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SHORT COMMUNICATION

Imprinted or innate food preferences in the model mite *Archegozetes longisetosus* (Actinotrichida, Oribatida, Trhypochthoniidae)

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Abstract

Most oribatid mites are opportunistic feeders with a broad variety of different food sources. However, preferences for certain food such as dark pigmented fungi, led to the 'choosy generalist'-hypothesis. The mechanisms behind this idea and whether oribatid mites have an innate or learned preference for food are unknown. We used *Archegozetes longisetosus* Aoki to test whether mites prefer unknown high quality food or food they have experienced before. We found that *A. longisetosus* did not prefer known food, and that food preferences were innate and not due to imprinting/learning behavior.

Keywords Behavioral ecology | soil fauna | choosy generalist

1. Introduction

Oribatid mites (Actinotrichida, Oribatida) feed on a wide range of different resources (Schuster 1956, Luxton 1972, Behan-Pelletier & Hill 1983, Schneider et al. 2004) and show basically a low degree of specialization in other aspects such as microhabitat preferences (Maraun & Scheu 2000, Valdecasas et al. 2006, Wehner et al. 2016). The preference for certain food has been studied in oribatid mites by gut boli/fecal pellet analysis (Anderson 1975, Labandeira et al. 1997, Meier et al. 2002), enzymology (Siepel & de Ruiter-Dijkman 1993, Hubert et al. 2001) or feeding preference tests in the laboratory (Riha 1951, Pande & Berthet 1973, Maraun et al. 1998, Hubert & Lukesova 2001, Maraun et al. 2003, Schneider & Maraun 2005, Koukol et al. 2009). These studies have demonstrated a broad food spectrum for oribatid mites, including leaf-litter, algae, fungi, lichen and dead animals (e.g. collembolans and nematodes). Especially certain types of dark pigmented fungi (family: Dematiaceae Fr.) are readily eaten by oribatids in biotests, yet the reasons for this behavior still remain conspicuous (Maraun et al. 1998, Maraun et al. 2003, Schneider et al. 2004, Schneider & Maraun 2005). In summary, oribatid mites seem to be mostly opportunistic feeders 'choosy generalists'; (Schneider & Maraun 2005), but with preferences, possibly for more nutrient-rich or less toxic food.

Studies on the spider mite *Tetranychus urticae* Koch (Actinotrichida, Prostigmata) and the predatory mite *Neoseiulus californicus* McGregor (Anactinotrichida, Mesostigmata) demonstrated effects of learned food preferences and foraging behavior, respectively (Egas & Sabelis 2001, Egas et al. 2003, Schausberger & Peneder 2017). For example, *T. urticae* with cucumber as food plant induced strong preferences for cucumber (for tomato mite strains), while exposure to tomato induced a strong aversion for tomato in cucumber mite strains (Egas & Sabelis 2001, Egas et al. 2004). Since cucumber as host plant yielded higher reproductive output (= high quality food), compared to tomato (= low quality food) and since both mite strains learned to prefer cucumber over tomato, learning seemed adaptive (Agrawal et al. 2002, Egas et al. 2003).

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This raises the question whether oribatid mites have an innate or imprinted food preference; i.e. do they exhibit an inborn preference for certain resources, which does not change *via* experience of higher quality food (= no learning effects/innate) or do they show preferences for higher quality resources in case they have fed on it before (= learning/imprinted). To test this we used *Archegozetes longisetosus* Aoki (Oribatida, Trhypochthoniidae) – a well-known model species for soil ecology and cell/developmental biology (Heethoff et al. 2007, Heethoff et al. 2013, Heethoff & Scheu 2016, Brückner et al. 2017) – raised on four resources of differing nutritional quality, ultimately resulting in variable reproductive output (for more details see Brückner et al. 2018b).

2. Materials and methods

Archegozetes longisetosus ran (Heethoff et al. 2007) stock cultures were kept in polypropylene boxes grounded with a mixture of plaster of Paris: activated charcoal (9:1) at 28°C and approximately 85–90 % relative humidity in complete darkness. *Archegozetes longisetosus* cultures were fed *ad libitum* with either *Chlorella* powder (Naturya, Bath, UK), lupine flour (Govinda Natur GmbH, Neuhofen, Germany), wheat grass powder (wheat; Naturya, Bath, UK) or dry yeast (Rapunzel Naturkost GmbH, Legau, Germany) three times a week. We offered *Chlorella* powder, lupine flour, wheat grass powder and grinded dry yeast to *A. longisetosus* which have been cultured on one of the four resources (= origin) for at three generations ($n_{Chlorella}$= 120 specimens; n_{lupine}= 590 specimens; n_{wheat}= 300 specimens; n_{yeast}= 300 specimens; different numbers are due to different breeding successes over the three generations), to test whether oribatid mites are imprinted to a resource they experienced as juvenile instars or possess an innate preference for certain food. The experiments were performed in plastic petri-dishes (4.5 × 1.5 cm) grounded with moist analytical filter paper (both, Hartenstein GmbH, Würzburg, Germany), and the food powders were placed marginally in a circle to guarantee maximum distance. Ten specimens were used for every replicate (n = 131). After one hour we counted the number of specimens resting on each of the offered resources. Unresponsive individuals were not counted and excluded from the analysis. We used a generalized mixed effect model (GLMM) with overall oribatid mite counts as response variable, origin and resource choice as fixed factors and experimental ID as random factor. The GLMM was fitted with a negative-binomial error distribution (goodness-of-fit test for the response variable: χ^2 = 6.9; p = 0.44) and log as link-function. Overall preference differences among the food sources were accessed using Wilcoxon signed-rank tests with affiliated false-discovery rate correction (Benjamini & Hochberg 1995). Statistics were performed in R 3.3.1 'Bug in Your Hair' (R Core Team 2016) using the R packages 'nlme' (Pinheiro et al. 2017), 'lme4' (Bates et al. 2015) and 'car' (Fox & Weisberg 2011).

3. Results

Archegozetes longisetosus preferred distinct resources (resource choice: Wald-χ2 = 9.6; df = 3; P = 0.022; Tab. 1), but origin had no effect (origin: Wald-χ2 = 4.36; df = 3; P = 0.215). Accordingly, preferences were not influenced by the resources the specimens developed on (interaction resource choice x origin: Wald-χ2 = 2.84; df = 9; P = 0.971). Overall, *A. longisetosus* individuals were mostly attracted by lupine, to a lesser extent by wheat and yeast, and least by *Chlorella* (see pairwise tests in Tab. 1).

4. Discussion

Archegozetes longisetosus did not prefer well-known resources, but rather showed an innate general preference (Tab. 1). Interestingly, this innate behaviour was not related to reproductive fitness, because the most preferred resource, lupine (number off offspring per female: 18.98 ± 4.48; mean ± SD), does not generate the highest number of offspring compared to the other three resource (chlorella: 1.44 ± 0.56; wheat: 44.76 ± 5.41; yeast: 22.20 ± 2.01), but rather represents a food with intermediate offspring production (numbers are extracted from Brückner et al. 2018b). The lack of any imprinting was rather surprising, because the used mite stock-cultures

Table 1. Proportions of *Archegozetes longisetosus* individuals counted on the different food sources depending on their origin and the total mean proportion (± SD) of mites on each chosen resource. The same letters indicate no differences among groups (P > 0.05) in pairwise Wilcoxon test comparisons of the overall resource choice after false discovery rate correction.

origin	**resource choice**			
	chlorella	lupine	wheat	yeast
chlorella	20	44	19	17
lupine	14	35	25	26
wheat	17	25	28	30
yeast	17	36	25	22
total	**17 ± 2 a**	**35 ± 7 c**	**24 ± 3 b**	**24 ± 5 b**

had exclusively been raised on one of the four offered resources for several generations before the experiment. Based on the learning effect found in *T. urticae* (e.g. Egas et al. 2003, Egas et al. 2004) we had expected to find at least a certain imprinted preference of wheat/yeast raised mite for their resource or a general switch to the resource which results in the highest reproductive output. This was, however, not the case and the strong innate preference for lupine may thus be caused by other than fitness related attributes (e.g., olfactory signals). Indeed, lupine powder was the food with the highest fatty acid content (Brückner et al. 2017) of all offered resource, supporting the idea that fatty acids could serve as important olfactory signals in *A. longisetosus* (see Brückner et al. 2018a).

Furthermore, food preference imprinting may be not beneficial for a highly opportunistic/generalist oribatid mite species like *A. longisetosus*, since such species need to switch food resources quite regularly to obtain exploitable nutrients in an environment with patchy distributed resources (Farley & Fitter 1999, Hodge 2006), and high densities of potential competitors (Hassall et al. 1986). Additionally, compared to plant parasites and predators (Egas & Sabelis 2001, Egas et al. 2003, Schausberger & Peneder 2017), learned associations may not be necessary for detritivores (see also Sitvarin et al. 2015), since they actually 'live' in their own food substrate and thus do not need to forage for distant food sources, a process often related to higher energetic costs (e.g. Schowalter 2016).

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6. Authors' contributions

MH and AB designed the research; RS, TS and AB performed bioassays; AB analysed the data; AB and MH wrote the paper. All authors read, discussed and approved the final version.

7. Competing financial interests

The authors declare no competing financial interests.

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