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## Females as intraguild predators of males in cross-pairing experiments with phytoseiid mites

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**Abstract** Studies on intraguild interactions between phytoseiid species have shown that intraguild predation occurs and is most commonly manifested as adult females of one species feeding on juveniles of another. Whether such intraguild interactions can also occur between adult females of one species and adult males of another, is not known. Herein, we report on intraguild interactions between adults of the two sexes in cross-pairing experiments involving three related phytoseiid species (*Neoseiulus paspalivorus*, *N. baraki* and *N. neobaraki*) that are potential candidates for controlling the coconut mite *Aceria guerreronis*, a serious pest of coconut palms in tropical countries. For comparative reasons, the experiments were repeated with larvae instead of males, and with only males or only females of two different species together. In the presence of an ample supply of prey, females of *N. neobaraki* never fed on individuals of their own species, yet appeared to be very aggressive against males, as well as larvae of the other two phytoseiid species. They also fed on females of *N. paspalivorus*, but rarely on females of *N. baraki*. Males of *N. neobaraki* did not suffer mortality when together with females of either of the two other phytoseiid species. Males of *N. baraki* did not suffer predation from females of *N. paspalivorus*, but males of *N. paspalivorus* suffered some mortality (15 %) from *N. baraki* females. Larvae of each of the three species were vulnerable to intraguild predation by heterospecific adult females, except for *N. neobaraki* larvae when together with *N. baraki* females. The absence or presence of intraguild predation is largely explained by the size ratios of the individuals that were put together: large individuals feed on smaller ones, but never the reverse. For each sex, size declines in the following order: *N. neobaraki* >

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*N. baraki* > *N. paspalivorus*. Moreover, for each species, females are larger than males and males are larger than larvae. Strikingly, however, females did not kill males and larvae of their own species. We propose that niche competition between related phytoseiid species is not only determined by intraguild predation on heterospecific larvae, but also by imposing great mortality on males from the intraguild prey because phytoseiid females being pseudo-arrhenotokous require insemination to produce offspring of both sexes.

**Keywords** Cross-breeding · Intraguild predation · Species recognition · Niche competition · Biological control · Phytoseiidae · Coconut mite · Eriophyidae

## Introduction

There is a growing awareness that biological control agents can be involved in intraguild interactions (Rosenheim et al. 1995; Zannou et al. 2005; Negloh et al. 2012). Intraguild predation may interfere with the goals of biological control, especially when a less effective predator feeds on another, resulting in an overall decrease in predation pressure on the target pest (Rosenheim et al. 1995; Schausberger and Croft 2000; Zannou et al. 2005; Negloh et al. 2012). Such interactions may be relevant especially when different predator species are used to control a single pest. This is the case with respect to the coconut mite *Aceria guerreronis* Keifer, a serious pest of coconut palms in South and Central America, the Caribbean and Africa, because there are three candidate predators of the target prey: *Neoseiulus paspalivorus* DeLeon, *N. baraki* Athias-Henriot and *N. neobaraki* Zannou, Moraes and Oliveira. The first two species were reported from surveys conducted in Africa, South America and Asia, while the latter was found in Africa only (Moraes et al. 2004; Lawson-Balagbo et al. 2008; Negloh et al. 2011; Zannou et al. unpublished data). The three species, particularly *N. baraki* and *N. neobaraki*, are morphologically very similar, and can be separated only on the basis of a few morphological characters (Moraes et al. 2004; Zannou et al. 2006; Famah Sourassou et al. 2012).

As part of a series of studies on their taxonomic relationships (Moraes et al. 2004; Zannou et al. 2006), we carried out cross-pairing experiments with the aim to assess reproductive barriers between *N. baraki* and *N. neobaraki*. Instead of interspecific mating and hybridization, however, we observed that females of one species exhibited high tendency to kill males of the other in all pairings (Famah Sourassou, personal observations). Field surveys conducted in Benin and Tanzania showed that the three species are rarely observed together under the bracts of *Aceria*-infested coconut fruits, although it is possible to find them sharing the same palm (Negloh et al. 2011; I. Zannou, pers. comm.). This behaviour, together with the spatially segregated distribution of the three phytoseiids species on coconut palms, underscores the need to investigate intraguild interactions between females and males of the three phytoseiid species. In this article, we report on intraguild predation between females and males in cross-pairing experiments with *N. neobaraki*, *N. baraki* and *N. paspalivorus*.

## Materials and methods

### Predators and rearing methods

The predators used in this study originate from colonies of the three species *N. neobaraki*, *N. baraki* and *N. paspalivorus* (see Table 1 for information about collection), maintained at

**Table 1** Collection localities, host plant, geographic coordinates and date of collection of predatory mites used in this study

Species	Country	Locality	Host plant	Latitude	Longitude	Collection date	No. colonizing females
<i>N. paspaliivorus</i>	Benin	Ouidah	<i>Cocos nucifera</i>	06°21'N	02°09'E	October 2005	52
	Ghana	Winneba	<i>Cocos nucifera</i>	05°22'N	00°38'W	December 2008	11
	Brazil	Itamaraca	<i>Cocos nucifera</i>	07°46'N	34°52'W	September 2006	5
<i>N. baraki</i>	Benin	Gbehoue	<i>Cocos nucifera</i>	06°21'S	01°55'E	February 2009	4
	Tanzania	Nachenjele	<i>Cocos nucifera</i>	08°78'S	39°41'E	June 2010	5
	Brazil	Itamaraca	<i>Cocos nucifera</i>	07°46'S	34°52'W	July 2006	8
<i>N. neobaraki</i>	Benin	Gbehoue	<i>Cocos nucifera</i>	06°21'S	01°55'E	November 2005	11
	Tanzania	Kiparanganda	<i>Cocos nucifera</i>	07°07'S	39°12'E	June 2010	Unknown

25–27 °C, 70–90 % relative humidity and a 12–12 h light–dark cycle at the IITA-Benin Acarology Laboratory. Their rearing units consisted of a black PVC tile (4 × 4 × 0.1 cm) placed on top of a foam pad (4 × 4 × 1 cm) resting in a Petri dish (14.5 cm in diameter and 1 cm in height). The edges of the tile (and part of the foam pad) were covered with a band of tissue paper. To prevent mites from escaping, distilled water was supplied to the Petri dish to create a barrier and this was maintained on a daily basis to keep the foam pad and the tissue paper wet. A small tuft of hydrophobic cotton wool covered by a piece of transparent plastic was placed in the center of each rearing unit to serve as an oviposition site for the predators. All colonies were provided with a fresh supply of prey consisting of eggs of *Tetranychus urticae* Koch.

### Experimental set up

The experiment was initiated with a cohort of eggs obtained from gravid females of each of the three species. One hundred females were collected from the established colonies and confined to rearing units similar to that described above. After 24 h, each egg laid by the predator was transferred to a new unit, again similar to that described above, except that there was now a 2.5 cm diameter black PVC disk. The nymphal stages of the three species were reared on all stages of *A. guerreronis* supplied ad libitum. When reaching the adult stage, predators were sexed and females and males of each population were kept apart for the subsequent cross-pairing experiments. All possible combinations involving females and males of the three species were created in cross-pairing experiments in the presence of *A. guerreronis*, being their natural prey. All experiments were set up as a single pair crossing between virgin females and males. Each pair (female–male) was observed daily and occurrence of intraguild predation between females and males of the three species was assessed after 48 h. Evidence of intraguild predation in the arenas of a given female–male combination was determined by the presence of a shrivelled corpse of one of the two individuals (female or male) paired together. For comparative reasons, we also examined pairings between males ('male × male') and between females ('female × female') of the three species under study, as well as pairings between females and heterospecific larvae ('female × larva').

Following the findings from the first set of experiments on a high aggressiveness of *N. neobaraki* females, we performed the following treatments (see Table 5): (a) *N. neobaraki* females were paired with *N. baraki* male and the mortality was recorded for 48 h; (b) all dead males were removed and replaced by *N. neobaraki* males; (c) After 48 h, surviving *N. neobaraki* males were removed and replaced by *N. baraki* males; (d) *N. neobaraki* females were paired with two different males, a conspecific and a *N. baraki* male. For comparative reasons, we also examined pairings between males ('male × male') and between females ('female × female') of the three species under study, as well as pairings between females and heterospecific larvae ('female × larva'). The experiments were conducted under laboratory conditions (25–27 °C, 70–90 % relative humidity and a 12–12 h light–dark cycle), in arenas consisting of 2.5 cm diameter black PVC tiles placed on moist cotton wool in a 14.5 cm diameter Petri dish. The experiments were replicated with new pairs of individuals for 20–40 times.

The number of heterospecifics (males, female or larvae) killed after 48 h was used as a proxy for intraguild predation. Occurrence of intraguild predation for each cross-pairing experiment was expressed as a percentage calculated from the ratio of the scored number of pairings yielding individuals (males, or females, or larvae) killed (i.e., the scored number of pairings with dead individuals) to the total number (N) of pairings for that

cross-pairing experiment. We arranged data in  $2 \times 2$  contingency tables and performed a Fisher's Exact test and a Chi square test of independence (using SAS version 9.2, SAS Institute 2005) to test whether the occurrence of intraguild predation and cross-pairing type (interspecific pairings vs intraspecific pairings) are independent. Both tests gave qualitatively the same conclusions, thus only results from the former test were presented.

In addition, we compared the body size of female and male specimens of the three predator species used in the experiments. The length and the width of dorsal shield were used as a proxy for body size. Twenty females and 15 males of each species were slide-mounted in Hoyer's medium and examined with respect to the length and width (at the level of seta s4) of the dorsal shield. Measurements were done with an ocular micrometer at  $400 \times$  magnification. For each species and sex, mean and standard error were calculated using the MEANS procedure (PROC MEANS, SAS Institute 2005). Differences among the three species in dorsal shield lengths and widths were tested by one-way analysis of variance (PROC ANOVA, SAS Institute 2005) followed by a Newman-Keuls multiple comparison test at  $p < 0.05$ .

## Results

In pairings with heterospecific males of *N. baraki* and *N. paspalivorus*, *N. neobaraki* females killed all males (100 % male mortality; Table 2). Moreover, when paired with females of the two other species, *N. neobaraki* females killed all *N. paspalivorus* females, but only 10 % of the *N. baraki* females (Table 3). In pairings with *N. paspalivorus* males, *N. baraki* females killed 15 % of the males. However, *N. paspalivorus* females did not kill

**Table 2** Percent mortality in interspecific and intraspecific pairings between females and males of three phytoseiid (*Neoseiulus*) species. The  $2 \times 2$  contingency table and Fisher's Exact test are given below

Cross-pairings (♀ × ♂)	N	Mortality (%)				
		Males killed	Females killed			
<b>Inter-species pairings</b>						
<i>N. neobaraki</i> × <i>N. paspalivorus</i>	40	100	0			
<i>N. neobaraki</i> × <i>N. baraki</i>	40	100	0			
<i>N. baraki</i> × <i>N. paspalivorus</i>	40	15	0			
<i>N. baraki</i> × <i>N. neobaraki</i>	40	0	0			
<i>N. paspalivorus</i> × <i>N. baraki</i>	40	0	0			
<i>N. paspalivorus</i> × <i>N. neobaraki</i>	40	0	0			
<b>Intra-species pairings</b>						
<i>N. paspalivorus</i> × <i>N. paspalivorus</i>	20	0	0			
<i>N. baraki</i> × <i>N. baraki</i>	20	0	0			
<i>N. neobaraki</i> × <i>N. neobaraki</i>	20	0	0			
<b>Cross</b>	<b>Dead</b>	<b>Alive</b>	<b>Total</b>	<b><math>X^2</math></b>	<b><i>df</i></b>	<b>Two-sided P</b>
<i>Fisher's Exact Test</i>						
Inter-specific pairings	86	154	240	30.1	1	1.3E-10
Intra-specific pairings	0	60	60			
Total	86	214	300			

**Table 3** Percent mortality in intra- and interspecific pairings between females of three phytoseiid (*Neoseiulus*) species. The 2 × 2 contingency table and Fisher’s Exact test are given below

	N	Mortality (%)			$X^2$	df	Two-sided P
		<i>N. paspalivorus</i>	<i>N. baraki</i>	<i>N. neobaraki</i>			
<i>N. paspalivorus</i>	20	0					
<i>N. baraki</i>	20	0	0				
<i>N. neobaraki</i>	20	100	10	0			
Cross	Dead	Alive	Total	$X^2$	df	Two-sided P	
<i>Fisher’s Exact test</i>							
Inter-specific pairings	22	38	60	26.9	1	4.5E–8	
Intra-specific pairings	0	60	60				
Total	22	98	120				

**Table 4** Percent mortality in interspecific and intraspecific pairings between females and larvae of three phytoseiid (*Neoseiulus*) species. The 2 × 2 contingency table and Fisher’s Exact test are given below

Female	×	Larva	N	Mortality (%)		
<b>Interspecific pairings</b>						
<i>N. neobaraki</i>	×	<i>N. paspalivorus</i>	40	100		
<i>N. neobaraki</i>	×	<i>N. baraki</i>	40	100		
<i>N. baraki</i>	×	<i>N. paspalivorus</i>	40	100		
<i>N. baraki</i>	×	<i>N. neobaraki</i>	40	0		
<i>N. paspalivorus</i>	×	<i>N. baraki</i>	40	35		
<i>N. paspalivorus</i>	×	<i>N. neobaraki</i>	40	15		
<b>Intraspecific pairings</b>						
<i>N. neobaraki</i>	×	<i>N. neobaraki</i>	40	2.5		
<i>N. baraki</i>	×	<i>N. baraki</i>	40	0		
<i>N. paspalivorus</i>	×	<i>N. paspalivorus</i>	40	0		
Females	Dead	Alive	Total	$X^2$	df	Two-sided P
<i>Fisher’s Exact test</i>						
Inter-specific pairings	140	100	240	111.0	1	2.0E–32
Intra-specific pairings	1	119	120			
Total	141	219	360			

any males of *N. baraki*. No mortality was recorded when pairing only females of the latter two species (Table 3). Male mortalities recorded in interspecific pairings were significantly different from those in intraspecific pairings (control) (Table 2), as were female mortalities in interspecific pairings when tested against intraspecific pairings (Table 3). There was no mortality in all pairings involving only males of the three species ( $n = 20$ ; killed = 0).

To assess whether the conditions under which we observed intraguild predation among adults, also allowed for predation by females of one species on larvae of the other, we paired *N. neobaraki* females with larvae of *N. baraki* or larvae of *N. paspalivorus* and

**Table 5** Male mortality in a series of experiments involving *Neoseiulus neobaraki* females on the one hand and conspecific and/or heterospecific (*Neoseiulus baraki*) males on the other hand

	% Males killed			
	(a) 1 ♂ <i>N. baraki</i>	(b) 1 ♂ <i>N. neobaraki</i>	(c) 1 ♂ <i>N. baraki</i>	(d) 1 ♂ <i>N. baraki</i> + 1 ♂ <i>N. neobaraki</i>
♀ <i>N. neobaraki</i> (N = 20)	100	0	100	100+0

**Table 6** Mean ( $\pm$ SD) length and width (micrometers) of dorsal shield measured on adult females and males of three predator species (females  $n = 20$ ; males  $n = 15$ ). Means within a column with different letters are significantly different (SNK,  $p < 0.05$ )

Species	Dorsal shield length		Dorsal shield width	
	Female	Male	Female	Male
<i>Neoseiulus paspalivorus</i>	340.7 $\pm$ 3.2 c	257.1 $\pm$ 3.6 c	138.7 $\pm$ 3.6 c	124.9 $\pm$ 1.6 c
<i>Neoseiulus baraki</i>	364.9 $\pm$ 4.8 b	277.0 $\pm$ 3.8 b	162.8 $\pm$ 3.0 b	141.1 $\pm$ 2.8 b
<i>Neoseiulus neobaraki</i>	380.1 $\pm$ 5.6 a	334.5 $\pm$ 5.9 a	184.5 $\pm$ 5.2 a	149.2 $\pm$ 2.4 a

found 100 % larval mortality within 24 h, in all cases. Also, *N. baraki* females killed all *N. paspalivorus* larvae, but they killed none of the *N. neobaraki* larvae. Finally *N. paspalivorus* females killed only few *N. neobaraki* larvae (15 %) and not many *N. baraki* larvae (35 %) (Table 4). Larval mortalities recorded in interspecific pairings were significantly different from those recorded in control pairings (Table 4).

To assess the individual ability of *N. neobaraki* females to discriminate interspecifically, we carried an additional series of experiments in which we confronted them with either heterospecific or conspecific males or both in a sequence of 4 experimental rounds. In first round, *N. neobaraki* females paired with *N. baraki* males killed all heterospecific males within 48 h (Table 5a). In the second round, after removal of the dead heterospecific males and replacement by conspecific males, none of the latter males was killed (Table 5b). In the third round, after removal of the conspecific males and replacement by heterospecific males again, all of the latter males were killed (Table 5c). In the fourth (last) round, when given a simultaneous choice between a conspecific male and an heterospecific male, all *N. baraki* males were killed, whereas all conspecific males survived (Table 5d). We conclude that females of *N. neobaraki* can discriminate between conspecific and heterospecific males, because they kill only the latter.

With respect to body size, specimens of *N. neobaraki* appeared larger than *N. baraki* specimens, which in turn were larger than those of *N. paspalivorus* (Table 6).

## Discussion

To the best of our knowledge (see Croft 1970; Monetti and Croft 1997; McMurtry et al. 1976; Hoying and Croft 1977; Mahr and McMurtry 1979; Congdon and McMurtry 1986) our results are the first to show that phytoseiid females can act as intraguild predators of heterospecific males, whereas they do not kill conspecific males (Table 2). This ability to discriminate between con- and heterospecific prey in cannibalism and intraguild predation



has been reported for many phytoseiid species (Croft et al. 1996; Schausberger and Croft 2000; Schausberger 2003). In terms of aggressiveness between species, *N. neobaraki* was superior over *N. baraki* and, *N. baraki* was superior over *N. paspalivorus*. When paired with a conspecific male and a heterospecific male together, each *N. neobaraki* female discriminated and killed only the heterospecific male (Table 5). This implicates species recognition prior to the decision to attack an intraguild prey. Strikingly, we never observed an attempt of males to mount a heterospecific female, let alone to mate with her. Thus, discrimination probably occurs prior to courtship.

We have no reason to suppose that phytoseiid females specifically aim to attack heterospecific males because they also attack heterospecific larvae, and in some cases even intraguild predation between females was observed (Table 4) (see also Croft et al. 1996, the only other reference to such a phenomenon). Size differences matter to who is the intraguild predator and who is the intraguild prey (Lucas et al. 1998; Hindayana et al. 2001; Sato et al. 2003; Janssen et al. 2007): large individuals feed on smaller ones, but never the reverse. For each sex, size declines in the following species order: *N. neobaraki* > *N. baraki* > *N. paspalivorus* (Table 6). Moreover, for each species, females are larger than males and males are larger than larvae. We conclude that the data in Table 2–4 largely confirm that the intraguild predator is larger in size than the intraguild prey and that predation of females on heterospecific males is no exception to this rule. We cannot, however, explain why *N. baraki* females did not prey on *N. neobaraki* larvae. This requires further scrutiny.

When sizes differed only little, as in pairings involving females of *N. neobaraki* and females of *N. baraki*, mortality was very low. While this again confirms the rule that differential size matters, behavioural observations on these females also showed that there is an alternative to being killed: *N. neobaraki* females stayed in the centre of the discs where the prey was placed, but *N. baraki* females moved along the edges of the discs. This may be interpreted as escape behaviour, a response commonly observed in intraguild prey (Hindayana et al. 2001; Yasuda et al. 2001; Michaud and Grant 2003; Janssen et al. 2007). In our experiments individuals cannot escape, but, under field conditions, individuals may move away (e.g. out of the area under the perianth) upon encountering an intraguild predator. Thus, caution should be exercised when extrapolating laboratory observations to the field.

Intraguild predation decreases as the density of the shared, extraguild prey increases (Schausberger 2003; Zannou et al. 2005). Indeed, *N. paspalivorus* females become less aggressive towards larvae of *N. neobaraki* when the density of coconut mites, their prey, increases (Negloh et al. 2012). However, in our study where we offered coconut mites as prey to mimick conditions where they feed and compete for prey, *N. neobaraki* females exhibited intraguild predation on heterospecific larvae, females and males despite the presence of prey. This implies that niche competition between phytoseiid species is not only determined by food competition and intraguild predation on immature life stages of smaller species (Negloh et al. 2012), but also by imposing greater mortality on males than on females of the other species. Since phytoseiid females reproduce by pseudo-arrhenotoky and thus require insemination to produce daughters and sons (Sabelis et al. 2002), smaller phytoseiid species may go extinct when males become too rare due to intraguild predation, unless there is a refuge where they can escape predation. These mechanisms may explain why the three phytoseiid species under study were not, or rarely, found co-occurring under the same perianth of an *Aceria*-infested coconut fruit. In Tanzania where *N. neobaraki* is prevalent, only one out of the 18 locations surveyed had *N. neobaraki* and *N. paspalivorus* occurring together on two nuts from two different palms (Negloh et al. 2011), but

unfortunately no information was provided on the sex of the co-occurring individuals of the two species.

If it is true that intraguild predation limits co-occurrence of phytoseiid species under the perianth of the same coconut, then there would be little room for complementary effects between the three phytoseiid species and therefore also no reason for strategies to combat coconut mites with all three species together. However, if there are refuges from intraguild predation under the perianth (e.g. *N. paspalivorus* occupying below-perianth space too narrow for the other two species), then coexistence may be possible, and possibly also complementary effects of two or more phytoseiid species on suppression of coconut mites. We consider this to be a key issue for future research on multiple predator species that are used to control coconut mites.

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