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1 Prey-specific impact of cold pre-exposure on kill rate 2 and reproduction

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15

16

17 Abstract

- 18 1. Temperature influences biological processes of ectotherms including ecological
19 interactions, but interaction strengths may depend on species-specific traits. Furthermore,
20 ectotherms acclimate to prevailing thermal conditions by adjusting physiological
21 parameters, which often implies costs to other fitness-related parameters. Both predators
22 and prey may therefore pay thermal acclimation costs following exposure to suboptimal
23 temperatures. However, these costs may be asymmetrical between predator and prey, and
24 between the predator and different species of concurrent prey.
- 25 2. We investigated whether thermal pre-exposure affected subsequent kill rate and predator
26 fitness when foraging on prey that differ in ease of capture, and whether changes were
27 primarily caused by predator or by prey pre-exposure effects. Specifically, we were
28 interested in whether there were interactions between predator pre-exposed temperature and
29 specific prey.
- 30 3. Using the mesostigmatid mite *Gaeolaelaps aculeifer* as a generalist predator and the
31 collembolans *Folsomia candida* and *Protaphorura fimata* as prey, we measured the impact
32 of present temperature, predator pre-exposure temperature, prey pre-exposure temperature
33 (all 10 or 20°C), prey species, and all interactions on prey numbers killed, predator eggs
34 produced, and exploitation of killed prey in a full factorial design.
- 35 4. Mites killed *P. fimata* in equal numbers independent of the presence of *F. candida*, but
36 killed *F. candida* when *P. fimata* were absent. Mite kill rate and reproduction were
37 significantly affected by mite pre-exposure temperature and test temperature, but not by
38 prey pre-exposure temperature. Significantly more of the slower prey was killed than of the
39 quicker prey. Importantly, we found significant synergistic negative interaction effects

between predator cold pre-exposure and hunting prey of higher agility on predator kill rate and reproduction.

5. Our findings show that the negative effects of cold and cold pre-exposure on kill rate and reproduction may be more severe when predators forage on quick prey. The study implies that predator cold exposure has consequences for specific prey survival following cold due to altered predation pressures, which in nature should influence specific prey population dynamics and apparent competition outcomes. The findings exemplify how not only current but also preceding conditions affect ecological interactions, and that effect strength depends on the species involved.

KEYWORDS

cold acclimation, Collembola, Mesostigmata, predator-prey interactions, prey exploitation, reproductive output, temperature, thermal pre-exposure

55 1 | INTRODUCTION

56 Thermal conditions affect ecological processes including predator-prey interactions by influencing
57 factors such as predator attack rate and prey handling efficiency (Frazer & Gilbert, 1976;
58 Thompson, 1978). The predation pressure on prey increases at higher temperature, so the intensity
59 of predator-prey interactions is stronger at higher temperature (Rall et al., 2010; Dell, Pawar, &
60 Savage, 2014; Gilbert et al., 2014; Sentis, Morisson, & Boukal, 2015; Thakur et al., 2017).
61 Furthermore, temperature affects species composition by changing competition outcomes among
62 prey species that overlap in resource use (Grainger, Rego, & Gilbert, 2018), and adding the effects
63 of a predator to such systems might affect the apparent competition outcome between different
64 prey (Holt & Lawton, 1994). In nature, temperatures are rarely constant but fluctuate on a daily
65 and weekly basis. Nevertheless, it has been little investigated how shifting temperatures affect
66 ecological interactions, and thus whether effects of acclimation to temperatures may affect
67 processes at temperatures experienced in subsequent periods (Ferris & Wilson, 2012; Sentis,
68 Morisson, & Boukal, 2015). Moreover, it has not been investigated whether such carry over effects
69 on ecological interactions would be species specific, i.e. whether the strengths of some interactions
70 would be more affected than those of others.

71 Organisms have evolved adaptations to perform under changing temperatures (Prosser,
72 1955; Angilletta, 2009). A large part of these adaptations are expressed as phenotypic plasticity,
73 whereby individuals thermally acclimate to their environment by physiological adjustments that
74 are highly beneficial under shifting thermal conditions (Johnston & Bennett, 1996; DeWitt, Sih, &
75 Wilson, 1998; Chown & Terblanche, 2007; Kristensen et al., 2008; Harrison, Woods, & Roberts,
76 2012; Teets & Denlinger, 2013; Overgaard & MacMillan, 2017). This is particularly true for cold
77 acclimation that can markedly alter lower thermal limits of individuals (Klok & Chown, 2003;

78 Sinclair & Roberts, 2005; Sørensen, Kristensen, & Overgaard, 2016). However, effects of
79 predator-prey interactions in multispecies systems under the influence of rapidly changing biotic
80 and abiotic conditions may be difficult to predict (Symondson, Sunderland, & Greenstone, 2002),
81 which may be due to potentially asymmetric changes in responses between predator and prey, and
82 in between different prey species. Some predators and parasites are found to prey and parasitize
83 more efficiently at cold temperature after cold acclimation (Sørensen, Toft, & Kristensen, 2013;
84 Terblanche, 2014; Cascone et al., 2015). However, the reverse is true for others, which prey and
85 parasitize at a lower rate following cold acclimation across temperatures compared to warm
86 acclimated individuals as an apparent trade-off with cold tolerance (Prasad, Roitberg, &
87 Henderson, 2002; Helgadóttir, Toft, & Sigsgaard, 2017; Jensen et al., 2017).

88 The ecological consequences of phenotypic responses to environmental change for species
89 interactions and ecological communities remain largely unexplored (Gilman et al., 2010; Yang &
90 Rudolf, 2010). Because species differ in their responses to temperature fluctuations, the relative
91 abilities of species to acclimate or adapt to temperature shifts will affect the outcome of
92 interspecific interactions (Stireman et al., 2005). In a thermal acclimation experiment on fish,
93 warm (25°C) acclimated Australian bass, *Macquaria novemaculeata* (Steindachner, 1866), made
94 more attacks on mosquitofish, *Gambusia holbrooki* (Girard, 1859), prey than cold (15°C)
95 acclimated bass across test temperatures (Grigaltchik, Ward, & Seebacher, 2012). Another
96 interesting study on a parasitic trematode, *Ribeiroia ondatrae* (Looss, 1907), and its snail,
97 *Planorbella (Helisoma) trivolvis* (Say, 1817), intermediate host showed that when parasite and
98 host were acclimated at cold temperature before being shifted to warm, they released more
99 parasites than if continuously maintained at warm temperature, showing that acclimation
100 temperature affects the parasite-host interaction (Paull et al., 2015). In this study, however, parasite

101 and host were acclimated together and the separate effects of acclimation on each species could not
102 be examined.

103 Prey species differ in agility and ease of capture. For actively hunting predators, fast
104 species are harder to catch than slow species, and ease of capture might likely be temperature
105 dependent (Kruse, Toft, & Sunderland, 2008). Whereas the focus of thermal effects on predator-
106 prey interactions has this far been addressing effects of high temperature acclimation in a climate
107 change context, cold and cold acclimation has received less attention. However, intermittent cold
108 periods may have significant effects on population dynamics, particularly if there are carry-over
109 effects after thermal shifts due to physiological acclimation responses. Additionally, cold
110 acclimation physiology and its effect on the ecology and interactions between predators and prey
111 also has relevance in a more applied context, as cold storage is an important feature of the
112 industrial production of biological control agents before release (Luczynski, Nyrop, & Shi, 2008;
113 Colinet & Boivin, 2011). The impact of cold storage on the performance of biological control
114 agents in relation to target and alternative prey following release might therefore influence their
115 efficiency and performance in the field, in interaction with field temperature. The impact of cold
116 storage may further interact with the agility and catchability of different prey such as target versus
117 alternative prey, thus affecting the overall species-specific ecosystem balances.

118 Collembolans are abundant in agricultural fields and are important prey to generalist
119 arthropod predators (Bilde, Axelsen, & Toft, 2000). Furthermore, their species composition may
120 have implications further down the food chain and affect ecosystem functioning (Crowther, Boddy,
121 & Jones, 2011; Eisenhauer, Sabais, & Scheu, 2011). Moreover, some collembolans are pests in
122 agriculture by feeding on seedlings and roots of certain crops, thereby reducing yields (Spencer &
123 Stracener, 1930; Scott, 1964; Baker & Dunning, 1975). Here, we used the mesostigmatid mite
124 *Gaeolaelaps aculeifer* Canestrini as a generalist model predator. This species occurs naturally

125 across Europe (Krogh, 1995; Navarro-Campos et al., 2012), and serves as a biological control
126 agent against a range of crop pests in greenhouses and agroecosystems (Lesna, Sabelis, & Conijn,
127 1996; Berndt, Poehling, & Meyhöfer, 2004; Jess & Bingham, 2004; Gerson & Weintraub, 2007;
128 Navarro-Campos, Wäckers, & Pekas, 2016). Cold acclimation was recently shown to significantly
129 reduce consumption and reproduction across test temperatures in *G. aculeifer* feeding on eggs of
130 the flour moth *Ephesia kuehniella* Zeller (Jensen et al., 2017). However, thermal pre-exposure and
131 test temperature may asymmetrically affect predator-prey interactions with interactive effects
132 depending on prey species and agility. Such asymmetric effects would differently influence the
133 top-down potential of predators on specific species of prey, and may therefore differentially affect
134 prey populations.

135 We tested the effects of independent thermal acclimation of a predator and two species of
136 collembolan prey in a factorial design, including a slow, easy prey (*Protaphorura fimata* Gisin)
137 and a quick, more difficult prey (*Folsomia candida* Willem). We hypothesized that test
138 temperature and prey species would independently affect predator kill rate and reproduction, and
139 that temperature would affect predation on the quick prey more than on the slow prey. We
140 furthermore hypothesized that both predator and prey pre-exposure temperature would affect
141 predator kill rate and reproduction such that cold pre-exposure would reduce capture and escape
142 rates, but that predator pre-exposure temperature affected predator kill rate and reproduction more
143 than prey pre-exposure temperature. Finally and importantly, we hypothesized that predator
144 thermal pre-exposure effects on kill rate and reproduction would be more pronounced when
145 preying on difficult prey than on easy prey. Our study has implications for understanding specific
146 prey and predator population dynamics in thermally fluctuating environments. It furthermore has
147 implications for cold storage of biological control agents before release in the field relative to the
148 agility of the target prey.

149

150 2 | MATERIALS AND METHODS

151 2.1 | Study species

152 We used adult female *G. aculeifer* (Acari: Laelapidae) as predators, and the springtails *F. candida*
153 (Collembola: Isotomidae) and *P. fimata* (Collembola: Onychiuridae) as prey differing in ease of
154 capture. *Protaphorura fimata* are slow moving and lack a furcula (the appendage with which some
155 springtails can jump), and are therefore easy prey to capture for adult *G. aculeifer*. In contrast, *F.*
156 *candida* are fast and possess a furcula and are therefore more difficult for *G. aculeifer* to catch.
157 *Folsomia candida* is known to be a high-quality prey for *G. aculeifer* (Krogh, 1995; Heckmann et
158 al., 2007), whereas the nutritional quality of *P. fimata* for *G. aculeifer* has not been reported.
159 Physiological acclimation responses to cold are documented in both *F. candida* (Waagner et al.,
160 2013) and *P. fimata* (Holmstrup & Slotsbo, 2017), and likely involve costs to other traits such as
161 heat tolerance (Alemu et al., 2017). Whereas *F. candida* is not considered an agricultural pest
162 (Fountain & Hopkin, 2005), *P. fimata* occurs as a pest in weed-free crops including lettuce and
163 sugar-beet by damaging seedlings and roots (Baker & Dunning, 1975; Endlweber, Ruess, & Scheu,
164 2009; Joseph et al., 2015).

165

166 2.2 | Animals and maintenance

167 A culture of predominantly adult *G. aculeifer* was purchased from ÖRE Bio-Protect
168 (Schwentinental, Germany). The mites had been raised on vermiculite as substrate with mould
169 mites (*Tyrophagus putrescentiae* Schrank) as prey, and were set up in experiments within two days
170 of arrival. In both experiments, large juveniles of the two springtail species (*F. candida* and *P.*
171 *fimata*) were used as prey. The juveniles for each species were picked at a size where they were

close to adulthood but were still not laying eggs. Since *P. fimata* start laying eggs at a larger size than *F. candida*, the provided *P. fimata* were larger than the provided *F. candida* in the two experiments. Measurements of 50 randomly collected individuals within the size class used as prey for each springtail species showed that provided *F. candida* had a median length of 94 μm (25th quartile (q): 86 μm ; 75th q: 97 μm) and a fresh mass of 30 μg (25th q: 26 μg ; 75th q: 35 μg), and that provided *P. fimata* had a median length of 127 μm (25th q: 122 μm ; 75th q: 137 μm) and a fresh mass of 79 μg (25th q: 68 μg ; 75th q: 91 μg). As larger prey are more difficult to capture and handle for *G. aculeifer* within the prey range used (Baatrup, Bayley, & Axelsen, 2006), larger size of *P. fimata* (slow-moving) than of *F. candida* (fast-moving) has a conservative effect on the predation outcome with regard to prey agility. All prey were provided live. Both prey species were obtained from our long-term laboratory colonies reared on baker's yeast. Before pre-treatments, we heat-extracted the mites over two hours into transparent plastic cups (7.0 cm diameter $\times$ 4.5 cm height) with water-saturated Plaster of Paris and charcoal (8:1 ratio) bottoms, to a density of less than 100 mites per cup. Only adult female mites were used in experiments. The mites were kept at a 12:12 h light:dark cycle and near 100% relative humidity throughout. In both experimental tests, mites were maintained individually in 24-well plates with water-saturated Plaster of Paris and charcoal (8:1) bottoms. Numbers of killed prey items of each species was recorded daily while any remnants were removed. Both experiments were run over a period of seven days.

190

191 2.3 | Effects of prey species pre-exposure on *G. aculeifer* kill rate

192 Cups with adult female *G. aculeifer* were supplemented with either *F. candida* or *P. fimata* to pre-
193 expose the mites to either prey (12 cups per prey species). In the pre-treatment, a mix of juveniles
194 and adults of either prey species was provided, ensuring availability of early-instar stages that

195 could be readily killed. After 20 days, 72 adult female *G. aculeifer* pre-fed either prey species were
196 allocated to individual wells in six 24-well plates, including four of each of the six pre-exposure
197 and test prey combinations within each plate. From each prey pre-treatment, 24 mites were then
198 provided with the same prey as they were pre-fed while another 24 mites were given the other
199 prey, and the last 24 mites were given choice of both prey. Access to six live prey items was
200 ensured daily, providing three prey of each species in the choice treatment. The experiment was
201 performed at 20°C. The experimental setup is summarized in Figure S1.

202

203 2.4 | Effects of pre-exposure temperature, test temperature, and prey species on kill 204 rate and reproduction

205 Petri dishes with water-saturated Plaster of Paris and charcoal (8:1) bottoms containing *F. candida*
206 or *P. fimata* and yeast were placed at 10°C or 20°C for 19 days prior to experimental tests.
207 Similarly, cups with adult female *G. aculeifer* were placed at either 10°C or 20°C (10 cups per
208 temperature) to thermally acclimate the mites before experimental tests. Mites used in the
209 experiment were taken at random across cups within each pre-treatment temperature. We ensured
210 access to *ad libitum* feeding on early-instar *F. candida* in all cups. After 12 days of thermal
211 acclimation, 96 adult female *G. aculeifer* from each temperature were allocated to individual wells
212 in four 24-well plates (eight plates in total) and given one day of starvation before a consecutive
213 seven-day test period. Two plates with mites from each acclimation temperature were maintained
214 at 10°C while the other two were maintained at 20°C. Within each test temperature, mites in one
215 plate were given springtails acclimated at 10°C and mites in the other plate were given springtails
216 acclimated at 20°C. Within plates, mites in rows 1, 3, and 5 were given *F. candida*, and mites in
217 rows 2, 4, and 6 were given *P. fimata*. All mites were given four large juveniles of either springtail

species by the start of the test period. Killed springtails were recorded daily and replaced with new individuals from the same species and acclimation temperature, and laid mite eggs were counted daily and removed. Only in very few cases were all four prey individuals killed and in these cases most prey was left largely uneaten. Consumption from each killed prey was estimated visually to each quarter animal. Exploitation of killed prey for reproduction was calculated as the number of eggs laid divided by the number of prey killed per individual *G. aculeifer* over the test period. The experimental setup is summarized in Figure S2.

2.5 | Statistical analysis

Nonparametric tests were selected for all analyses because variances were unequal (Bartlett tests, $P < 0.05$) and because the data were in many cases not normally distributed (Shapiro-Wilk tests, $P < 0.05$). Effects of prey pre-exposure (*F. candida* or *P. fimata*), prey species provided during the test (*F. candida* or *P. fimata*), and their interaction on the number of prey individuals killed were analysed using a proportional hazard test (Cox, 1975). Similarly, effects of predator acclimation temperature (10 or 20°C), prey acclimation temperature (10 or 20°C), test temperature (10 or 20°C), prey species (*F. candida* or *P. fimata*), and their interactions on the number of prey individuals killed and mite eggs laid during the test period were analysed using proportional hazard tests. Effects of all factors on the exploitation of killed prey for reproduction was analysed by adding the number of killed prey as a covariate to the model for egg production. Effects of predator acclimation temperature, test temperature, and their interaction were furthermore tested within each prey species using the number of killed prey as a covariate in proportional hazard tests. The Wald statistic was used in all proportional hazard tests (Bangdiwala, 1989). Overall effects across pre-exposure and provided prey, and across predator acclimation temperatures, test

temperatures, and prey species were also compared using Wilcoxon tests, and individual treatment groups were compared using Wilcoxon comparison of each pair. Consumption from killed individuals of each prey species was similarly compared using a Wilcoxon test. All analyses were performed in JMP 13.0.0 (SAS Institute Inc., Cary, NC, USA).

245

3 | RESULTS

3.1 | Effects of prey species pre-exposure on prey-specific kill rate and prey selection

Pre-exposure to one or the other species of prey during 20 days prior to testing did not affect predator kill rate or reproduction (Proportional hazard: $\chi^2_{1,144} = 0.034$, $P = 0.85$). However, mites provided with *P. fimata* during the test killed significantly more prey than mites only given *F. candida* ($\chi^2_{1,144} = 20.34$, $P < 0.0001$, Figure 3). There was no interaction between prey species pre-exposure and test prey on kill rate ($\chi^2_{1,144} = 0.52$, $P = 0.77$). Equal numbers of *P. fimata* were killed regardless of the presence or absence of *F. candida* (Figure 1). Under choice conditions very few *F. candida* were killed. If only *F. candida* was available, however, they were killed in significantly higher numbers than under choice conditions. This demonstrates that the female *G. aculeifer* were fully capable of catching and killing the provided *F. candida*, but that they only did so when an easier alternative (*P. fimata*) was not available.

258

3.2 | Effects of pre-exposure temperature and prey species on kill rate and reproduction

Mite kill rate and egg production were significantly higher at 20°C than at 10°C (Table 1, Figure 2a and b). More interestingly, also the acclimation temperature of mites affected their kill rate and

263 reproduction (Table 1, Figure 2a and b). Mites that were acclimated at 20°C had significantly
 264 higher kill rate and reproduction than mites acclimated at 10°C regardless of test temperature and
 265 prey species (Table 1, Figure 2a and b). In contrast, the acclimation temperature of the prey did
 266 neither significantly affect predator kill rate nor reproductive output (Table 1), and we therefore
 267 pooled prey acclimation groups in Figure 2. Also the species of prey provided highly influenced
 268 kill rate and reproduction across treatments (Table 1). Mites killed more prey individuals and laid
 269 more eggs when given *P. fimata* than when restricted to prey on *F. candida* (Table 1, Figure 2a
 270 and b). Prey species interacted significantly with test temperature on predator kill rate and
 271 reproduction (Table 1), which reflects a stronger positive effect of high (20°C) test temperature on
 272 predation and reproduction in mites fed *P. fimata* than in mites fed *F. candida* (Figure 2a and b).
 273 Moreover, prey species interacted significantly with predator acclimation temperature (Table 1),
 274 reflecting a stronger negative effect of cold acclimation on predation and egg production in mites
 275 fed *F. candida* than in mites given *P. fimata* (Figure 2a and b). A significant interaction between
 276 predator acclimation temperature and test temperature on reproduction, but not on kill rate,
 277 furthermore shows that warm acclimated mites exploited killed prey better at warm temperature
 278 than did cold acclimated mites (Table 1, Figure 2a and b). Overall, the exploitation efficiency of
 279 killed prey was not affected by prey species (Table 1). However, we found a significant three-level
 280 interaction between test temperature, predator acclimation temperature, and prey species (Table 1).
 281 This reflects significant effects of acclimation temperature, test temperature, and their interaction
 282 on the exploitation of killed *F. candida* (Table 2, Figure 2c), whereas only test temperature
 283 affected the exploitation of killed *P. fimata* (Table 2, Figure 2c). Mites exploited killed *F. candida*
 284 at higher efficiency for egg production than killed *P. fimata* when warm acclimated, but not when
 285 cold acclimated (Table 2, Figure 2c). Mites consumed killed *F. candida* more completely than
 286 killed *P. fimata* (Wilcoxon: $\chi^2_{1,168} = 37.12$, $P < 0.0001$). A median of approximately 49% (25th q:

287 26%; 75th q: 73%) of killed *F. candida* and 78% (25th q: 64%; 75th q: 92%) of killed *P. fīmata*
288 biomass were left uneaten by mites that killed at least one prey.

289

290 4 | DISCUSSION

291 Temperature plays a major role in the interaction intensity between predators and prey (Laws,
292 2017). Higher temperature increases predation rate relative to prey reproduction, which intensifies
293 top-down control of prey (Kishi et al., 2005; Hoekman, 2010; Rosenblatt & Schmitz, 2016).
294 Moreover, different prey alternatives within a habitat may vary widely in their ease of capture as
295 some prey species are faster and more agile than others. Our experiment demonstrated that not
296 only current but also preceding thermal conditions significantly influence predator-prey
297 interactions. Furthermore, we show that the effects of temperature and pre-exposure temperature
298 significantly depends on and interacts with prey species. Predatory mites killed significantly fewer
299 prey and laid fewer eggs after cold acclimation, and this effect was exacerbated when hunting a
300 fast compared to a slow species of prey (Table 1, Figure 2a and b). In contrast, individuals of the
301 fast prey were more efficiently exploited once killed than individuals of the slow prey at high
302 temperature.

303 Adult female *G. aculeifer* were capable of catching and killing large juvenile *F. candida*,
304 but only did so when easier prey was not available, which demonstrates a clear preference for the
305 easier prey (Figure 1). This is consistent with a study on the pirate bug *Orius insidiosus* Say, which
306 in the presence of two congeneric thrips species, *Frankliniella bispinosa* Morgan and *Frankliniella*
307 *occidentalis* Pergande, preyed significantly more on the larger and slower species when both prey
308 were equally abundant, but were capable of killing either prey in equal numbers when only one
309 species was present (Reitz, Funderburk, & Waring, 2006). This preference is not to confuse with a
310 selective preference based on taste or nutritional quality of the prey (Lang & Gsödl, 2001; Provost,

311 Lucas, & Coderre, 2006). The lack of an effect of prey pre-exposure on species-specific predation
312 over the subsequent eight days further justifies using *F. candida* as the only prey during thermal
313 pre-exposure in the subsequent experiment.

314 It has previously been shown that predators have higher attack rate at higher temperature
315 (Lang, Rall, & Brose, 2012; Gilbert et al., 2014; Thakur et al., 2017), and that temperature
316 differently affects the hunting success of different predators depending on their hunting strategy
317 (Kruse, Toft, & Sunderland, 2008). As in previous studies, we found a higher predation intensity at
318 higher temperature, but the thermal effect was highly dependent on prey species and most
319 pronounced for mites hunting the slower prey (Table 1, Figure 2a). We furthermore found a
320 significant effect of previous thermal exposure, such that predation intensity was higher in predators
321 that had also experienced higher previous temperature. A similar response to thermal acclimation
322 was found for larvae of the dragonfly *Sympetrum vulgatum* Linnaeus feeding on *Daphnia magna*
323 Straus (Sentis, Morisson, & Boukal, 2015). Here, we further show that the specific prey
324 significantly influences the impact of not only test temperature but also of predator thermal
325 acclimation temperature on the predator-prey interaction. While predator pre-exposure temperature
326 significantly affected the rate of catching and killing prey, thermal pre-exposure of the prey did not
327 significantly affect predator capture and kill rate, indicating that prey acclimation costs to cold
328 exposure do not significantly affect their ability to escape. In accordance, cold acclimated
329 Australian bass showed a decrease in burst swimming performance at warm temperature, while
330 their cold acclimated mosquitofish prey maintained high burst swimming performance
331 (Grigaltchik, Ward, & Seebacher, 2012). The cold acclimation costs on the ability of predators to
332 catch prey are therefore apparently higher than the cold acclimation costs on the ability of prey to
333 escape.

334 The exploitation of killed prey for egg production was significantly higher for warm-
335 acclimated mites feeding on *F. candida* at warm temperature than for mites feeding on *P. fimata*,
336 which was only affected by test temperature (Table 1 and 2, Figure 2c). This can probably be
337 explained by more complete consumption of killed *F. candida* by warm-acclimated mites at warm
338 temperature, as many and large parts of killed *P. fimata* were observed to typically be left uneaten.
339 Warm-acclimated mites might further have the physiological machinery adjusted toward
340 reproduction, and might therefore more readily exploit ingested nutrients for egg production, while
341 cold-acclimated mites allocate more resources toward hibernation (Teets & Denlinger, 2013; Jensen
342 et al., 2017). Because *F. candida* were harder to catch than *P. fimata* and therefore more rarely
343 caught, each caught individual would be more valuable and was therefore more completely
344 exploited. Instead, *P. fimata* were often discarded without complete consumption and a new
345 individual could more readily be killed, also known as superfluous killing (Lang & Gsödl, 2003;
346 Fantinou et al., 2008). Therefore, the predator may have equal performance despite lower impact on
347 prey populations when hunting difficult compared to easy prey, as prey are more completely
348 exploited when more rarely caught (Figure 2).

349 Since easy prey were readily killed and individuals were poorly exploited, mites would
350 have higher negative impact on the population of easy prey (*P. fimata*) than on the difficult prey
351 (*F. candida*). When both prey were available in equal proportion, easy prey were killed in the same
352 numbers as when difficult prey were absent, even though easy prey were at half the density (Figure
353 1). This indicates that under natural conditions, there would be uneven predation pressure on the
354 two prey populations. Furthermore, our study shows that prey-specific predation pressures would
355 depend on temperature, and even more interestingly, on effects from preceding thermal conditions
356 on predator kill rate. This impacts the apparent competition between prey species (Holt & Lawton,
357 1994), which further influences prey-specific grazing pressures down the food chain (Crowther,

358 Boddy, & Jones, 2011). As temperatures in nature are rarely constant but continuously fluctuate,
359 our study aids in understanding predator-prey driven population dynamics in nature by
360 demonstrating that previous temperatures subsequently affect prey-specific predator-prey
361 interactions.

362 Biological control of a pest can be enhanced if alternative prey support persistence of the
363 predator when the target prey are scarce (Nomikou et al., 2002). The present study system is a
364 good example that alternative prey may enhance biological control by supporting the control agent
365 without inhibiting control of the target prey. If using *G. aculeifer* to control *P. fimata* in the field,
366 alternative prey like *F. candida* is typically present and will support *G. aculeifer* when *P. fimata*
367 populations are low. However, *P. fimata* is more readily preyed upon when the population is high
368 because of its ease of capture. We therefore propose that *G. aculeifer* would be a good biocontrol
369 agent against *P. fimata* in agriculture, and that the presence of *F. candida* as an additional food
370 would further enhance the control potential of *G. aculeifer* against *P. fimata*. Whereas cold storage
371 extends the shelf life of biocontrol agents before use (Luczynski, Nyrop, & Shi, 2008; Colinet &
372 Boivin, 2011), the present study shows that the agility of the target prey should be taken into
373 account when considering cold storage of predatory arthropods before use in biological control.

374 Many studies consider interaction strengths to be fairly fixed when applied in ecological
375 models (e.g. Berlow et al., 2009), although it is well known that temperature affects predation rates
376 (Dell, Pawar, & Savage, 2011; Laws, 2017). However, it is little studied how temperature and
377 thermal history affects predator-prey interactions as well as parameters essential for these
378 interactions such as predator locomotion and metabolic physiology (Clusella-Trullas, Terblanche, &
379 Chown, 2010; McCue et al., 2016; Williams et al., 2016). Further studies on the effects of thermal
380 history on predator physiological and behavioural performance would be useful to disentangle the
381 mechanisms that govern predator-prey dynamics. Additionally, effects of thermal history on e.g.

382 predator functional response to prey density would be of high ecological relevance for further
383 studies (Skalski & Gilliam, 2001; Englund et al., 2011).

384

385 5 | CONCLUSIONS

386 In conclusion, our study shows that the predation pressure of a generalist arthropod predator
387 depends on both current and previously experienced temperature, and that the effects of predator
388 thermal exposure and pre-exposure are prey-specific. Effects of both present and pre-exposure
389 temperature on predator kill rate and reproduction are larger when hunting a fast compared to a
390 slow prey. Predators compensate for the difficulty of catching fast prey by utilizing killed
391 individuals of the fast prey more completely, however only at warm temperature after warm pre-
392 exposure, supporting earlier findings that *G. aculeifer* acclimated to cold have adjusted their
393 physiology toward higher environmental robustness at the cost of reproduction (Jensen et al., 2017).
394 Our study further indicates that *G. aculeifer* would be an efficient control agent against *P. fimbata*,
395 and that the presence of alternative prey would enhance rather than limit the control of this pest.
396 Finally, considerations on cold storage of *G. aculeifer* and likely other predatory arthropods used in
397 biological control should include the agility of the target pest relative to alternative prey, as the
398 intensity of predator-prey interactions involving quick prey is more negatively affected after cold
399 storage of the predator than the intensity of predator-prey interactions involving slow prey. This
400 underlines the complexity of environmental effects and experienced environmental history on
401 ecological interactions, and emphasizes that not only current but also previous conditions affect
402 animal ecology.

403

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407

408 AUTHORS' CONTRIBUTIONS

409 K.J., S.T., L.S., J.G.S, and M.H. conceived the experiment. K.J. performed the experiment and
410 analyzed the data. K.J. wrote the first draft, and all authors contributed to the final draft.

411

412 DATA ACCESSIBILITY

413 Data available from the Dryad Digital Repository: doi:10.5061/dryad.pr06nk2 (Jensen et al., 2018).

414

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417

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626

TABLE 1 Proportional hazard tests on prey kill rate, reproductive output, and exploitation of killed prey for reproduction by female *Gaeolaelaps aculeifer* depending on pre-exposure temperature (predator PT; 10 or 20°C), prey pre-exposure temperature (prey PT; 10 or 20°C), test temperature (TT; 10 or 20°C), prey species (*Folsomia candida* or *Protaphorura fimata*), and their interactions. Adult female *G. aculeifer* were given thirteen days at either pre-exposure temperature feeding ad libitum on early-instar *F. candida* over the first twelve days followed by one day of starvation. They were then given seven days at either test temperature feeding *ad libitum* on either prey species. Both species of prey were given 19 days of pre-exposure at either temperature before the test period. Significant values are shown in bold

Factor	Prey individuals killed			<i>G. aculeifer</i> eggs laid			Exploitation of killed prey		
	<i>df</i>	χ^2	<i>P</i>	<i>df</i>	χ^2	<i>P</i>	<i>df</i>	χ^2	<i>P</i>
Predator PT	1	31.2637	<0.0001	1	24.3714	<0.0001	1	8.0802	0.0045
Prey PT	1	3.6790	0.0551	1	3.2723	0.0705	1	0.3382	0.5609
TT	1	106.6667	<0.0001	1	89.1814	<0.0001	1	21.3483	<0.0001
Prey species	1	40.8460	<0.0001	1	10.1660	0.0014	1	0.0969	0.7556
Predator PT × prey PT	1	0.0102	0.9196	1	0.6574	0.4175	1	0.7166	0.3972
Predator PT × TT	1	0.3819	0.5366	1	8.3697	0.0038	1	8.0849	0.0045
Predator PT × prey species	1	6.0574	0.0138	1	4.1842	0.0408	1	2.3790	0.1230
Prey PT × TT	1	0.3394	0.5602	1	1.2183	0.2697	1	0.7584	0.3838
Prey PT × prey species	1	0.1368	0.7114	1	0.0837	0.7723	1	0.0002	0.9880
TT × prey species	1	8.1160	0.0044	1	7.7874	0.0053	1	0.3941	0.5302
Predator PT × prey PT × TT	1	1.2502	0.2635	1	0.4781	0.4893	1	2.5517	0.1102
Predator PT × prey PT × prey species	1	3.0662	0.0799	1	0.4375	0.5083	1	0.0004	0.9835
Predator PT × TT × prey species	1	0.1632	0.6862	1	5.9921	0.0144	1	5.8552	0.0155
Prey PT × TT × prey species	1	0.0492	0.8245	1	0.1078	0.7427	1	0.0599	0.8067
Predator PT × prey PT × TT × prey species	1	0.8033	0.3701	1	0.4905	0.4837	1	0.1622	0.6871
Prey individuals killed	-	-	-	-	-	-	1	35.8651	<0.0001

635

636

637 **TABLE 2** Proportional hazard tests on the exploitation efficiency of killed prey for reproduction
 638 by female *Gaeolaelaps aculeifer* for each prey species (*Folsomia candida* or *Protaphorura fimata*),
 639 depending on predator pre-exposure temperature (predator PT; 10 or 20°C), test temperature (TT;
 640 10 or 20°C), and their interaction. Adult female *G. aculeifer* were given thirteen days at either pre-
 641 exposure temperature feeding *ad libitum* on early-instar *F. candida* over the first twelve days
 642 followed by one day of starvation. They were then given seven days at either test temperature
 643 feeding *ad libitum* on either prey species. Both species of prey were given 19 days of pre-exposure
 644 to either temperature before the test period. Significant values are shown in bold

Factor	<i>F. candida</i>			<i>P. fimata</i>		
	<i>df</i>	χ^2	<i>P</i>	<i>df</i>	χ^2	<i>P</i>
Predator PT	1	8.0859	0.0045	1	0.8665	0.3519
TT	1	16.0461	<0.0001	1	6.9073	0.0086
Predator PT × TT	1	11.0051	0.0009	1	0.0835	0.7727
Prey individuals killed	1	17.9548	<0.0001	1	17.2316	<0.0001

645

646

647 **Figure legends**

648

649 **FIGURE 1** Number of springtails killed by female *Gaeolaelaps aculeifer* during seven days of
650 feeding *ad libitum* on *Folsomia candida*, *Protaphorura fimata*, or a choice of both, following 20
651 days of restricted pre-exposure to either prey species. Pre-exposure and tests were conducted at
652 20°C. Boxes show median and 10th, 25th, 75th and 90th percentiles plus outliers. The *P*-values are
653 from Wilcoxon tests across all treatments. Different letters indicate significant differences
654 (Wilcoxon each pair comparison at $\alpha = 0.05$)

655

656 **FIGURE 2** (a) Number of springtails killed, (b) number of eggs laid, and (c) exploitation of killed
657 prey for egg production by female *Gaeolaelaps aculeifer* during seven days of feeding *ad libitum*
658 on *Folsomia candida* or *Protaphorura fimata* at either 10 or 20°C, following twelve days of pre-
659 exposure to either temperature. Prey pre-exposure temperature is not included as a factor on the
660 figure because it did not significantly affect predator kill rate and reproduction (Table 1). Boxes
661 show median and 10th, 25th, 75th and 90th percentiles plus outliers. The *P*-values are from Wilcoxon
662 tests across all treatments. Different letters indicate significant differences (Wilcoxon each pair
663 comparison at $\alpha = 0.05$)

664

665 **FIGURE S1** Design of the experiment investigating effects of restricted pre-exposure to different
666 prey

667

668 **FIGURE S2** Design of the experiment investigating effects of predator pre-exposure
669 temperature, prey pre-exposure temperature, test temperature, and prey species

670

671 **FIGURE 1**

672

675

676 **FIGURE S1**

Test prey = *Folsomia candida*

Pre-exposure prey = <i>F. candida</i>	Pre-exposure prey = <i>P. fimata</i>
--	---

Test prey = *Protaphorura fimata*

Pre-exposure prey = <i>F. candida</i>	Pre-exposure prey = <i>P. fimata</i>
--	---

Test prey = choice of both

Pre-exposure prey = <i>F. candida</i>	Pre-exposure prey = <i>P. fimata</i>
--	---

N = 24 in all treatment combinations

677

678

679 **FIGURE S2**

Test temperature = 10°C		Test temperature = 20°C	
Prey = <i>Folsomia candida</i>	Mite pre-exposure at 10°C Prey pre-exposure at 10°C	Mite pre-exposure at 10°C Prey pre-exposure at 20°C	Mite pre-exposure at 10°C Prey pre-exposure at 10°C
	Mite pre-exposure at 20°C Prey pre-exposure at 10°C	Mite pre-exposure at 20°C Prey pre-exposure at 20°C	Mite pre-exposure at 20°C Prey pre-exposure at 20°C
Prey = <i>Protaphorura fimata</i>	Mite pre-exposure at 10°C Prey pre-exposure at 10°C	Mite pre-exposure at 10°C Prey pre-exposure at 20°C	Mite pre-exposure at 10°C Prey pre-exposure at 20°C
	Mite pre-exposure at 20°C Prey pre-exposure at 10°C	Mite pre-exposure at 20°C Prey pre-exposure at 20°C	Mite pre-exposure at 20°C Prey pre-exposure at 20°C

N = 12 in all treatment combinations

680

681