



Dosage-dependent and prey stage-specific non-consumptive effects of predators on prey: interactions between *Neoseiulus cucumeris* and *Tyrophagus putrescentiae**

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*In: Zhang, Z.-Q., Fan, Q.-H., Heath, A.C.G. & Minor, M.A. (Eds) (2022) *Acarological Frontiers: Proceedings of the XVI International Congress of Acarology (1–5 Dec. 2022, Auckland, New Zealand)*. Magnolia Press, Auckland, 328 pp.

Predators can affect prey both directly through consumption and indirectly through non-consumptive effects such as predation risk. The latter has been less studied than consumptive effects in predator-prey interactions, although many studies have shown that non-consumptive effects could significantly affect various life history traits of the prey (Clinchy *et al.* 2013; Gurr *et al.* 2017; Hawlena & Schmitz 2010; Hermann & Thaler 2014; McCauley *et al.* 2011; Peckarsky *et al.* 2002; Skelhorn *et al.* 2011; Stoks 2001; Zanette *et al.* 2011), such as development, reproduction and lifespan in mite prey-predator systems (Choh & Takabayashi 2010; Freinschlag & Schausberger 2016; Grostal & Dicke 1999; Li & Zhang 2019; Ristyadi *et al.* 2022; Škaloudová *et al.* 2007; Wei & Zhang 2019, 2022). Most published studies examined the short-term effects of predation risk on prey immature development, reproduction and behaviour (e.g. Abrams & Rowe 1996; Choh *et al.* 2010; Majchrzak *et al.* 2022; Oku *et al.* 2003; Oliveira & Moraes 2021; Rocha *et al.* 2020; Saavedra *et al.* 2022; Warkentin 1995). In this study, we examined the effects of predation risk on short-term as well as long-term traits such as fecundity and lifespan. In addition, we also compared the effects of exposure to predation risks for long versus short duration.

We hypothesized that mild predation stress such as short-term exposure to predation risk might have positive fitness effects, inspired by insights from studies on short-term cold or heat stress. Although exposure to extreme nonlethal chilling or heat could decrease the longevities of mite females (e.g. Jiao *et al.* 2016; Ristyadi *et al.* 2022; Søvik & Leinaas 2003; Zhang *et al.* 2016), repeat transient heat as a relatively mild form of heat stress could increase the longevity and later heat resistance in fruit flies (Hercus *et al.* 2003) and in oriental fruit moths (Zheng *et al.* 2017). Furthermore, fluctuating heat was found to increase the longevity of female mites (Søvik & Leinaas 2003). Likewise, long-term fluctuating cold temperatures could increase the longevity in solitary bees because the fluctuations could protect chill injury by triggering immune responses and reducing oxidative stress (Torson *et al.* 2015).

In this study, we used a mite predator-prey system (*Neoseiulus cucumeris* and *Tyrophagus putrescentiae*), which allows relatively easy application of long-term and flexible predation stress (Wei & Zhang 2019). We aimed to examine whether the effects of predator-induced stress are dosage-dependent, and if the relatively “mild” stress of shorter duration could have different effects on prey.

In the first experiment, we examined the effects of mild and strong predation stress as different levels of predation cues generated by different numbers of predators (0, 1, 3, and 5 predators, respectively). We showed that with the increased level of predation stress, prey individuals had longer developmental time, lower fecundities (for females), shorter lifespans and lower survival rates (Wei & Zhang 2022). However, for the two former parameters, there were no statistic differences between the median level and high level groups; and for the latter two parameters, there were no statistic differences between the median level and low level groups. Thus, we demonstrated that the effects of predation stress were dosage-dependent to some extents. However, the “mild” stress did not show opposite effects of the “strong” stress as demonstrated in previous studies using heat stress (Hercus *et al.* 2003; Søvik & Leinaas 2003; Zheng *et al.* 2017). It is possible that the “mild” predation stress generated by one predator used in this experiment was not mild enough, because in all group, the predation stress was supplied during the whole lifespan of the prey (Wei & Zhang 2022).

We went further to test the influences generated by the predation stress given during different life stages of the prey, including the immature stage, oviposition period, and post-oviposition period. We also included the control group without predation stress and the full group with predation stress given during the whole life. Then we found that predation stress applied during immature stage definitely delayed the development of the prey. Compared with the control group, the predation stress given during oviposition stage reduced fecundity dramatically by 50.7%, while predation stress given during immature stage just reduced fecundity by 7.3%. The highlight of this study was that the predation stress supplied during earlier life (immature stage) extended lifespans of the prey by 9.7%, whereas the stress supplied during later life (oviposition and post-oviposition stages) reduced lifespans of the prey by 24.8% and 28.7%, respectively (Wei *et al.* 2022b). This indicated that the predation risk either supplied during relatively short-term (the immature stage was relatively shorter compared with other stages), or supplied during earlier life, or combination of the two conditions, could have positive effects on the prey in prolonging the lifespan of the prey.

To understand whether it is the predation stress given during a short-term or the stress given during one of the specific immature stages of the prey that generated positive effects on lifespan of the prey, the exposure of predation stress was applied during different specific developmental stages, including the larval, protonymphal, and tritonymphal stages; and also including the first five days of the oviposition stage. The exposure to predation stress during the larval or protonymphal stage delayed development, reduced fecundity and prolonged lifespan of the prey, while the exposure during the tritonymphal stage reduced lifespan slightly and the exposure during the first five days of the oviposition period showed the same lifespan with those of the control (Wei *et al.* 2022a). This indicated that it was not, or at least not only, because of the exposure during short-term, that generated positive effects on lifespan of the prey.

Overall, our studies showed dosage-dependent and prey stage-specific effects of predation stress on prey fitness. In particular, the larval stage and protonymphal stage were very important to the prey and the exposure to predation stress during these two stages was the key to extension of prey lifespan.

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