

# A thelytokous predatory mite is more cannibalistic towards distant kin

Keshi Zhang<sup>a,b, </sup> and Zhi-Qiang Zhang<sup>a,b,\* </sup>

<sup>a</sup>School of Biological Sciences, University of Auckland, 3A Symonds Street, Auckland, 1072, New Zealand and

<sup>b</sup>Manaaki Whenua – Landcare Research, 231 Morrin Road, Auckland, 1072, New Zealand

\*Address correspondence to Zhi-Qiang Zhang. E-mail: [zhangz@landcareresearch.co.nz](mailto:zhangz@landcareresearch.co.nz)

Handling editor: Zhi-Yun JIA

## Abstract

Kin recognition has been widely observed in various taxa. Cannibalism avoidance may be a strong driver for the evolution of kin recognition, as it may avoid a reduction in inclusive fitness. Kin recognition has recently been observed in a generalist phytoseiid, *Amblyseius herbiocolus* (Acari: Phytoseiidae). This study experimentally examined the degree of relatedness needed between prey larvae and cannibal adults of *A. herbiocolus* for the occurrence of kin discrimination. The adults were individually placed in enclosed arenas with two prey, a daughter and a more distant related larva, to observe their cannibalizing choice. The adults of *A. herbiocolus* did not discriminate between close relatives (daughter versus niece) but preferably cannibalized more distant kin (i.e., first and second cousins once removed). Phenotype matching and familiarization seem prominent as recognition mechanisms used by *A. herbiocolus* adults. The effect of learning on kin recognition through prior contact in *A. herbiocolus* requires further investigation. Studies on other adaptive functions of kin recognition of *A. herbiocolus*, such as cooperation and parental care, may provide meaningful insights.

**Key words:** Acari, cannibalism, choice test, close kin, discrimination, kin recognition.

## Abstract

Identifying relatedness is significant to the evolution of social behavior, and the knowledge of how relatedness and behavior are interrelated is essential to predicting species ecology (Breed 1998; Penn and Frommen 2010; Fisher et al. 2021). Kin recognition, the ability to discriminate and treat conspecifics differently according to their genetic relatedness, has been widely observed across the animal kingdom (Hamilton 1964; Holmes and Sherman 1983; Tang-Martinez 2001; West et al. 2007; Penn and Frommen 2010; Clemens and Brecht 2021). The perception and identification of individually associated cues can instigate different actions toward individuals of varying relatedness (Mateo 2004; Penn and Frommen 2010; Godoy et al. 2016). Kin recognition is used in social interactions, including parental care, cooperation, competition, cannibalism and group living (Waldman 1988; Pfennig and Frankino 1997; Fellowes 1998; Pfennig et al. 1998; Penn and Frommen 2010). Prior association and phenotype matching are among the most reported kin recognition mechanisms (Mateo 2004; Penn and Frommen 2010; Henkel et al. 2011; Clemens and Brecht 2021). Prior association is the direct learning of individual's phenotypic cues that can be used to recognize familiar relatives from unfamiliar conspecifics later encountered (Mateo 2004; Penn and Frommen 2010). Phenotype matching is the generalization of a template from assessing own or other conspecific's characteristics to allowing the discrimination between indirectly familiar and unfamiliar phenotypes later encountered (Mateo 2004; Penn and Frommen 2010; Henkel et al. 2011; Clemens and Brecht

2021). Other recognition mechanisms were also reported (Penn and Frommen 2010). For example, contextual (or spatial) cues, such as locality (e.g., nests or burrows) can provide information on the kinship of individuals encountered (Mateo 2004; Penn and Frommen 2010). Genetic recognition, where recognition alleles mediate the recognition process, has also been suggested (Mateo 2004; Penn and Frommen 2010; Leedale et al. 2020). Inbreeding avoidance and increased inclusive fitness have been suggested as the ultimate causes of kin recognition (Hamilton 1964; Holmes and Sherman 1983; West et al. 2007; Johnstone and Cant 2008; Penn and Frommen 2010). Individuals would avoid inbreeding when it is deleterious to do so, and show altruistic behaviors to increase their own and relatives' reproductive success (Penn and Frommen 2010).

Phytoseiidae (Acari: Mesostigmata) contains many cannibalistic predatory mites (Schausberger 2003). Cannibalism has been suggested as a cause for the evolution of kin recognition in invertebrates (Schausberger and Croft 2001; Fisher et al. 2021). Identifying between kin and non-kin is essential to the inclusive fitness of a cannibal (Schausberger 2003): by preferentially eating non-kin, cannibals can gain nutritional benefits without reducing their inclusive fitness (Schausberger 2003; Khodaei and Long 2020). Several phytoseiids have been found to recognize kin, including the specialist predators, *Phytoseiulus persimilis*, and *P. macropilis* (Schausberger and Croft 2001), and generalist predators, *Amblyseius herbiocolus*, *Gynaeseius liturivorus*, *Iphiseius degenerans*, and *Neoseiulus californicus* (Faraji et al. 2000; Christiansen

Received 6 July 2022; accepted 14 September 2022

© The Author(s) 2022. Published by Oxford University Press on behalf of Editorial Office, Current Zoology.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)

and Schausberger 2017; Saitoh and Choh 2018; Zhang and Zhang 2022). Prior association and phenotype matching were mostly reported in phytoseiids (Schausberger 2005, 2007; Christiansen and Schausberger 2017; Schausberger and Çekin 2020). However, the two mechanisms are not mutually exclusive. Without prior association, *P. persimilis* preferred the cannibalism of non-kin (Schausberger and Croft 2001). However, when familiarization was allowed, unfamiliar kin were favored by *P. persimilis* cannibals over familiar non-kin (Schausberger 2007). These results indicate the ability of *P. persimilis* to use multiple kin recognition mechanisms, which can be modified through learning.

Sexually produced diploid organisms share half of their genetic material with their parents (Makowicz et al. 2018). However, with no fertilization, meiosis and fusion of gametes (syngamy) do not occur during parthenogenesis or thelytoky (Normark and Kirkendall 2009; Stenberg and Saura 2009). Therefore, the degree of genetic relatedness between a mother and her offspring, and among offspring is higher in thelytokous than sexually reproducing species (Makowicz et al. 2016). Kin recognition in species with extreme intra-specific genetic similarities is less understood than in sexually reproducing individuals (Makowicz et al. 2016). The thelytokous raider ant (*Cerapachys biroi*) can distinguish between nest and non-nest mates (Kronauer et al. 2013). The clonal species, Amazon mollies (*Poecilia formosa*), are more aggressive towards distant kin (non-sister clones) compared to clonal sisters (Makowicz et al. 2018). We recently observed kin recognition (kin versus non-kin) ability in a thelytokous phytoseiid *A. herbicolus* (Zhang and Zhang 2022). Most studies on kin recognition focused on discrete classes of kin and non-kin (Ryan and Lacy 2003; Cassinello and Calabuig 2008). Fine-scale kin discrimination (small difference in their kinship) has only been reported in several vertebrate species (e.g., mice, *Peromyscus polionotus rhoadsi*, aoudad *Ammotragus lervia*, and Siberian jays *Perisoreus infaustus*) (Ryan and Lacy 2003; Cassinello and Calabuig 2008; Griesser et al. 2015). However, it is uncertain whether the asexually reproduced *A. herbicolus* can show fine-scale discrimination of relatives regarding the degree of their relatedness. Since *A. herbicolus* reproduce asexually, parents and offspring would share remarkable genetic similarities (Makowicz et al. 2018). Therefore, we hypothesize that individuals would be less likely to discriminate between close relatives (i.e., mother, daughter, and niece). As a result, those more distantly related individuals will be preferably cannibalized. To test this hypothesis, the difference in relatedness needed between prey larvae and cannibal adults of *A. herbicolus* for the occurrence of kin discrimination was examined experimentally.

## Materials and methods

### Mite rearing

*Amblyseius herbicolus* adults were field-collected from naturally infested nightshade *Solanum nigrum* leaves at Manaaki Whenua—Landcare Research, St Johns, Auckland, and from a garden in Epsom, Auckland, and maintained under laboratory conditions during early 2021. The dried fruit mite *Carpoglyphus lactis* (Acari: Astigmata), obtained from Bioforce Limited (Karaka, Auckland), was fed to *A. herbicolus* (see Zhang and Zhang 2021, for details). Cultures were checked weekly, and yeasts and *C. lactis* were replenished when needed. Culturing arenas and experiments were maintained at  $25 \pm 1$  °C,  $80 \pm 5\%$  relative humidity, and 16:8 h (L:D).

### Experimental set-ups

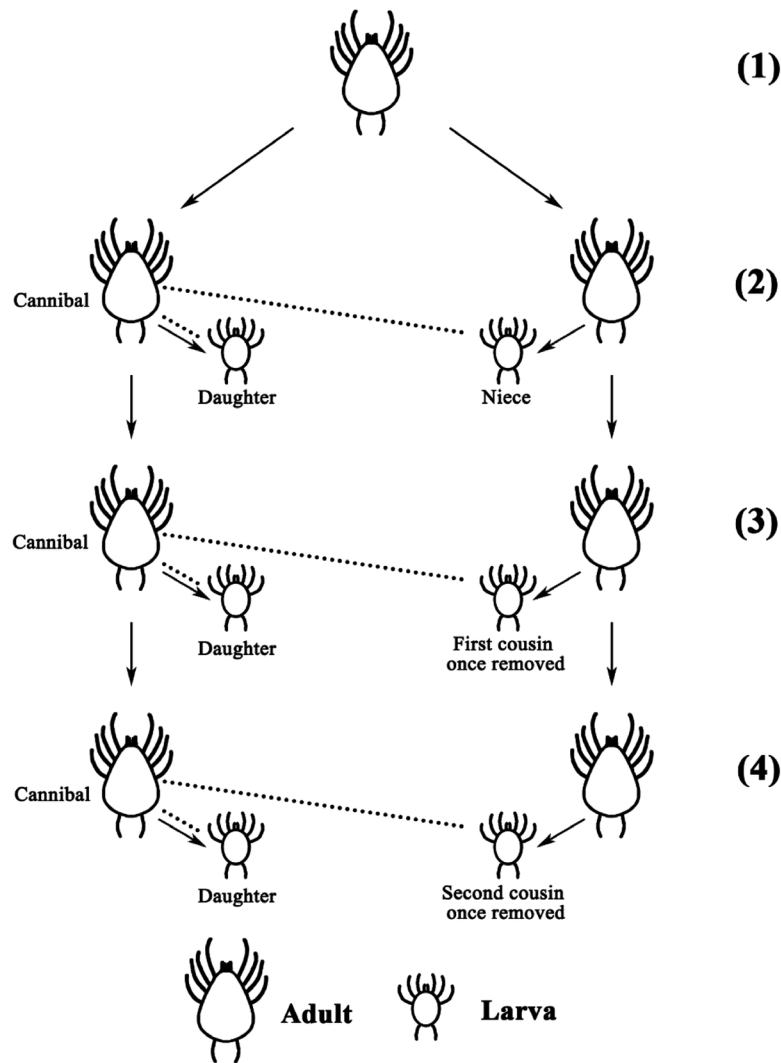
A choice experiment was done using the methods of Schausberger and Croft (2001) and Zhang and Zhang (2022). Modified Munger cells were used for rearing and testing (see Zhang and Zhang 2021, for details). Eggs of *A. herbicolus* (collected from cultures using 2-cm long purple threads) were reared singly with ad libitum mixed stages of *C. lactis* using the modified Munger cells to breed different families (Figure 1). For each family, the first adult (common ancestor) was not used in the choice test but allowed to lay eggs to breed the second generation. The eggs were hatched individually in new Munger cells and reared until oviposition. More than four eggs were harvested from each adult of the second generation. Rearing cells were checked twice a day, and eggs laid by the prospective cannibals were removed immediately and placed into new cells individually for hatching. Thus, contact between adults and their hatched larvae before the choice test was limited to few hours. One egg laid by the adults from the second generation was reared for the third generation, while others were used as prey in the choice test. The choice of eggs being used as prey or to start the next generation was randomly assigned (using a random number generator). The same steps were repeated for the fourth generation. Adults from the second, third, and fourth generations were tested as cannibals in the choice experiment. Cannibals and prey were tested separately between generations. Twenty families were replicated, and a total of 80 testing subjects (i.e., 20 families with 4 cannibals per generation) were available for each generation (second, third, and fourth). A subset of the testing subjects was lost due to human errors or death from random causes. Each choice combination was replicated more than 60 times (daughter versus niece:  $n = 62$ ; first cousin once removed:  $n = 62$ , and second cousin once removed = 70).

Adult cannibals used in the experiment were at the beginning of their oviposition period (3–9 days after the final molt), and larvae were within 20 h post-hatching. To ensure they were of similar sizes, larvae were not fed. Hunger level can modulate kin discrimination in *A. herbicolus* (Zhang and Zhang 2022). With extended starvation, the benefit of cannibalism can outweigh the cost of eliminating kin (Van den Beuken et al. 2019). Therefore, the cannibals were not starved before the choice test in this study.

### Experimental procedures

For the choice test, one adult and two prey were placed into the cell (Figure 1). No food (*C. lactis*) except water was provided to the choice test cells. One prey was the daughter of the cannibal and the other prey was close kin (nieces), intermediate kin (first cousin once removed), or distant kin (second cousin once removed). Randomly selected colors were marked on the dorsal shields of both prey for distinction. Mites in the cells were checked every 30 min until the death of one prey individual. Choice and latency (time elapsed from the start of the experiment to the cannibalism of one larva) were recorded. Cells were monitored for 6–8 h during the day and unmonitored overnight.

Each cannibal and prey individual was used only once in the experiment. Live subjects were returned to the culture. During the choice test, newly laid eggs by the cannibals were removed immediately from the cell. Cells were excluded from the experiment when a larva starved to death (body not deflated), when cannibals ate both prey before observation, or when the cannibal died before eating a larva.



**Figure 1.** Family tree of *Amblyseius herbicolus*. The relatedness of adults within the same generation is: common ancestor (1), siblings (2), first cousins (3), and second cousins (4). Arrows point to the descendants. Dotted lines denote larvae used as prey for the choice test, and the relatedness of the prey to the cannibals are indicated.

### Statistical analysis

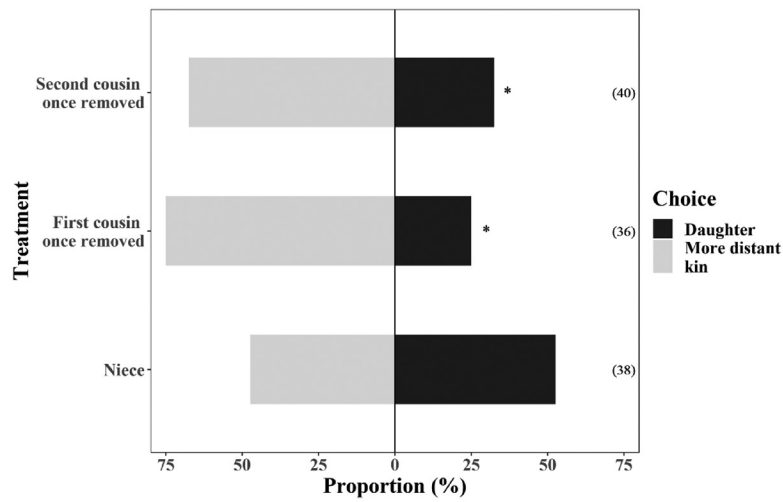
R version 4.0.5 (R Development Core Team 2021) was used for statistical analysis and package ggplot2 (Wickham 2016) for generating graphs. The preference of *A. herbicolus* was determined using a two-tailed binomial test, with the probability of eating daughters being 0.5. The mixed effects logistic regression (Bates et al. 2015) was used to determine the effect of latency to cannibalism on the choice (daughter or more distant kin) made by the cannibals, which included random effects of the longitudinal design and individuals' relatedness. Overdispersion test was done on the mixed effects logistic regression model. The amount of cannibalism was summarized with proportion and standard errors. Proportions were compared using the chi-square test. An alpha level of 0.05 was used.

### Results

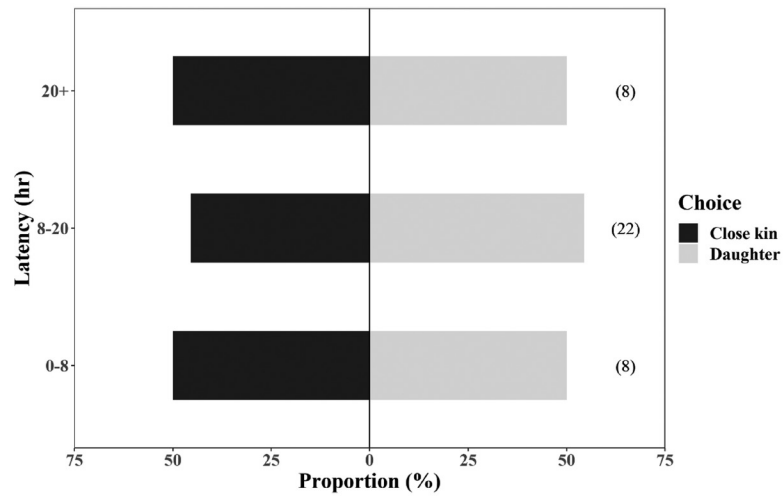
Adults of *A. herbicolus* did not show a preference for either their daughters or their nieces when given a choice ( $P = 0.871$ ) (Figure 2). When the distance of genetic relatedness

increased, adults of *A. herbicolus* displayed a statistically significant preference towards larvae of their first ( $P = 0.004$ ) and second ( $P = 0.039$ ) cousins over their daughters.

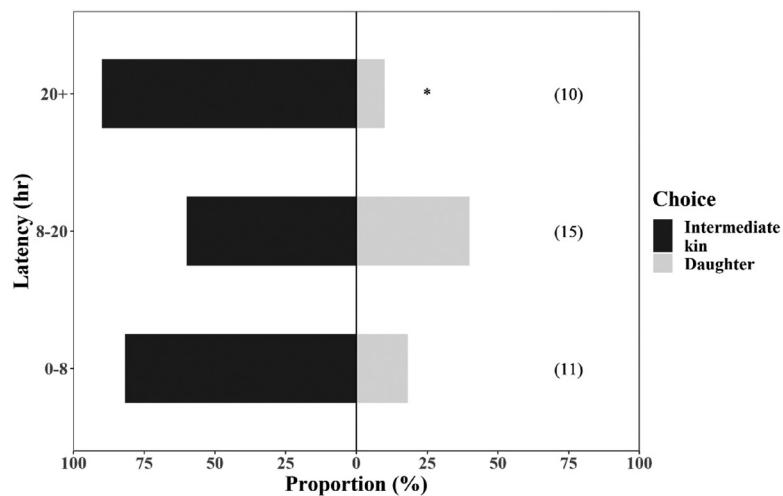
The cannibalism preference was not affected by the latency to cannibalism (mixed effects logistic regression: likelihood ratio test = 0.020,  $df = 1$ ,  $P = 0.887$ ). No significant overdispersion was detected (overdispersion ratio = 1.003,  $P = 0.473$ ). The early attackers (0–8 h) and late attackers (8–20 and > 20 h) were all non-discriminant between daughters and nieces (Figure 3). The preference to cannibalize the first cousin's larva rather than their own within the first 8 h, between 8 and 20 h (overnight predation), and after 20 h was marginally non-significant ( $P = 0.065$ ), non-significant ( $P = 0.607$ ), and significant ( $P = 0.021$ ), respectively (Figure 4). The early attackers (0–8 h) and late attackers (8–20) had non-significant ( $P = 0.344$ ) and marginally non-significant ( $P = 0.064$ ) preferences, respectively, to cannibalize the second cousin's larva rather than their own (Figure 5). Adults showed no preference ( $P = 1$ ) towards second cousin's larvae rather than their own for cannibalism that occurred after 20 h.



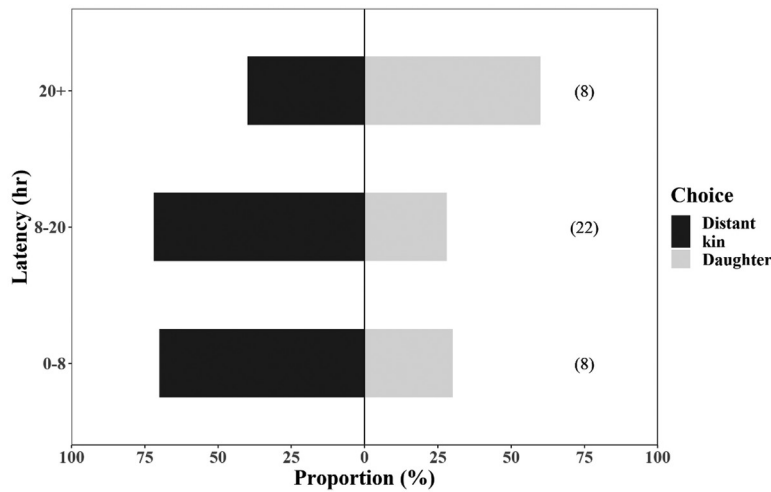
**Figure 2.** Prey cannibalized by *Amblyseius herbicolus* adults with a choice between daughters versus niece, daughters versus first cousin once removed, and daughters versus second cousin once removed. Sample sizes are in parentheses for each treatment. Asterisks denote significant differences in the adults' choice (two-tailed binomial test:  $P = 0.039$  and  $0.004$  from top to bottom).



**Figure 3.** Prey cannibalized by *Amblyseius herbicolus* adults, choosing between daughters and nieces at different latency periods. Sample sizes are in parentheses for each period. Chi-square test on the proportion between different periods:  $X^2(2) = 0.077$ ,  $P = 0.962$ .



**Figure 4.** Prey cannibalized by *Amblyseius herbicolus* adults, choosing between daughters and first cousin's larvae at different latency periods. Sample sizes are in parentheses for each period. Asterisks denote significant differences in the adults' choice (two-tailed binomial test:  $P = 0.021$ ). Chi-square test on the proportion between different periods:  $X^2(2) = 3.273$ ,  $P = 0.195$ .



**Figure 5.** Prey cannibalized by *Amblyseius herbicolus* adults, choosing between daughters and second cousin's larvae at different latency periods. Sample sizes are in parentheses for each period. Chi-square test on the proportion between different periods:  $X^2(2) = 1.983$ ,  $P = 0.371$ .

Most adults of *A. herbicolus* cannibalized a conspecific larva during the experiment: 92.7% (daughter versus niece), 87.8% (daughter versus first cousin once removed), and 93% (daughter versus second cousin once removed). The proportion of cannibalism between different choice groups was statistically similar [chi-square test:  $X^2(2) = 0.879$ ,  $P = 0.644$ ]. The proportion of cannibalism at different latencies (i.e., 0–8, 8–20 and 20+ h) did not vary significantly between different treatments [chi-square test:  $X^2(4) = 4.516$ ,  $P = 0.341$ ] (Figure 6). The latency to cannibalism varied between 0.5 and 35.1 h. However, most cannibalism occurred more than 8 h after the cannibal and prey were placed into the choice cell.

## Discussion

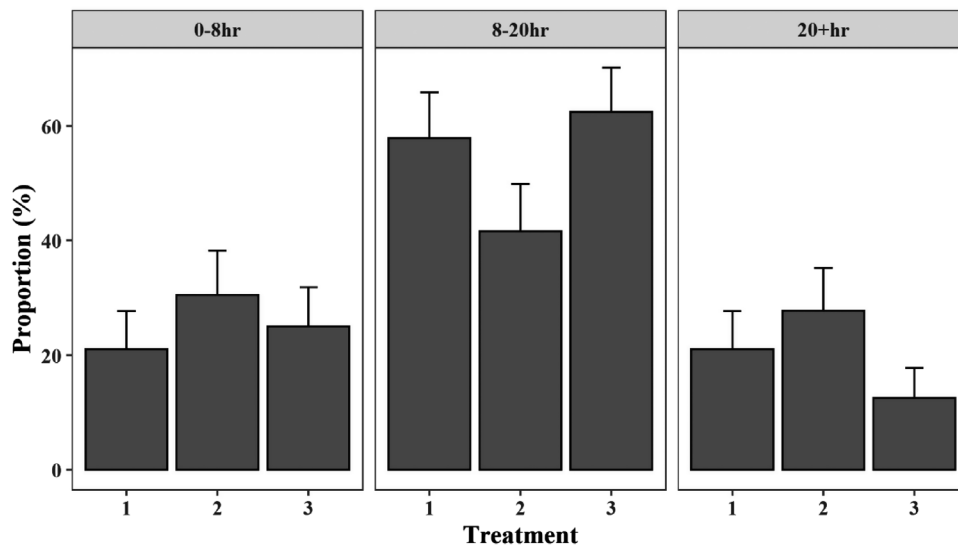
Relatively fine-scale discrimination to other invertebrates was found in *A. herbicolus*, where adults preferentially cannibalized cousin's larvae over their own daughters. To our knowledge, only limited invertebrate species have been reported with this relatively fine-scale kin discrimination; most were eusocial insects. For example, honey bees *Apis mellifera* can have multiple patrines within a colony, where workers were found to cooperate with full-sisters but were aggressive against half-sisters (reviewed in Carlin 1988). The cuticular profiles of the leafcutter ant *Acromyrmex octospinosus* are genetically polymorphic and can potentially allow the discrimination between full- and half-sister workers (Nehring et al. 2011). The ponerine ant *Pachycondyla villosa* and paper wasp *Polistes fuscatus* can recognize individual nest mates (Tibbetts 2002; D'Ettorre and Heinz 2005). The recognition of conspecific individuals based on familiarity was also found in the predatory mite *P. persimilis* (Schausberger 2005, 2007). However, it has been suggested that compared to noneusocial species, highly cooperative eusocial species with a division of labor would face a higher cost of nepotism, and fine-scale discrimination of different matrines or patrines would be less likely (Lihoreau et al. 2016).

In contrast, many vertebrate species show fine-scale discrimination among close relatives. The mandrill *Mandrillus sphinx* performed more grooming towards close kin (mother, offspring, and maternal half-siblings) compared with more distant kin (grandmother, aunt, uncle, and cousin) and

non-kin, despite the richness of groomees' contagious parasite load (Poirotte and Charpentier 2020). Female freshwater rainbowfish *Melanotaenia eachamensis* preferred shoaling with full-sib sisters over half-sib sisters and non-kin, but preferred shoaling with non-kin brothers over half- and full-sib brothers (Arnold 2000). Belding's ground squirrels *Spermophilus beldingi* recognize close kin (mother, sisters, and daughters) from distant kin (grandmother, aunts, and cousins) by producing more alarm calls (Sherman 1977; Mateo 2002). Our study suggests that the thelytokous invertebrate species such as *A. herbicolus* can have relatively fine-scale kin discrimination compared to vertebrate species. Whether *A. herbicolus* can show a preference towards cannibalizing distant kin (i.e., cousin's larvae) versus non-kin may be interesting for further investigation.

The choice test found that adults of *A. herbicolus* did not show a preference in cannibalism between close relatives (i.e., daughter and niece). Likewise, the gregarious cockroaches *Blattella germanica* had similar preferences to rest with full-siblings and half-siblings or cousins (Lihoreau et al. 2016). Although *B. germanica* had enough variations in the chemical properties of their cuticular hydrocarbon profiles to allow accurate discrimination between close relatives, behaviorally, they did not. Chinook salmon *Oncorhynchus tshawytscha* discriminated against non-kin and kin behaviorally but showed similar aggressiveness towards full- and half-siblings (Henkel et al. 2011). Due to a lack of specificity or an insignificant benefit, individuals may not show a preference between close and more distant relatives. Additionally, the diverse mating systems may affect the variation in kin recognition across different species (Henkel et al. 2011).

Like our previous study, most *A. herbicolus* adults were cannibalistic (Zhang and Zhang 2022). For most species, food shortage and starvation are the main drivers of cannibalism (Schausberger 2003; Van den Beuken et al. 2019). Although the benefit of cannibalizing kin is increased with extended starvation (Van den Beuken et al. 2019), no difference in the choice made was seen between the early and late attackers. In this study, the cannibals were not starved before the choice test. Thus, they were not cannibalistic at the start of the experiment. Adults had multiple physical encounters with the prey during the choice test before cannibalism since



**Figure 6.** The proportion of cannibalism by adults of *Amblyseius herbicolus* when given a choice between daughters versus niece (1), daughters versus first cousin once removed (2), and daughters versus second cousin once removed (3), at different latency intervals.

arenas had small dimensions favoring frequent encounters among them (personal observation). As hunger develops with extended starvation, adults might choose the prey based on the previous contact. However, our study eliminated dispersal. During food scarcity, *A. herbicolus* adults may disperse rather than cannibalize due to their wide range of prey. Thus, cannibalism prevalence can be much lower in nature (Walzer et al. 1999).

Adults of *A. herbicolus* are likely to use an innate recognition mechanism or phenotype matching in kin discrimination (Zhang and Zhang 2022). Phenotype matching and prior association are likely to be used by *A. herbicolus* in kin discrimination. In this study, the adults could have contacted their eggs and by this way learned the kin labels during oviposition. Eggs can provide cues to be used potentially as a template in future kin recognition (Faraji et al. 2000; Saitoh and Choh 2018; Saitoh et al. 2020). The self-referent phenotype matching, where individuals compare themselves as a template to others, is possible since adults can access their eggshells and shed skins after molting and memorizing these characteristics (Schausberger 2004; Penn and Frommen 2010). The adult cannibals of *A. herbicolus* can compare prey larvae against the template generalized by accessing themselves or eggs laid for dissimilarities. Daughters of *A. herbicolus* would be genetically and phenotypically more similar to nieces than cousin's offspring. Hence, more dissimilar larvae (i.e., cousin's larvae) over daughters were preferentially cannibalized by *A. herbicolus* cannibals.

The discrimination among relatives was observed in the adults of *A. herbicolus*. This relatively fine-scale kin discrimination of *A. herbicolus* has rarely been reported in invertebrates, especially among mites. Phenotype matching and familiarization seems likely as promising recognition mechanisms used by *A. herbicolus* adults to avoid kin cannibalism. The influence of learning through familiarization in kin recognition of *A. herbicolus* requires further investigation. Studies on other adaptive functions of kin recognition of *A. herbicolus*, such as cooperation and parental care, may provide important insights.

## Acknowledgments

We thank Bioforce Ltd for providing the initial population of *Carpoglyphus lactis*. We thank Dr Aaron Harmer and Ms Anne Austin (Manaaki Whenua – Landcare Research) for their constructive comments and suggestions that improved this manuscript.

## Funding

This study was supported in part by New Zealand Government core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group.

## Conflict of Interest Statement

The authors have no relevant financial or non-financial interests to disclose.

## References

- Arnold KE, 2000. Kin recognition in rainbowfish *Melanotaenia eachamensis*: Sex, sibs and shoaling. *Behav Ecol Sociobiol* 48(5):385–391.
- Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48.
- Breed M, 1998. Chemical cues in kin recognition: Criteria for identification, experimental approaches, and the honey bee as an example. In: Robert K, Vander M, Michael B, Karl EE, Mark LW, editors. *Pheromone Communication in Social Insects*. Boca Raton: CRC Press, 57–78.
- Carlin NF, 1988. Discrimination between and within colonies of social insects: Two null hypotheses. *Neth J Zool* 39(1–12):86–100.
- Cassinello J, Calabuig G, 2008. Spatial association in a highly inbred ungulate population: Evidence of fine-scale kin recognition. *Ethology* 114(2):124–132.
- Christiansen IC, Schausberger P, 2017. Interference in early dual-task learning by predatory mites. *Anim Behav* 133:21–28.
- Clemens AM, Brecht M, 2021. Neural representations of kinship. *Curr Opin Neurobiol* 68:116–123.

- D'Ettorre P, Heinz J, 2005. Individual recognition in ant queens. *Curr Biol* 15:2170–2174.
- Faraji F, Janssen A, Van Rijn P, Sabelis M, 2000. Kin recognition by the predatory mite *Iphiseius degenerans*: Discrimination among own, conspecific, and heterospecific eggs. *Ecol Entol* 25:147–1155.
- Fellowes MDE, 1998. Do non-social insects get the (kin) recognition they deserve? *Ecol Entomol* 23(2):223–1227.
- Fisher AM, Le Page S, Manser A, Lewis DR, Holwell GI et al., 2021. Relatedness modulates density-dependent cannibalism rates in drosophila. *Funct Ecol* 35(12):2707–2716.
- Godoy I, Vigilant L, Perry SE, 2016. Cues to kinship and close relatedness during infancy in white-faced capuchin monkeys *Cebus capucinus*. *Anim Behav* 116:139–151.
- Griesser M, Halvarsson P, Drobniak SM, Vilà C, 2015. Fine-scale kin recognition in the absence of social familiarity in the Siberian jay, a monogamous bird species. *Mol Ecol* 24(22):5726–5738.
- Hamilton WD, 1964. The genetical evolution of social behaviour I and II. *J Theor Biol* 7:1–52.
- Henkel AJ, Garner SR, Neff BD, 2011. Effects of paternal reproductive tactic on juvenile behaviour and kin recognition in chinook salmon *Oncorhynchus tshawytscha*. *Ethology* 117(5):451–458.
- Holmes WG, Sherman PW, 1983. Kin recognition in animals: The prevalence of nepotism among animals raises basic questions about how and why they distinguish relatives from unrelated individuals. *Am Sci* 71(1):46–55.
- Johnstone RA, Cant MA, 2008. Sex differences in dispersal and the evolution of helping and harming. *Am Nat* 172:318–330.
- Khodaei L, Long TAF, 2020. Kin recognition and egg cannibalism by *Drosophila melanogaster* larvae. *J Insect Behav* 33(1):20–29.
- Kronauer DJC, Tsuji K, Pierce NE, Keller L, 2013. Non-nest mate discrimination and clonal colony structure in the parthenogenetic ant *Cerapachys biroi*. *Behav Ecol* 24(3):617–622.
- Leedale AE, Li J, Hatchwell BJ, 2020. Kith or kin? Familiarity as a cue to kinship in social birds. *Front Ecol Evol* 8(77):1–13.
- Lihoreau M, Rivault C, van Zweden JS, 2016. Kin discrimination increases with odor distance in the German cockroach. *Behav Ecol* 27(6):1694–1701.
- Makowicz AM, Moore T, Schlupp I, 2018. Clonal fish are more aggressive to distant relatives in a low resource environment. *Behaviour* 155(5):351–367.
- Makowicz AM, Tiedemann R, Steele RN, Schlupp I, 2016. Kin recognition in a clonal fish *Poecilia formosa*. *PLoS ONE* 11(8):e0158442.
- Mateo JM, 2002. Kin-recognition abilities and nepotism as a function of sociality. *Proc R Soc B: Biol Sci* 269(1492):721–727.
- Mateo JM, 2004. Recognition systems and biological organization: The perception component of social recognition. *Ann Zool Fenn* 41(6):729–745.
- Nehring V, Evison SEF, Santorelli LA, d'Ettorre P, Hughes WOH, 2011. Kin-informative recognition cues in ants. *Proc Biol Sci* 278(1714):1942–1948.
- Normark BB, Kirkendall LR, 2009. Chapter 192 - parthenogenesis in insects and mites. In: Resh VH, Cardé RT, editors. *Encyclopedia of Insects*. 2nd edn. San Diego: Academic Press, 753–757.
- Penn D, Frommen J, 2010. Kin recognition: An overview of conceptual issues, mechanisms and evolutionary theory. In: Kappeler P, editor. *Animal Behaviour: Evolution and Mechanisms*. Berlin, Heidelberg: Springer, 55–85.
- Pfennig DW, Frankino WA, 1997. Kin-mediated morphogenesis in facultatively cannibalistic tadpoles. *Evolution* 51:1993–1999.
- Pfennig DW, Ho SG, Hoffman EA, 1998. Pathogen transmission as a selective force against cannibalism. *Anim Behav* 55(5):1255–1261.
- Poirotte C, Charpentier MJE, 2020. Unconditional care from close maternal kin in the face of parasites. *Biol Lett* 16(2):20190869.
- R Development Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing [cited 2022 April]. Available from: <http://www.R-project.org/>.
- Ryan KK, Lacy RC, 2003. Monogamous male mice bias behaviour towards females according to very small differences in kinship. *Anim Behav* 65(2):379–384.
- Saitoh F, Choh Y, 2018. Role of kin recognition in oviposition preference and cannibalism by the predatory mite *Gynaeseius liturivorus*. *Exp Appl Acarol* 76(2):149–160.
- Saitoh F, Janssen A, Choh Y, 2020. The use of volatile cues in recognition of kin eggs by predatory mites. *Ecol Entomol* 45(5):1220–1223.
- Schausberger P, 2003. Cannibalism among phytoseiid mites: A review. *Exp Appl Acarol* 29(1–4):173–191.
- Schausberger P, 2004. Ontogenetic isolation favours sibling cannibalism in mites. *Anim Behav* 67(6):1031–1035.
- Schausberger P, 2005. The predatory mite phytoseiulus persimilis manipulates imprinting among offspring through egg placement. *Behav Ecol Sociobiol* 58(1):53–59.
- Schausberger P, 2007. Kin recognition by juvenile predatory mites: Prior association or phenotype matching? *Behav Ecol Sociobiol* 62(1):119–125.
- Schausberger P, Çekin D, 2020. Plastic female choice to optimally balance (k)in- and out-breeding in a predatory mite. *Sci Rep* 10(7861):1–8.
- Schausberger P, Croft B, 2001. Kin recognition and larval cannibalism by adult females in specialist predaceous mites. *Anim Behav* 61:459–464.
- Sherman PW, 1977. Nepotism and the evolution of alarm calls. *Science* 197(4310):1246–1253.
- Stenberg P, Saura A, 2009. Cytology of asexual animals. In: Schön I, Martens K, Dijk P, editors. *Lost Sex*. Dordrecht: Springer, 63–74.
- Tang-Martinez Z, 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: A critical re-evaluation. *Behav Process* 53:21–40.
- Tibbetts EA, 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc Royal Soc B* 269:1423–1428.
- Van den Beuken TPG, Stockwell LW, Smallegange IM, 2019. Et tu, brother? Kinship and increased nutrition lower the incidence of cannibalism in male bulb mites. *Anim Behav* 152:45–52.
- Waldman B, 1988. The ecology of kin recognition. *Annu Rev Ecol Syst* 19(1):543–571.
- Walzer A, Schausberger P, Schausberger P, 1999. Predation preferences and discrimination between con- and heterospecific prey by the phytoseiid mites phytoseiulus persimilis and neoseiulus californicus. *BioControl* 43(4):469–478.
- West SA, Griffin AS, Gardner A, 2007. Evolutionary explanations for cooperation. *Curr Biol* 17:661–672.
- Wickham H, 2016. *Ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Zhang K, Zhang Z-Q, 2021. The dried fruit mite *Carpoglyphus lactis* (Acari: Carpoglyphidae) is a suitable alternative prey for *Amblyseius herbicolus* (Acari: Phytoseiidae). *Syst Appl Acarol* 26(11):2167–2176.
- Zhang K, Zhang Z-Q, 2022. Kin recognition by cannibals is modulated by hunger level in a generalist predatory mite *Amblyseius herbicolus* (Chant) (Acari: Phytoseiidae). *J Appl Entomol* 146(5):579–585.