

To be an intra-guild predator or a cannibal: is prey quality decisive?

MARTA MONTSERRAT, ARNE JANSSEN, SARA MAGALHÃES and MAURICE W. SABELIS Institute for Biodiversity and Ecosystem Dynamics, Department of Population Biology, University of Amsterdam, the Netherlands

Abstract. 1. Many cannibalistic species are also intra-guild predators. Such predators will often face the decision whether to consume a conspecific or a heterospecific prey from the same guild. This decision may depend on the relative quality and abundance of the prey but also on other factors such as relatedness by descent, prey-specific defence and the probability of the victim harbouring shared diseases.

2. Here, intra-guild interactions among two cannibalistic species of predatory mites, *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari: Phytoseiidae) that belong to closely related genera were studied.

3. Individuals of *I. degenerans* were offered a diet of conspecifics or heterospecifics. Because *I. degenerans* is capable of recognising kin individuals from non-kin, and they were exclusively offered conspecifics that were either distantly related or non-kin, it was expected that it would not refrain from cannibalising for reasons of possible relatedness.

4. When corrected for numbers of victims eaten, survival, and juvenile development of predators fed with intra-guild prey was higher than that of cannibals. This was probably caused by a higher quality of heterospecific victims, even though conspecific victims were larger and therefore potentially contained more food. This led to the prediction that the predators should strongly prefer heterospecific prey. This was indeed borne out in independent choice experiments. Thus, the choice of predators between heterospecific and conspecific prey is not only affected by avoidance of consuming conspecifics, but also by relative prey quality.

Key words. *Iphiseius degenerans*, juvenile survival, *Neoseiulus cucumeris*, Phytoseiidae, prey preference.

Introduction

Cannibalism, or the killing and consuming of conspecifics (Elgar & Crespi, 1992) and intra-guild predation, the killing and consumption of heterospecific competitors (Polis *et al.*, 1989), are widespread in the animal kingdom (Fox, 1975; Polis, 1981; Polis *et al.*, 1989; Elgar & Crespi, 1992; Polis & Holt, 1992; Rosenheim *et al.*, 1995). Both cannibalism and intra-guild predation often occur when extra-guild prey densities are low (Polis, 1981; Polis *et al.*, 1989; but see Hironori & Katsuhiko,

1997 and Lucas *et al.*, 1998), which suggests that extra-guild prey are preferred to intra-guild prey or conspecifics. The reason for this may be that the quality of intra-guild prey and conspecifics is low relative to the quality of extra-guild prey (Polis, 1981; Polis *et al.*, 1989). Additionally, the costs that are associated with cannibalism and intra-guild predation may be higher than the costs of attacking and consuming extra-guild prey. Several types of costs have been suggested to be associated with cannibalism (Polis, 1981; Elgar & Crespi, 1992). First, because the victim itself is a predator, the cannibal runs an increased risk of being injured or killed by the victim. Second, because of the phylogenetic relatedness of predator and victim, they may share diseases and the predator may therefore run an increased risk of contracting diseases carried by the victim (Polis, 1981; Pfennig *et al.*, 1998). Finally, cannibalism has the added cost of loss of

Correspondence: Marta Montserrat, Institute for Biodiversity and Ecosystem Dynamics, Department of Population Biology, University of Amsterdam, PO Box 94084, 1090 GB Amsterdam, the Netherlands. E-mail: montserr@science.uva.nl

inclusive fitness when cannibal and victim are related (Polis, 1981). Ignoring the loss of inclusive fitness, the direct fitness costs of intra-guild predation often converge to those of cannibalism with increasing phylogenetic similarity of predator and victim. Apart from the acquisition of food, both intra-guild predation and cannibalism share the benefits of eliminating both competitors for the shared resource and possible future predators of their offspring (Polis, 1981).

At low availability of extra-guild prey, predators have the choice of attacking conspecifics or intra-guild prey. Other things being equal, the possible kinship among conspecifics implies that the costs of intra-guild predation are lower, hence, predators should prefer attacking intra-guild prey to conspecifics. This has often been suggested as a reason for the preference of predators to feed on intra-guild prey (Schausberger & Croft, 2000a, 2001). Another explanation for this preference, however, is that intra-guild prey may have a higher quality than conspecifics. These two explanations are not mutually exclusive, but, to our knowledge, the aspect of the quality of the prey has not been studied before.

In this paper the benefits associated with cannibalism and intra-guild predation were compared. Specifically, the quality of both types of prey, expressed as the survival and developmental rates of consumers feeding on either conspecific or heterospecific prey, were compared. To rule out the possible effect of kinship, the relatedness between conspecific victims and consumers was minimised. Subsequently, it was tested whether consumers preferred feeding on conspecific or heterospecific prey in a choice test, and whether this preference can be explained by differences in prey quality.

The experimental system

Intra-guild predation and cannibalism are common phenomena among phytoseiid mites (Schausberger & Croft, 1999). Predatory mites often co-occur in patches with conspecifics and/or intra-guild predatory species, where they search for the same resources. In those patches, encounters between conspecific and heterospecifics might result in attack, with the final outcome depending on the relative vulnerability of the opponents.

The experimental system here consisted of the two predatory mites species *Iphiseius degenerans* (Berl.) and *Neoseiulus cucumeris* (Oudemans). These two species are currently being used as biological control agents of thrips in greenhouses (van Houten & van Stratum, 1995), and co-occur in the Mediterranean area (Algeria, Egypt, Greece, Israel, Italy, and Morocco; DeMoraes *et al.*, 2004). Adults and juveniles of both species cannibalise on younger stages, and the species are reciprocal intra-guild predators. The attack rates of *I. degenerans*, however, both as cannibal and as intra-guild predator of *N. cucumeris* are much higher than those of *N. cucumeris* (M. Montserrat and A. Janssen, unpubl. data). *Iphiseius degenerans* is known to discriminate between kin and non-kin conspecifics (Faraji *et al.*, 2000), whereas it is unknown whether *N. cucumeris* can do so. Therefore, *I. degenerans* was chosen as the focal species for both cannibalistic and intra-guild interactions, with *N. cucumeris*

serving as intra-guild prey. Both species have five different developmental stages: egg, larva, protonymph, deutonymph, and adult. The eggs are largely invulnerable to predation by other predatory mites (DeCourcy Williams *et al.*, 2004), and all mobile stages are generally attacked by equal-sized or larger individuals of a more advanced stage of development.

Materials and methods

Phytoseiid mite cultures and experimental set-up

The origin and culture methodology for *I. degenerans* and *N. cucumeris* are described in Faraji *et al.* (2000) and van Rijn and Tanigoshi, (1999). Two strains of *I. degenerans* were used for the experiments: one originating from Morocco, referred to here as the M-strain, in culture since 1995, and another originating from Israel (the I-strain) in culture since 2000 (Faraji *et al.*, 2000). The predators were fed pollen twice per week, *I. degenerans* received birch pollen (*Betula pubescens* Ehrh.), and *N. cucumeris* was fed *Typha* sp. pollen. Pollen was collected from birch and *Typha* sp. plants located at the campus of the University of Amsterdam. Male flowers were dried in a stove at 45 °C for 24 h, and sieved (350 µm) to collect pollen. This was subsequently stored in a freezer (−10 °C) until use. The two species were reared on plastic arenas (35 × 20 cm for *I. degenerans* and 15 × 8 cm for *N. cucumeris*) placed on top of wet sponges in water-containing trays. The edges of the arenas were covered with tissue paper that contacted the sponge and the water, and served as a barrier as well as a water source. The arenas of *I. degenerans* were divided into four subunits with three strips of moist filter paper (20 × 1 cm) placed across the arena. In each subunit, a piece of sewing thread was placed to serve as oviposition site. Cohorts were created by transferring the threats with the eggs to the corresponding subunit of a new arena. Although females can walk on the moist filter paper, they normally stay within the area of each subunit. To minimise the chance of confronting kin predators and conspecific victims, they were always collected from subunits that were furthest away from each other. Because *I. degenerans* discriminates between kin and distantly related individuals from the same strain (Faraji *et al.*, 2000), it was expected no effect of kinship between cannibal and victim on the propensity to cannibalise.

The experimental set-up consisted of plastic arenas (15 × 8 cm) placed on top of a sponge inside a water-filled plastic tray. The margins of the arena were covered with tissue paper that was kept moist through contact with the sponge and the water, serving as a supply of water for the mites. Each arena was divided into 10 cells (≈ 1.5 × 1.5 cm) with thin strips of filter paper that remained wet through contact with the paper covering the margins. Cells were further isolated from each other with a line of Tanglefoot that was applied on top of the paper surrounding each cell. One *I. degenerans* larva (M-strain, 2–3 days old from egg deposition) was put in each cell. The following day, when the larvae had moulted to protonymph (*I. degenerans* larvae do not require food to moult to protonymph – van Rijn & Tanigoshi, 1999), they were offered one of two different food regimes, each consisting of three different treatments: (i) low food supply,

consisting either of one *I. degenerans* larva (M-strain) per day, one *N. cucumeris* larva per day, or no food; (ii) high food supply, consisting of either five *I. degenerans* larvae (M-strain) per day, five *N. cucumeris* larvae per day, or ample *Typha* sp. pollen. The number of replicas varied between 29 and 40 per treatment. To recognise the target protonymph (i.e. the consumer), it was marked by applying blue fluorescent powder to its dorsum. This procedure was applied in all treatments to exclude potential effects of the powder on survival of the consumer. Every 24 h, the following variables were recorded: (i) survival of the target individual; (ii) moulting of the target individual; and (iii) the number of non-target individuals eaten. The experiment lasted for a maximum of 10 days. By this time, the individuals had either developed into adults or they had died. Rates of intra-guild predation and cannibalism were assessed under each of the two food supply rates, and were analysed using a Welch *t*-test for unequal variances.

The effect of being a cannibal or an intra-guild predator on the mortality risk

The effect of consuming conspecifics or heterospecifics on the mortality of the target individual was compared. Mortality data were analysed using the Cox's proportional hazard model (Cox, 1972; Fox, 2001), which allows the inclusion of censored data obtained in time-dependent experiments such as ours. Data were fitted to the equation

$$\lambda(t;Z) = \lambda_0(t) \exp[\beta_1 z_1 + \beta_2 z_2],$$

where *t* is the time since the beginning of the experiment, *Z* is the vector representing the variables that may influence the probability of dying, $\lambda(t;Z)$ is the probability of dying at time *t*, given that the individual has not died before, *z*₁ and *z*₂ are variables that are used to code for the effect of each treatment on the probability of dying, $\lambda_0(t)$ is the baseline probability of dying independent of treatment, and β_1 and β_2 are regression coefficients (Haccou & Hemerik, 1985). Two separate analyses were performed, one for each food supply rate. In the treatments with low prey supply, the treatment without any food was used as the control [thus being $\lambda_0(t)$]. For high food supply, the treatment with pollen was taken as control, because pollen has proven to have a high nutritional quality (van Rijn & Tanigoshi, 1999). Statistical differences between the regression coefficients were assessed with the Wald test (Haccou & Hemerik, 1985).

The effect of being a cannibal or an intra-guild predator on development

The number of individuals that moulted to the next developmental stage (i.e. from larva to protonymph, from protonymph to deutonymph, and from deutonymph to adult) at each of the two food supply regimes (low or high), were compared among treatments with an overall χ^2 test followed by pair-wise χ^2 tests corrected using the sequential Bonferroni

method, provided that the overall test was significant (Rice, 1989; Sokal & Rohlf, 1995).

The effect of prey quality

Differences in mortality and development of the predators when cannibalising or preying on heterospecifics may arise for several reasons. First, predators may consume intra-guild prey at higher rates than conspecifics. Second, heterospecific and conspecific prey may be of different quality. To discriminate between these two possibilities, a Cox regression analysis was performed in which the number of larvae eaten per day until death or until reaching adulthood was incorporated as a new covariate. The model used was

$$\lambda(t;Z) = \lambda_0(t) \exp[\beta_3 z_3 + \beta_4 z_4 + \beta_{3*4} z_3 z_4],$$

with *z*₃ coding for the type of larvae (heterospecific or distantly related conspecific) and *z*₄ the number of prey items eaten per day until death or adulthood. If prey species were of different quality, a significant interaction term between these two factors is expected.

Prey preference

Because protonymphs only kill zero to two larvae per day, detecting prey preference using protonymphs is potentially hampered by low statistical power. Therefore, adult females were chosen as consumers and larvae as prey to test prey preference, assuming that prey quality is similar for all developmental stages. This assumption is based on experiments done with this predatory mite species, in which the relative quality of three different prey types, expressed as developmental and oviposition rates was the same for juveniles than for females (van Rijn & Tanigoshi, 1999). To minimise the influence of kinship between potential victims and consumers on prey preference, female predators and conspecific potential victims of the M-strain were taken from opposite rearing units (see above), and a treatment with conspecific victims from the I-strain was included. Experiments were done on a plastic oval arena (26 × 52 mm) floating on water-saturated cotton wool in a plastic container (100 ml, 6.7 cm high, lower diameter 5.1 cm, upper 6.5, Greiner no. 724201). One *I. degenerans* female from the M-strain (10–12 days old since egg stage) was added per arena with six larvae of *N. cucumeris* together with either six larvae of *I. degenerans* from the M-strain or six larvae of *I. degenerans* from the I-strain. A treatment without females was done to control for background mortality (only with six larvae of *I. degenerans* from the M-strain and six larvae of *N. cucumeris*). Four hours after the addition of the female predatory mite to the arena, we counted the number of larvae eaten (dead in the control), the number of larva that were alive, and the number of larvae that were found in the water surrounding the arena. There were 10/11 replicates per treatment. Differences in predation (or dead individuals in the control), or individuals found in the water, between species and within each replica were analysed with Wilcoxon matched-paired signed-rank tests. Differences among treatments for each of the two species of larvae were analysed with Kruskal–Wallis ANOVA tests with planned comparisons (Siegel & Castellan, 1988).

Results

Predation rates

The predation rate on conspecific larvae was consistently lower than on heterospecific larvae, both when the predators were offered one or five larvae per day (Fig. 1).

The effect of being a cannibal or an intra-guild predator on the mortality risk

Predators on a diet of one conspecific or heterospecific larva per day had significantly lower mortality than predators that were deprived of food (Fig. 2a) (overall test: $\chi^2_2 = 24.0$, $P < 0.0001$; multiple comparisons: one *N. cucumeris* larva per day vs. no food: $\beta = -2.13$, Wald = 17.7, $P = 0.00014$; one *I. degenerans* larva per day vs. no food: $\beta = -0.85$, Wald = 7.1, $P = 0.028$). When predators were feeding on conspecifics, their mortality was 3.6 times higher than when they were feeding on heterospecifics (1 *I. degenerans* larva per day vs. 1 *N. cucumeris* larva per day: $\beta = 1.28$, Wald = 6.4, $P = 0.040$) (Fig. 2a).

When pollen, five conspecific larvae, or five heterospecific larvae were offered per day, mortality risk was low compared with that of the individuals that had a low supply of food (Fig. 2b). There was no significant difference among treatments

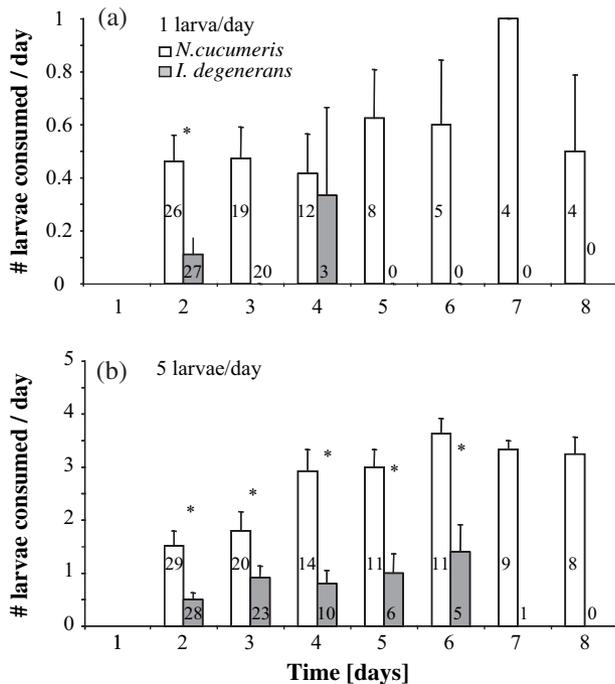


Fig. 1. Daily predation rate (average \pm SE) of *I. degenerans* juveniles on either conspecific larvae (grey bars) or heterospecific (*N. cucumeris*) larvae (white bars), when supplied with either (a) one larva per day, or (b) five larvae per day. * Indicates a significant difference between predation rates of the two species of larvae. The number of predators tested (numbers inside bars) decreased with time due to mortality.

(overall test: $\chi^2_2 = 1.6$, $P = 0.457$). Two days before the end of the experiment, however, all the cannibals were dead (Fig. 2b).

The effect of being a cannibal or an intra-guild predator on development

There was no significant difference in the fraction of larvae moulting to protonymph among treatments (Figs 3a,b, first group of bars, low food supply: $\chi^2_2 = 0.7$, $P > 0.5$; High food supply: $\chi^2_2 = 2.1$, $P > 0.25$). Differences among treatments, however, were found for the fraction of individuals moulting to deutonymph and to adult (Fig. 3). At low food supply, there was a significant effect of the type of food supplied on the fraction of individuals developing from protonymph to deutonymph ($\chi^2_2 = 12.5$, $P = 0.0019$). A higher fraction of individuals moulted from protonymph to deutonymph when the larva offered was heterospecific than when it was a conspecific or when no food was supplied (no food vs. one *N. cucumeris* larva per day: $\chi^2_1 = 7.6$, $P = 0.02$ after sequential Bonferroni correction;

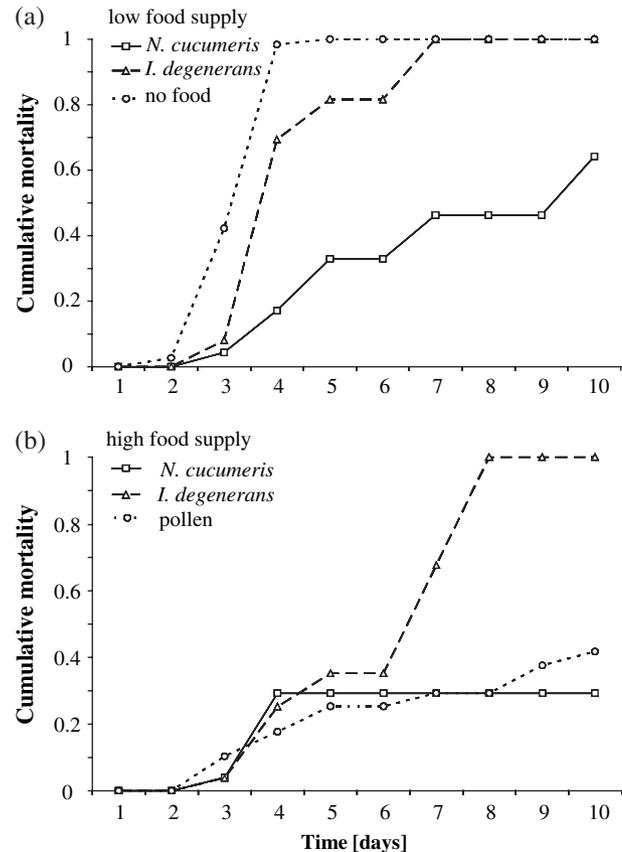


Fig. 2. Cumulative mortality (fraction of individuals dying through time) of immature *I. degenerans* subjected (a) to a low supply of food, i.e. one heterospecific (*N. cucumeris*) larva per day, one conspecific (*I. degenerans*) larva per day, or no food, or (b) to a high supply of food, i.e. five heterospecific (*N. cucumeris*) larvae per day, five conspecific (*I. degenerans*) larvae per day, or pollen.

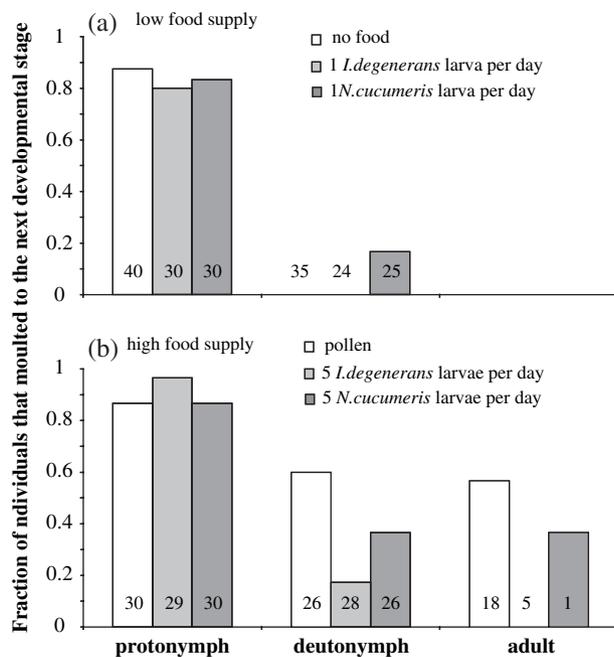


Fig. 3. Fraction of individuals that moulted to the next developmental stage (i.e. from larvae to protonymph, from protonymph to deutonymph, and from deutonymph to adult), when the food supply was either (a) low or (b) high. Individuals were given a diet of conspecific larvae (light grey bars), heterospecific larvae (dark grey bars), or received no food (to compare with low food supply) or abundant pollen (as control for high food supply) (white bars). Numbers inside bars are number of replicates. The number of predators tested (numbers inside bars) decreased with time due to mortality.

one *I. degenerans* larva per day vs. one *N. cucumeris* larva per day: $\chi^2_1 = 5.3$, $P_{\text{Bonferroni}} = 0.04$) (Fig. 3a). No individuals moulted to adult.

At high food supply, the fraction of individuals that moulted from protonymph to deutonymph on a diet of pollen was higher than the fraction of individuals that were offered five conspecific larvae per day, but not different from the fraction of individuals fed with five heterospecific larvae per day (Fig. 3b) (overall: $\chi^2_2 = 14.6$, $P < 0.001$; pollen vs. five *I. degenerans* larvae day: $\chi^2_1 = 14.5$, $P_{\text{Bonferroni}} < 0.001$; pollen vs. five *N. cucumeris* larvae per day: $\chi^2_1 = 3.8$, $P_{\text{Bonferroni}} = 0.1$). This fraction was not significantly different for predators that fed on

conspecifics or heterospecifics (Fig. 3b) (five *I. degenerans* larvae per day vs. five *N. cucumeris* larvae per day: $\chi^2_1 = 3.9$, $P_{\text{Bonferroni}} = 0.2$). The fraction of individuals moulting to adult was not different between individuals fed with pollen or fed with five heterospecific larvae per day ($\chi^2_1 = 0.6$, $P_{\text{Bonferroni}} = 0.85$). None of the individuals fed with five conspecific larvae per day reached adulthood (Fig. 3b).

The effect of prey quality

To separate the effects of predation rates and prey quality, the number of prey items eaten per day and per predator were included as a new variable in the survival analysis. We found no significant effect of prey type, but there was a significant effect of the number of victims eaten and a significant interaction between these two factors, showing that there is a significant effect of prey quality (Table 1). Indeed, survival of predators that consumed similar number of victims was higher when the victims were heterospecific than when conspecific, especially when more than one victim was consumed (Fig. 4). Given this difference, we would expect strong preference for heterospecific prey when both non-kin conspecifics and heterospecifics were offered together.

Prey preference

Females of *I. degenerans* killed and ate a higher number of heterospecific larvae than conspecific larvae, independently of whether conspecific larvae were of the same strain than the females or different (Fig. 5a) (M-strain *I. degenerans* larvae vs. *N. cucumeris* larvae: $Z = 3.6$, $P = 0.0022$; I-strain *I. degenerans* larvae vs. *N. cucumeris* larvae: $Z = 2.84$, $P = 0.0045$). The number of larvae killed (or dead) at the end of the experiment was similar between treatments for *I. degenerans* larvae (Fig. 5a, $\chi^2_2 = 3.96$, $P = 0.14$), but significantly higher for *N. cucumeris* when a female of *I. degenerans* was present in the arena (Fig. 5a, $\chi^2_2 = 22.05$, $P < 0.0001$). The number of larvae of *I. degenerans* that tried to escape and ended up in the cotton wool did not differ between treatments (Fig. 5b, $\chi^2_2 = 0.67$, $P = 0.71$), which indicates that the presence of the conspecific female did not affect the tendency of *I. degenerans* larvae for leaving the arena.

Thus, we conclude that females of *I. degenerans* displayed a clear preference for heterospecific larvae.

Table 1. Mortality of predators on a diet of conspecific or heterospecific prey, corrected for the number of prey consumed until death or reaching adulthood. The Cox's proportional hazard model applied was $\lambda(t;Z) = \lambda_0(t) \exp[\beta_3 z_3 + \beta_4 z_4 + \beta_{3*4} z_3 z_4]$. The interaction coefficient β_{3*4} indicates whether the mortality risk of individuals that ate the same number of prey items differed with prey species. The χ^2 -value for the overall test was $\chi^2_3 = 27.9$ ($P < 0.0001$).

Factors	β	SE	Wald	d.f.	P
Species of larvae (β_3)	-0.25	0.35	0.54	3	0.91
No. larvae consumed day ⁻¹ (β_4)	6.01	1.45	17.2	3	0.0006
Interaction (β_{3*4})	4.30	1.30	10.9	3	0.012

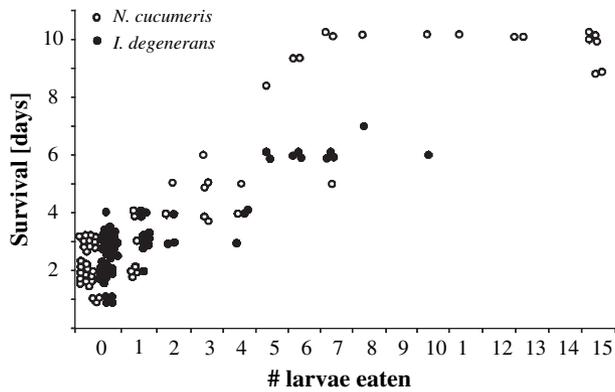


Fig. 4. The survival of *I. degenerans* juveniles as a function of the number of larvae eaten. The experiment lasted for 10 days. By this time, the individuals had either developed into adults or had died. Open dots refer to individuals that fed on heterospecific prey (*N. cucumeris*), closed dots are individuals fed on conspecifics (*I. degenerans*).

Discussion

The mortality risk of predators that were either engaged in intra-guild predation or cannibalism was studied. It was shown here that intra-guild predators have higher survival and developmental rates than cannibals. This was also true when survival was corrected for the number of victims eaten, even though conspecific larvae are larger than heterospecifics ($\approx 0.022 \times 0.017$ mm vs. 0.020×0.012 mm respectively), and, hence, are expected to provide more food per prey item. This suggests that quality of intra-guild prey is higher than that of conspecific victims. If the quality of intra-guild prey would be higher than that of conspecifics, it is expected that predators would prefer intra-guild prey to conspecifics. This is indeed what was found.

Predation rates on heterospecifics were consistently much higher than on conspecifics, which ultimately led to a 3.6-fold difference in mortality in the cannibal vs. that of the intra-guild predator. This raises the question of why cannibalistic individuals do not consume more conspecifics in order to survive and develop into adulthood. One reason might be that larvae of *I. degenerans* are difficult to capture and subdue by conspecific immatures, because both are armed with the same weapons, thus increasing the risk for the cannibal of becoming injured during the attack. The ability of conspecifics to defend themselves better than the intra-guild prey is probably an important factor in the differences in quality found for both types of prey. Another reason might be that predators refrain from cannibalising because of the probability to kill kin individuals. The probability that cannibals and potential victims were kin was minimised, however, and experiments with conspecifics from another strain showed the same trend. *Iphiseius degenerans* is able to discriminate between conspecific and heterospecific eggs and between kin and non-kin conspecific eggs (Faraji *et al.*, 2000) and immatures (F. Faraji, pers. obs.), and even between own and distantly related eggs (Faraji *et al.*, 2000). Therefore, it would not be expected the cannibals refraining

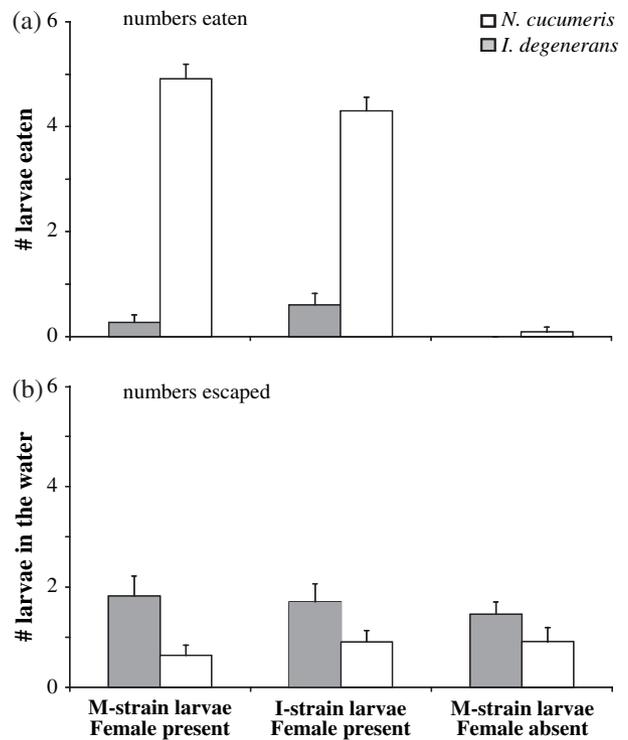


Fig. 5. Number (average \pm SE) of conspecific and heterospecific larvae (a) eaten, and (b) found in the water, in presence and absence of an adult female *I. degenerans*. These females were offered a choice between six conspecific larvae (grey bars) and six heterospecific larvae (white bars). The number of replicates was 10/11.

from consuming conspecifics. Several other experiments on intra-guild predation and cannibalism in predatory mites have also shown that consumption of heterospecifics results in higher survival and development of juvenile predatory mites than consumption of conspecifics (Schausberger & Croft, 2000b), and that predatory mites prefer intra-guild prey over conspecifics when both types of prey are given a choice (Schausberger & Croft, 2000a). These authors, however, attributed this preference to avoidance of predation on kin prey and not to differences in quality of conspecifics and heterospecifics. Here, it is suggested that choice of predators between heterospecific and conspecific prey is not only affected by avoidance of consuming conspecifics because it could lead to a decrease of inclusive fitness, but also by differences in quality of conspecific and heterospecific prey (Dong & Polis, 1992). In fact, when predators are capable of recognising kin, like our predators, they could avoid eating kin and only cannibalise on non-kin or distantly related victims. Hence, the only reason for preferring not to cannibalise on non-kin victims would be prey quality. Therefore, it is suggested here that experiments on diet choice of cannibals and intra-guild predators should consider whether cannibals are capable of kin recognition, and should include an analysis of the relative quality of both prey types.

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