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1 Prey-specific experience affects prey preference and time
2 to kill in the soil predatory mite *Gaeolaelaps aculeifer*
3 Canestrini

4

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7

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19

20 A B S T R A C T

21 Generalist predators potentially have access to a wide array of prey, but it is little studied how
22 experience with specific prey affects preference for this prey. In particular, it is unknown how
23 experience with pest prey affects predator foraging decisions in cases where the pest is nutritious
24 but protected by a repelling, potentially deadly defence. We investigated preference of the soil
25 predatory mite *Gaeolaelaps aculeifer* Canestrini for the risky pest springtail *Protaphorura fimata*
26 Gisin relative to the safe non-pest springtail *Folsomia candida* Willem. Egg production under
27 foraging on live or dead individuals of either prey showed that the two species had equal nutritional
28 quality for *G. aculeifer*, but indicated that live *F. candida* were more difficult to catch than live *P.*
29 *fimata*. Importantly, some *G. aculeifer* were killed by *P. fimata* defence secretions, demonstrating
30 that live *P. fimata* are risky prey. Preference for *P. fimata* was generally high when mites were
31 given a choice between a live individual of either prey, but this preference was reduced following
32 exposure to live individuals of this prey. Furthermore, fewer *G. aculeifer* killed a prey and time
33 until kill was longer after experience with live *P. fimata*. These findings indicate that live *P. fimata*
34 induced a partial aversion on *G. aculeifer* during exposure. Our study shows that generalist
35 predators can reduce their preference for risky prey following exposure. This indicates that
36 generalist predators used in biological control against risky prey are most efficient against this prey
37 if not exposed to it prior to release.

38

39 *Keywords:* Collembola; Mesostigmata; Predation; Pre-exposure; Prey selection; Risky prey

40

41

1. Introduction

Generalist predators do not feed randomly among available prey, but often show preference for some prey species over others (Sigsgaard, 2010; Toft, 1999; Whitney et al., 2018). When a certain prey species is common, generalist predators sometimes develop a preference for this prey as they learn to more efficiently catch and handle it (Ishii and Shimada, 2010). For use in biological control, it has been suggested that maintaining generalist control agents on a target pest increases preference for this prey or host (Cascone et al., 2015; Su et al., 2019). However, if prey possess deterrent defence mechanisms, predators may develop avoidance to these prey (e.g. Forbes, 1989), as defense mechanisms can sometimes harm or even kill the predator (Mukherjee and Heithaus, 2013). Some slow-moving prey possess deadly defense reactions including the secretion of adhesive and toxic fluids (Betz and Kölsch, 2004). Prey that are easy to catch can therefore be dangerous to handle, especially for generalist predators that have not evolved specialized adaptations to handling the challenge. Generalist predators may thus react to experience with such prey by learning how to handle the prey or by inducing an aversion and avoiding the prey, particularly if alternative prey is available (Barnhisel, 1991). For predators used in biological control of pests in greenhouses and agroecosystems, previous experience with a prey species could be important for their prey preference and selection under foraging. Thus, information about how prior prey exposure affects predator biological control potential has implications for how to optimally maintain predators prior to release.

Collembola species within the family Onychiuridae sometimes occur as pests in agriculture by feeding on plant parts in weed-cleared fields (Baker and Dunning, 1975; Edwards, 1962; Scott, 1964; Spencer and Stracener, 1930). In particular, the springtail *Protaphorura fimata* Gisin (Collembola: Onychiuridae) is reported to cause damage by feeding on seedlings of lettuce, *Lactuca sativa* Linnaeus, and sugar beet, *Beta vulgaris* Linnaeus, thereby impeding early growth and

66 reducing yields (Baker and Dunning, 1975; Hurej et al., 1992; Joseph, 2017; Joseph et al., 2015).
67 The species is also reported to feed on the roots of maize, *Zea mays* Linnaeus (Endlweber et al.,
68 2009). These Collembolans are slow moving and, in contrast to most other springtails, lack a
69 furcula for jumping to escape predators (Christiansen et al., 2009; Hopkin, 1997). Instead, they
70 possess pseudocelli from which they excrete a sticky, often toxic secretion from underlying glands
71 upon attack (Brown, 1983; Christiansen et al., 2009; Hopkin, 1997; Usher and Balogon, 1966).
72 During attacks on large *P. fimata*, predators thus risk getting their limbs and mouthparts glued to
73 their body by this secretion and will die if they are unable to free themselves.

74 Mesostigmatid mites are effective biological control agents in agroecosystems (Koehler,
75 1997; Moreira and de Moraes, 2015), and are widely used against a range of crop pests (Gerson and
76 Weintraub, 2007; Knapp et al., 2018). The soil predatory mite *Gaeolaelaps aculeifer* Canestrini
77 (Mesostigmata: Laelapidae) is used against various pests in greenhouses and agroecosystems
78 (Berndt et al., 2004a,b; Gerson and Weintraub, 2007; Jess and Bingham, 2004; Lesna et al., 1996;
79 Navarro-Campos et al., 2016), and occurs naturally in both northern and southern Europe (Karg,
80 1961; Krogh, 1995; Navarro-Campos et al., 2012). They can survive as scavengers (Vasseur et al.,
81 2018), and are reported to have inherent, genetically controlled prey preference (Lesna and Sabelis,
82 1999). We recently showed that *G. aculeifer* has promising potential as a biological control agent
83 against *P. fimata* (Jensen et al., 2019b). The isotomid springtail *Folsomia candida* Willem
84 (Collembola: Isotomidae) is another prey that can be reared in large quantity and serve as a
85 nutritious prey for *G. aculeifer* (Heckmann et al., 2007; Jensen et al., 2019a; Krogh, 1995). In
86 contrast to *P. fimata*, *F. candida* is fast moving and possesses a furcula, but has no pseudocelli. It is
87 furthermore common and widespread in temperate soils while no pest effects are reported (Fountain
88 and Hopkin, 2005).

89 It is important to increase the efficiency of biological control agents in integrated pest
90 management (Plouvier and Wajnberg, 2018), and priming generalist predators on the pest prey can
91 in some cases potentially target the predators towards the pest (Ishii and Shimada, 2010; Su et al.,
92 2019). Alternatively, priming the predator with a specific prey species may cause an aversion
93 against this species if it has a defence mechanism. Collembolans are mainly detritus feeders, but
94 their high abundance in crop fields makes them important alternative prey for predators (Bilde et
95 al., 2000), which can facilitate predator establishment and sustenance (Azevedo et al., 2019; Krey et
96 al., 2017; Muñoz-Cárdenas et al., 2017). Such indirect interactions among pest and alternative prey
97 may enhance the overall biological control service (Chailleux et al., 2014), although alternative prey
98 can in some cases impede control (Koss and Snyder, 2005; Symondson et al., 2006). In our system,
99 where we investigate different prey items of *G. aculeifer*, it might be that *F. candida* is less
100 preferred than *P. fimata*, and that it therefore might be feasible to use *F. candida* both as a safe
101 maintenance prey and as an alternative prey in the field.

102 In the present study, we used *G. aculeifer* to investigate how previous experience with *P.*
103 *fimata* affected kill rate, time to kill, and preference for this prey relative to an alternative prey (*F.*
104 *candida*). To enable distinguishing between effects of prey catchability or risk, and of prey
105 nutritional quality, we exposed adult female *G. aculeifer* to either live or dead *P. fimata* or *F.*
106 *candida*, or to starvation, and measured survival and egg production on the different treatments. The
107 live and dead prey tests allowed us to distinguish between effects of food quality and nutritional
108 quality as catchability plays a role for the overall food quality of the prey when prey is live, whereas
109 only nutritional quality affects predator performance when the prey is dead. After 8 days of pre-
110 exposure to either treatment, we measured preference for *P. fimata* relative to *F. candida* as well as
111 time until kill and proportion of mites killing a prey in a choice assay. As the physical handling
112 disturbance of test chambers and the resulting activity and catchability of *F. candida* appeared to

113 differ between the pre-treatment and the following choice test, we also investigated the effect of
114 regularly disturbing *F. candida* on the performance of *G. aculeifer*. Our results show that exposing
115 biological control agents to a risky pest prey may lower their kill rate and immediate preference for
116 the pest.

117

118 **2. Material and methods**

119 *2.1. Predatory mites*

120 A culture of predominantly adult *G. aculeifer* was purchased from ÖRE Bio-Protect GmbH
121 (Schwentinental, Germany), where they had been reared in vermiculite with mould mites
122 (*Tyrophagus putrescentiae* Schrank) as prey. Before pre-treatments, we heat-extracted the mites
123 over two hours into transparent plastic cups (7.0 cm diameter × 4.5 cm height) with water-
124 saturated Plaster of Paris and charcoal (8:1 ratio) bottoms, to a density of less than 100 mites per
125 cup. The mites were kept at 20 ± 1 °C, a 12:12 h light:dark cycle, and near 100% humidity. Adult
126 females were collected from the extracted mites with an aspirator and allocated randomly to
127 experimental treatments. Females are easily distinguished from nymphs and adult males by their
128 brown dorsal shield and larger size (OECD, 2008).

129

130 *2.2. Restriction to P. fimata, F. candida, or starvation diets*

131 During the experiments, adult female *G. aculeifer* were kept individually in 16 mm diameter 24-
132 well plate holes with 3 mm water-saturated Plaster of Paris and charcoal (8:1) bottoms. The holes
133 were clogged with rubber stoppers, giving an enclosure height of 1 cm. Plates were kept at 20 ± 1
134 °C and a 12:12 h light:dark cycle. Water was added daily to re-satiate the plaster of Paris bottoms

135 and maintain a high humidity. Each female *G. aculeifer* was then provided with juvenile
136 springtails *ad libitum* (15-30 individuals of either *P. fimata* or *F. candida*), ensuring access to a
137 variety of prey stages from many small to fewer large juveniles. Both prey species were obtained
138 from our long-term laboratory colonies reared on baker's yeast (*Saccharomyces cerevisiae*
139 Meyen). Prey was offered both as live ($n = 120$ *G. aculeifer* per prey species) and dead ($n = 96$ per
140 prey species) prey. We also included a starvation treatment where no prey was provided ($n = 96$).
141 Fresh prey and water were supplied daily to ensure high prey availability and humidity. Survival
142 and the number of eggs laid per mite were recorded daily and eggs were removed after counting.
143 Mortality due to *P. fimata* defence fluids was easily recognized as dead mites had their legs and
144 mouthparts glued to their own body.

145

146 2.3. Prey preference and time until kill

147 After the eight days of prey-specific diet or starvation, all prey was removed and mites were given
148 two to four hours in their containers without prey. They were then submitted to a choice
149 experiment where they were given the choice between one small juvenile of each species, which
150 were provided simultaneously with an aspirator. Small prey were chosen to maximize catchability
151 (Baatrup et al., 2006). A reference sample of 24 representative juveniles of each species showed a
152 similar average length of 56.6 ± 1.3 (S.E.) μm and 53.5 ± 1.1 μm for *P. fimata* and *F. candida*,
153 respectively (t -test: $t = 3.46$, $P = 0.069$). Individual mites were observed under microscope for up
154 to two hours, and time until the kill and prey species killed were recorded. The choice tests were
155 performed at daytime under light in a room at 23 ± 1 °C, after removing the top rubber stopper.
156 Water was added to the plaster of Paris bottoms before tests to ensure high humidity.

157

158 2.4. Disturbance effects on reproduction

159 As provisioning of live *F. candida* resulted in lower *G. aculeifer* egg production than other prey
160 treatments, likely due to low activity of *F. candida* combined with high efficiency of its jumping
161 response, we tested the hypothesis that disturbing the system would increase catchability and egg
162 production. The activity of *F. candida* is markedly increased by disturbance, and we predicted that
163 this increase in prey activity would enhance prey capture because mites would encounter prey
164 more frequently while the escape response might be impaired by the preceding jump. To test this,
165 we kept adult female *G. aculeifer* provided with *ad libitum* juvenile *F. candida* (15-30 individuals)
166 under either disturbed or undisturbed conditions over eight days ($n = 24$ per treatment) in
167 individual 24-well plate holes as described in section 2.2. Disturbance was induced by mildly but
168 abruptly shaking one of the 24-well plates with individual mites and *F. candida* prey for one
169 minute every half hour during ten hours each day, while the other 24-well plate was left
170 undisturbed except at the daily provisioning of fresh prey and water. Mite eggs laid were recorded
171 daily and removed.

172

173 2.5. Statistical analysis

174 Overall effects of pre-treatment diet and prey state on survival during pre-treatment, proportion of
175 mites killing a prey, and prey species killed were analysed using mixed effects nominal logistic
176 regressions. Effects on egg production during pre-treatment were analysed using a mixed effects
177 proportional hazard analysis. Overall effects of pre-treatment diet, prey state during pre-treatment,
178 and prey species selected on time until kill were similarly analysed using a mixed effects
179 proportional hazard analysis. Effects of pre-treatment diet on mite survival, kill rate, and prey
180 preference were further analysed using likelihood ratio tests. Effects of diet on the number of mite

eggs laid were analysed using an overall Wilcoxon test followed by a post-hoc test (Steel-Dwass at $\alpha = 0.05$). A similar test was used to assess effects of previous diet and selected prey on time to kill in the choice experiment. For mites previously provisioned with live prey, overall effects of previously provisioned prey and killed prey on time to kill under choice were furthermore analysed using the likelihood ratio test in a proportional hazard analysis. Effects of disturbance on egg production were analysed using a Wilcoxon test. Nonparametric tests were used because variances were unequal (Bartlett tests, $P < 0.05$), and because the data were generally not normally distributed (Shapiro-Wilk tests, $P < 0.05$). All analyses were performed in JMP 13.0.0 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Effects of prey species on survival and reproduction

We found effects of diet on both survival and egg production (Table 1). Egg production was furthermore affected by prey state and the interaction between diet and prey state (Table 1). All female *G. aculeifer* provided with live *F. candida* or dead prey of either springtail species survived the eight-day feeding period prior to choice tests. However, four individuals provided with live *P. fimata* died during this period as they were stuck in *P. fimata* defence fluids after failed attacks. As a consequence, survival of *G. aculeifer* was lower when feeding on live *P. fimata* than after feeding on live or dead *F. candida* or dead *P. fimata* (Fig. 1A). One *G. aculeifer* died under the eight days of starvation. Exposure to live *P. fimata* thus represents a more severe mortality risk than starvation, although not significantly so (Fig. 1A). Mites provided with live *F. candida* laid a median of only two eggs (Fig. 1B). This was fewer than mites provided with live *P. fimata* or dead prey of either species, which laid a median of 6.5 to 10 eggs (Fig. 1B). However, mites provided

204 with live *F. candida* laid more eggs than mites that were exposed to starvation, which laid a
205 median of only one egg (Fig. 1B).

206

207 3.2. Effects of preceding prey on kill rate, prey preference, and time until kill

208 Kill rate and prey preference were both affected by the preceding diet and prey state, as well as
209 their interaction (Table 1). When given a choice between live juvenile *P. fimata* and *F. candida*,
210 only 70% of mites previously provisioned with live *P. fimata* killed a prey (Fig. 2A). This was a
211 smaller proportion of mites killing a prey than in mites previously provisioned with live *F. candida*
212 or with dead prey of either species, all of which killed in more than 90% of cases (Fig. 2A). All
213 previously starved mites killed a prey (Fig. 2A). Mites previously restricted to live *P. fimata* killed
214 *F. candida* instead of *P. fimata* in 51% of cases (Fig. 2B). This was a lower preference for *P.*
215 *fimata* than for mites on all other pre-treatments, which killed *P. fimata* instead of *F. candida* in
216 68-78% of cases (Fig. 2B).

217 Time until kill was affected by all three factors (preceding diet, prey stage, and prey species
218 killed), and by the interactions between diet and prey stage and between prey stage and species
219 killed (Table 2). When analysing effects on time until kill after feeding on live prey alone, mites
220 previously given live *F. candida* attacked and killed a prey at a median of 2.45 minutes. This was
221 significantly sooner than mites previously given live *P. fimata* (Likelihood ratio test: $\chi^2_{1,194}$
222 = 48.35, $P < 0.0001$), which killed at a median of 9.05 minutes (Fig. 2C). Mites selecting *F.*
223 *candida* after foraging on live prey killed at a median of 3.22 minutes (Fig. 2C). This was
224 significantly sooner than mites selecting *P. fimata* after foraging on live prey ($\chi^2_{1,194} = 27.58$, $P <$
225 0.0001), which killed at a median of 4.41 minutes (Fig. 2C). There was no significant interaction
226 between previous exposure and selected prey on time until kill ($\chi^2_{1,194} = 1.06$, $P = 0.30$). After

227 being provisioned with dead prey or starved, mites killed at a median of 4.80 minutes with no
228 significant difference between treatments (Fig. 2C). Mites previously provisioned with live prey
229 likewise killed within this time frame when subsequently killing the other prey than they were pre-
230 fed (Fig. 2C). Interestingly, mites previously provided with live *F. candida* and that killed *F.*
231 *candida* in the choice test killed already at a median of 1.28 minutes, which was sooner than all
232 other groups (Fig. 2C). In contrast, the median time to kill in mites previously provisioned with
233 live *P. fimata* that also killed *P. fimata* in the choice test was 15.03 minutes and thus longer than
234 for any other group (Fig. 2C).

235

236 3.3. Effects of disturbance on reproduction

237 Mites preying on live *F. candida* that were regularly activated by disturbance laid a median of 6
238 (25th quartile (q): 3; 75th q: 9) eggs. This was significantly more than mites preying on undisturbed
239 *F. candida* (Wilcoxon: $\chi^2_{1,48} = 5.34$, $P = 0.021$), which laid a median of only 3 (25th q: 2; 75th q: 5)
240 eggs.

241

242 4. Discussion

243 Targeting generalist biocontrol agents towards a pest prey by priming them to the pest before
244 release is suggested as a way to improve efficiency in biological control (Cascone et al., 2015).
245 Such a response was recently indicated in the phytoseiid mite *Neoseiulus bicaudus* Wainstein (Su et
246 al., 2019), and can occur as predators learn to catch and handle abundant prey (Ishii and Shimada,
247 2010). However, if the target prey possesses a repelling defence, this may instead lead to an
248 aversion to such prey (Barnhisel, 1991). We found that *P. fimata* is a risky and occasionally deadly
249 prey to *G. aculeifer* because of its sticky defence secretions (Fig. 1A), and that *G. aculeifer*

250 subjected to live *P. fimata* subsequently had reduced preference for this prey (Fig. 2B). This lower
251 preference was accompanied by lower overall kill rate (Fig. 2A) and longer time to kill (Fig. 2C),
252 especially if the subsequent attack was targeting *P. fimata*. These results all indicate that *G.*
253 *aculeifer* learns from experience with the *P. fimata* defence mechanism under attacks and develop a
254 partial aversion against this prey following exposure.

255 During the eight days of experimental prey exposure, 4% of *G. aculeifer* feeding on *P.*
256 *fimata* were killed under attacks on this prey (Fig. 1A), and observations showed that many more
257 gained experience with the *P. fimata* defence fluids but survived the attack. Although the proportion
258 of lethal attacks appears relatively low, the risk of attacking *P. fimata* is substantial considering that
259 *G. aculeifer* has an adult lifespan of more than 100 days (Amin et al., 2014; Jensen et al., 2017).
260 Thus, it may be problematic to use such maintenance prey for extended periods, and an increased
261 preference for alternative high-quality prey would be an adaptive response. In aphids, a comparable
262 though rarely deadly defence mechanism is found (Dixon, 1958), and an aversion towards aphids
263 has previously been shown in wolf spiders provisioned with these prey (Toft, 1997). Our results
264 have implications for the understanding of predator-prey dynamics and in biological control by
265 demonstrating that experience with previous prey may affect predator foraging decisions. A
266 previous study, however, shows that the acquired aversion of *G. aculeifer* to *P. fimata* documented
267 in the current study is not maintained over a long period, at least not in the presence of large
268 juvenile *F. candida* as alternative prey (Jensen et al., 2019b).

269 Our results indicate that predators used to control *P. fimata* should not be maintained on this
270 prey as a priming treatment before release, since recent experience with live *P. fimata* increases
271 reluctance to kill and reduces preference for this pest. This suggests that naïve generalist predators
272 may be more efficient than experienced predators against risky target prey. Instead, maintaining the
273 control agent on an alternative high-quality and agile prey such as *F. candida*, keeps the predator

274 healthy while hungry and motivated to kill. Although 100% of starved mites attacked (Fig. 2A),
275 their longer time to kill than mites maintained on live *F. candida* indicates that these mites were
276 weaker and less active (Fig. 2C). To control *P. fimata* in the field, it might be advantageous to also
277 release *F. candida* as an alternative but more difficult prey especially if few *P. fimata* are available,
278 as these high-quality alternative prey might help sustain *G. aculeifer* in the field or facilitate
279 establishment (Azevedo et al., 2019; Brenard et al., 2018; Muñoz-Cárdenas et al., 2017; Rueda-
280 Ramírez et al., 2018). This is especially relevant since *F. candida* is harder to catch and generally
281 less preferred than *P. fimata* (Fig. 2B), while not damaging the crop (Fountain and Hopkin, 2005).

282 The tests with dead prey showed that the two springtail species used in the experiment had
283 equal nutritional quality, as attested by similar fecundity in the adult female *G. aculeifer* fed either
284 prey species (Fig. 1B). The lower fecundity of *G. aculeifer* fed live *F. candida* must therefore be
285 caused by lower catchability of the fast moving *F. candida* relative to slow moving *P. fimata* (Fig.
286 1B). Further evidence that *F. candida* were difficult to catch during the pretreatment period is given
287 by the higher fecundity of *G. aculeifer* exposed to disturbed *F. candida*. Disturbance stimulates
288 random movement of *F. candida*, which increases the preying success of *G. aculeifer*, and the
289 relative ease with which *G. aculeifer* caught *F. candida* during choice trials were facilitated by the
290 constant mild disturbance by the experimenter during these tests. In soil, such disturbance can be
291 caused by other animals within the soil fauna such as more active mesostigmatid mites, centipedes,
292 or ground beetles, and it has been shown experimentally that disturbance from one predator may
293 increase the availability of prey for another (Losey and Denno, 1998).

294 We conclude that *G. aculeifer* learn a partial immediate aversion against *P. fimata* following
295 eight days of maintenance on this species. Thus, priming on a risky prey with a deterrent defence
296 may lead to the opposite effect than intended, as the predator reduces its preference for the prey. In
297 the field, availability of alternative prey may be advantageous, as it would maintain preference for

the defended prey because of low risk that the predator develops an aversion. We encourage that more studies are performed to investigate the indirect interactions between pest- and alternative prey in agroecosystems managed with use of generalist predators for biological control.

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451

452 **Table 1.** Overall effects of pre-treatment diet (*Protaphorura fimata*, *Folsomia candida*, or
453 starvation) and prey state (live, dead, or absent) on survival and egg production during pre-
454 treatment, and proportion killing a prey and prey species killed (preference) under choice in the
455 adult female *Gaeolaelaps aculeifer*.

Factor	df	Survival		Egg production		Kill rate		Species killed	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Diet	1	5.61	0.0178	109.64	<0.0001	25.61	<0.0001	14.79	0.0001
Prey state	2	4.76	0.0924	586.34	<0.0001	49.05	<0.0001	16.53	0.0003
Diet × prey state	1	1.47e ⁻⁵	0.9969	47.82	<0.0001	10.77	0.0010	7.58	0.0059

456

457

458 **Table 2.** Overall effects of pre-treatment diet (*Protaphorura fimata*, *Folsomia candida*, or
459 starvation), prey state (live, dead, or absent), and prey species killed on time until kill under choice
460 in the adult female *Gaeolaelaps aculeifer*.

Factor	df	χ^2	<i>P</i>
Diet	1	222.06	<0.0001
Prey state	2	720.73	<0.0001
Species killed	1	30.82	<0.0001
Diet × prey state	1	143.75	<0.0001
Diet × species killed	1	1.63	0.2016
Prey stage × species killed	2	6.93	0.0312
Diet × prey state × species killed	1	3.70	0.0543

461

462

Figure legends

464

465 **Fig. 1.** Fitness measures of adult female *Gaeolaelaps aculeifer* during eight days of feeding on a
466 mixture of 15-30 small and larger juvenile *Folsomia candida* or *Protaphorura fimata*. (A) Survival
467 over the eight days. Different letters indicate significant differences (Likelihood ratio each pair
468 comparison at $\alpha = 0.05$). (B) Egg production over the eight days. Boxes show median and 10th,
469 25th, 75th, and 90th percentiles plus outliers. The *P*-value is from a Wilcoxon test across all groups.
470 Different letters indicate significant differences (Steel-Dwass test at $\alpha = 0.05$).

471

472 **Fig. 2.** Predation behaviour of adult female *Gaeolaelaps aculeifer* when given a choice between a
473 juvenile *Folsomia candida* or a juvenile *Protaphorura fimata* after eight days of feeding on either
474 prey. The mites were given two to four hours without prey before the choice assay and were
475 observed for up to two hours. (A) Proportion of *G. aculeifer* killing a prey within the two hours.
476 Different letters indicate significant differences (Likelihood ratio each pair comparison at $\alpha =$
477 0.05). (B) Proportion of either prey species selected by mites that attacked and killed a prey.
478 Different letters indicate significant differences (Likelihood ratio each pair comparison at $\alpha =$
479 0.05). (C) Time until first kill by mites that killed a prey. Boxes show median and 10th, 25th, 75th,
480 and 90th percentiles plus outliers. The *P*-value is from a Wilcoxon test across all groups. Different
481 letters indicate significant differences (Steel-Dwass test at $\alpha = 0.05$).

482

483

484 **Fig. 1**

485