchange. The mainly cohesive interactions between mice and male and young jirds resulted in a relatively high probability of flea transfer. Moreover, frequency of flea transfer as well as proportion of fleas transferred were correlated with behavioural characteristics of mouse-jird interactions.

Continuous transfer of fleas between different hosts may sometimes lead to establishment of a flea on an unusual host. For example, Hopkins (1957) and Holland (1964) suggested that the evolution of some bird fleas included transfer from mammalian hosts. Some fleas can become established on predators of their true hosts (King 1976). It is not clear if flea transfer between jirds and mice has any evolutionary consequences. It appears
interactions can potentially cause the spreading of disease and *M. meridianus* (see description in Rall 1938) and *M. musculus* (see description in Kucheruk 1983) burrows. Morphological limitations suggest the possible unsuitability of mouthparts, combs, claws etc. of a particular flea species to the pelage and skin structure of an unusual host (Deoras and Gokhale 1958). Interspecific difference in host behaviour (for example, intensity and pattern of grooming) can also be a restriction for flea establishment. Finally, physiological differences between hosts that are important for fleas include, for example, constituents of blood. Fecundity and egg hatchability of *Xenopsylla cheopis* were higher when fleas were fed upon *Rattus rattus* than upon *Bandicota bengalensis* (Prasad 1969).

Nevertheless, flea transfer between mice and jirds can have rather serious epidemiological consequences. Feral house mice seasonally migrate from natural habitats to human settlements and contact with commensal resident conspecifics (Khokhlova and Krasnov 1986). Commensal mice in the study region are infested by flea *Leptopsylla segnis* (Khokhlova and Knizaeva 1983, Suverneva et al. 1983). The latter is not an effective plague vector because plague bacteria are usually unable to block the alimentary canal at the proventriculus in this species (Vatschenok 1988). This blockage is the main mechanism determining the transmission of the plague pathogen by fleas. The contacts between feral and commensal mice has been reported to evoke the dispersal of fleas from natural habitats into human settlements and contact with commensal *M. musculus* (see description in Rall 1938) whereas *M. meridianus* has been indicated by a high degree of spatial overlap between the naturally occurring interactions between *M. meridianus* and *M. musculus* seem to be rather often. It is indicated by a high degree of spatial overlap between home ranges of these species (Krasnov 1984). In addition, the occurrence of “jird” fleas on *M. musculus* and “mouse” fleas on *M. meridianus* has been continuously observed (Shiranovich et al. 1959, Lavrovsky et al. 1983, Suverneva et al. 1983). Consequently, the transfer of fleas between *M. meridianus* and *M. musculus* mediated by behavioural interactions can potentially cause the spreading of disease into urban and suburban areas.

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