Compatibility of *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi*, candidate biocontrol agents of the coconut mite *Aceria guerreronis*: spatial niche use and intraguild predation

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Abstract The eriophyid mite *Aceria guerreronis* occurs in most coconut growing regions of the world and causes enormous damage to coconut fruits. The concealed environment of the fruit perianth under which the mite resides renders its control extremely difficult. Recent studies suggest that biological control could mitigate the problems caused by this pest. *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi* are two of the most frequently found predatory mites associated with *A. guerreronis* on coconut fruits. Regarding biological control, the former has an advantage in invading the tight areas under the coconut fruit perianth while the latter is more voracious on the pest mites and has a higher reproductive capacity. Based on the idea of the combined use/release of both predators on coconut fruits, we studied their compatibility in spatial niche use and intraguild predation (IGP). Spatial niche use on coconut fruits was examined on artificial arenas mimicking the area under the coconut fruit perianth and the open fruit surface. Both *N. paspalivorus* and *P. bickleyi* preferentially resided and oviposited inside the tight artificial chamber. Oviposition rate of *P. bickleyi* and residence time of *N. paspalivorus* inside the chamber were reduced in the presence of a conspecific female. Residence of *N. paspalivorus* inside the chamber was also influenced by the presence of *P. bickleyi*. Both *N. paspalivorus* and *P. bickleyi* preyed upon each other with relatively moderate IGP rates of adult females on larvae but neither species

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yielded nutritional benefits from IGP in terms of adult survival and oviposition. We discuss the relevance of our findings for a hypothetic combined use of both predators in biological control of *A. guerreronis*.

Introduction

Coconut is a key perennial cash crop in countries of the inter-tropical zone of the earth. The palm is of great versatility with over one hundred derivative products (e.g., Foale 2003). The coconut fruit is the most important plant part and often attacked by a range of herbivorous arthropods including the eriophyid mite *Aceria guerreronis* Keifer. Since the description of *A. guerreronis* from coconut fruits collected in the state Guerrero (Mexico) (Keifer 1965) the tiny eriophyid mite has been reported infesting coconut fruits in most coconut growing regions of Central and South America (Doreste 1968; Howard et al. 1990; Lawson-Balagbo et al. 2008), South Asia (Fernando et al. 2002), Africa (Mariau 1969; Seguni 2002; Koffi Negloh personal communication) and most recently from Oman (de Moraes personal observation).

Aceria guerreronis resides under the perianth of coconut fruits and feeds on its developing tissue. Damage due to *A. guerreronis* results in surface scars, growth distortion, copra (dried white flesh) reduction and premature fruit drop (Moore and Howard 1996; Nair 2002). Yield losses have been recorded as ranging between 30% and 60% of the production (Moore et al. 1989; Nair 2002; Seguni 2002). Chemical measures considered against the pest mites are expensive and difficult to apply because of the secluded environment in which *A. guerreronis* resides (Mariau and Tchibozo 1973; Hernandez 1977; Ramaraju et al. 2002). Considerable attention is being given to biological and integrated control strategies involving the use of entomopathogenic fungi and acarophagous natural enemies (Hall et al. 1980; Cabrera 2002; de Moraes and Zacarias 2002; Lawson-Balagbo et al. 2007a, b, 2008). Regarding the latter, the predatory mites *Neoseiulus paspalivorus* De Leon (Phytoseiidae) and *Proctolaelaps bickleyi* Bram (Ascidae) are two of the most frequently found predators of *A. guerreronis* on coconut fruits (Howard et al. 1990; de Moraes and Zacarias 2002; de Moraes et al. 2004a; Lawson-Balagbo et al. 2008; Koffi Negloh personal communication).

Both *N. paspalivorus* and *P. bickleyi* are considered promising candidates for classical or augmentative biological control of *A. guerreronis* (de Moraes and Zacarias 2002; Lawson-Balagbo et al. 2007a, b). Both predatory mites readily prey on *A. guerreronis* and have rather high population growth rates when offered *A. guerreronis* as prey (Lawson-Balagbo et al. 2007a). Moreover, recent observations revealed that *N. paspalivorus* and *P. bickleyi* occasionally co-occur on coconut fruits. The two predators have overlapping micro-habitats on the fruits but the latter is less often present in the tightest areas under the perianth (Lawson-Balagbo et al. 2007b, 2008). *Neoseiulus paspalivorus* is more dorso-ventrally flattened giving it an advantage in accessing the area under the bracts, whereas *P. bickleyi* is the more voracious predator and has a much higher intrinsic rate of increase with *A. guerreronis* as prey than *N. paspalivorus* (Lawson-Balagbo et al. 2007a). These complementary predator characteristics prompted the idea of using the two predators in combination for biological control of *A. guerreronis*.

However, before using two or more predators in combination for biological control of a given pest, knowledge of the predators' diet breadth and potential interactions is required

(Swirskii et al. 1970; McMurtry 1982; Rosenheim et al. 1995; McMurtry and Croft 1997; Schausberger 1997). Both predators are considered generalist predators, which may feed on animal and non-animal food (McMurtry and Croft 1997; Lawson-Balagbo et al. 2007a). In contrast, nothing is known about potential interactions between *N. paspalivorus* and *P. bickleyi*. In general, interactions between simultaneously released or co-occurring natural enemies may be direct and indirect. As with classical predator–prey interactions, direct interactions such as intraguild predation (IGP) may be lethal (Polis et al. 1989; Rosenheim et al. 1995) and non-lethal such as changes in behaviour due to perception of each other's presence (e.g., Bolker et al. 2003; Preisser et al. 2005). There exists a multitude of possible indirect interactions with competition for shared resources being a ubiquitous and highly important type (e.g., Janssen et al. 1998; Wajnberg et al. 2001; Reitz and Trumble 2002).

The overall objective of the present work was to evaluate the compatibility of *N. paspalivorus* and *P. bickleyi* in a hypothetic combined use against *A. guerreronis*. Among the possible direct and indirect interactions in the concealed habitat of *A. guerreronis*—in the tight chambers under the bracts of coconut fruits—we were most interested in competition for space and IGP between *N. paspalivorus* and *P. bickleyi*. Both interactions are considered key interactions between co-occurring natural enemies and have been shown to govern, among other factors, the local coexistence or displacement of the involved species and with that to potentially affect biological control of the shared prey (Yao and Chant 1989; Croft and MacRae 1992; Rosenheim et al. 1995; Schausberger 1998; Walzer and Schausberger 1999a; Walzer et al. 2001; Onzo et al. 2004). Specifically, we addressed the questions (1) whether the two predatory mites would share and co-inhabit the area under the perianth when released simultaneously against *A. guerreronis* and (2) whether the two predators would engage in IGP?

Materials and method

Predator source and rearing

Neoseiulus paspalivorus and *P. bickleyi* used for experiments derived from specimens collected in Acaraú and Itamaracá in the Brazilian states Ceará and Pernambuco, respectively. The stock colonies of both species were maintained on separate arenas consisting of a sheet of black PVC foil (12 × 12 cm), laid on a water-saturated foam mat (14 × 14 × 4 cm) placed in a plastic tray (20 × 20 × 6 cm). The margins of the sheet were covered by moist tissue paper serving as drinking water source and preventing the mites from escaping. Additionally, a narrow strip of an adhesive (Raupenleim®, Avenarius-Agro) was applied along the centre of the tissue paper. Colonies of *N. paspalivorus* and *P. bickleyi* were reared on *A. guerreronis* offered on small pieces of infested meristematic tissue of coconut fruits. Those pieces also served as oviposition sites and were replenished every third day. Eggs and mobile life-stages of the predators were removed from the old pieces before they were discarded. Mites were transferred to new arenas every two weeks. The rearing units were stored in a climatic chamber at 25 ± 1°C, 80–90% RH and 16:8 h L:D photoperiod.

Experimental procedures

Experiment 1: spatial niche use and oviposition site preference

Adult gravid females of both predators were taken randomly from rearing units and transferred to experimental units, each consisting of a black PVC foil (5.5 × 4.5 cm) placed on a

water-saturated foam mat ($5.5 \times 4.5 \times 3$ cm) inside a plastic tray ($10 \times 10 \times 5$ cm) half-filled with water. The edges of the sheet were covered with strips of moist tissue paper to provide access to free water. Surplus of *A. guerreronis* prey was provided by brushing mites onto the experimental units with a fine camel's hair brush. Half of the surface of each experimental unit was covered by a translucent microscope slide (5×2.5 cm) sealed on its edges by candle wax. The microscope slide rested on the moist tissue paper confining the arena and thereby created a $\sim$2 mm high chamber between the upper side of the plastic foil and the lower side of the microscope slide (mimicking the space beneath the perianth of coconut fruits). Only a 1-mm wide entrance point was left to allow access of the mites to the chamber and enable movement between the chamber and the uncovered half of the arena (representing the space on the fruit surface outside the perianth). Experiments were started by placing one or two gravid females on each arena; treatments were single females of either species, two conspecific females of either species and two heterospecific females (one female of each species). Experimental units were stored in a climatic chamber at $25 \pm 1°C$, $60 \pm 5\%$ RH and constant darkness.

For three consecutive days female position and survival were recorded hourly between 8:00 and 12:00 and at 16:00 on day one and three times daily at 8:00, 12:00 and 16:00 on days two and three. For observations experimental units were taken out from the climatic chamber one at a time and checked immediately thereupon to avoid any influence of extended light exposure on mite position. Time spent in- and outside the chamber was estimated by assigning full time intervals between two consecutive observations to a given location if the mite remained at the same location and assigning half intervals to either location if the mite had changed locations. Oviposition (location and number of eggs) was recorded once at the end of the experimental period (3 days) after opening the chamber. Within each species, total time spent and total number of eggs laid per female in- and outside the artificial chamber (considering only those females that survived until the end of the experiment) were compared by *T*-tests for dependent samples. For each species, daily oviposition rate (considering all females and calculated by dividing egg production through survival time) and time spent inside chambers were compared among treatments using univariate ANOVAs followed by Bonferroni post hoc tests (SPSS 15.0, SPSS Inc.). Data were checked for normal distribution (Kolmogorov–Smirnov test) and homogeneity of variances prior to statistical analyses. Log-transformed values of the number of eggs/female/day were used to correct variance heterogeneity and heteroskedasticity. Egg position was compared between treatment pairs using 2×2 Fisher's exact tests. Logistic regression was used to compare female survival between treatments (SPSS 15.0, SPSS Inc.).

Experiment 2: intraguild predation by adult females on larvae

Gravid females of both predators were taken randomly from rearing units and transferred singly into closed cages with free water available. Cages were cavities (1.5 cm diameter) drilled into rectangular pieces of acrylic glass ($8 \times 3.5 \times 0.3$ cm) with a fine mesh screen at the bottom (Schausberger 1997). Each rectangular piece had two cavities spaced apart 1.0 cm. A strip of tissue paper was placed on the lower side between the two cavities so that it slightly reached into the cavities. The tissue paper was kept moist during the experimental period to provide access to free water. The cavities were covered using a microscope slide (7.5×2.5 cm) and the whole unit was secured with a rubber band. Experimental units were stored in a climatic chamber at $25 \pm 1C$, $60 \pm 5\%$ RH and 16:8 h L:D photoperiod. Two treatments, with and without IG prey, were established for each species. In the former treatment and after 24 h starvation each female was offered three heterospecific larvae

randomly picked from the rearing unit. Once per day dead larvae and protonymphs were removed from the cages and replaced by new larvae. Prey loss, female survival and oviposition were recorded every 24 h during 10 days. Prey loss/day and oviposition/day were compared between the two predator species using *T*-tests for independent samples. Female survival (chance and time) was compared within each species between treatments (with and without prey) using Cox hazard regression (SPSS 15.0, SPSS Inc.).

Experiment 3: aggressiveness of adult females against heterospecific larvae

Aggressiveness was defined as chance and latency to attack by an adult female predator on a heterospecific larva. Aggressiveness tests were conducted in cages as described above. Gravid females were singly placed in cages and starved for 24 h. After starvation each female was offered one heterospecific larva. Cages were monitored for successful attacks by the female predators on the larvae every 10 min during the first hour and every 30 min later on for six consecutive hours. The experiment was carried out at 25 ± 1°C. Mean latency to successful attack of females on larvae was compared between predator species using *T*-test for independent samples. Aggressiveness (chance and time of attack) by females on larvae was compared between predator species by Cox hazard regression (SPSS 15.0, SPSS Inc.).

Results

Experiment 1: spatial niche use and oviposition site preference

Overall, the total time spent by *N. paspalivorus* and *P. bickleyi* inside the artificial chamber was either equal or higher than the time spent outside the chamber (Fig. 1). *Neoseiulus paspalivorus* alone or held with a conspecific female spent significantly more time inside the artificial chamber than outside (*T*-tests for dependent samples; $T_{14} = 6.71$, $P < 0.001$ and $T_{13} = 2.23$, $P = 0.044$, respectively). For *P. bickleyi*, time spent inside the chamber was significantly higher than outside when held alone ($T_{11} = 5.3$, $P < 0.001$) but the difference was not significant when held with a conspecific female ($T_7 = 1.77$, $P = 0.119$). For both species the time spent in and outside the chamber did not differ when held with a heterospecific female ($T_9 = 1.55$, $P = 0.155$ and $T_9 = 1.5$, $P = 0.167$, for *N. paspalivorus* and *P. bickleyi*, respectively).

Treatment affected the total time spent by *N. paspalivorus* inside the artificial chamber (ANOVA; $F_{2,36} = 3.58$, $P = 0.038$). *Neoseiulus paspalivorus* spent more time inside the chamber when held alone than with a conspecific female or mixed but differences were only significant between treatments alone and two conspecifics (Bonferroni; $P = 0.017$) (Fig. 1). In contrast, the total time spent by *P. bickleyi* inside the chamber did not differ among treatments (ANOVA; $F_{2,27} = 1.28$, $P = 0.293$) (Fig. 1).

Within each treatment either species placed significantly more eggs inside the artificial chamber than outside (*T*-tests for dependent samples; $T > 2.42$, $P < 0.05$) (Fig. 2). For each species, the proportion of eggs placed inside and outside the chamber did not differ among treatments (pairwise Fisher's exact tests; $P > 0.1$) (Fig. 2).

The daily oviposition rate of *N. paspalivorus* was similar among treatments (ANOVA; $F_{2,38} = 2.04$, $P = 0.144$). In contrast, *P. bickleyi* laid more eggs per day when held with *N. paspalivorus* or when held alone than when held with a conspecific female (ANOVA; $F_{2,33} = 2.04$, $P = 0.017$; Bonferroni, $P = 0.032$ for both pairwise comparisons) (Fig. 3).
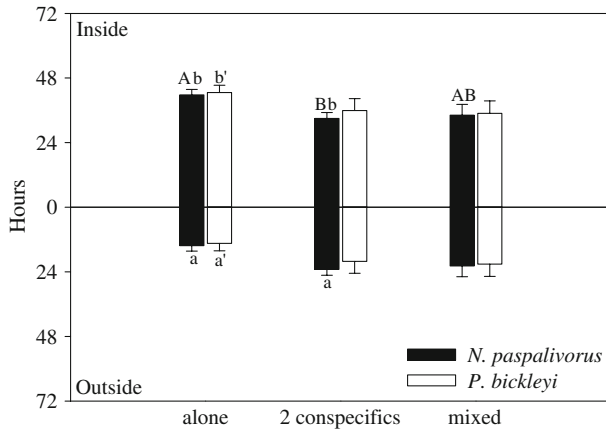
Fig. 1 Residence time (h, mean ± SE) of adult females of *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi* inside and outside the artificial chamber when held alone, with a conspecific female or with a heterospecific female (mixed). Different lower case letters on top of bars indicate significant differences between sites within treatments (*T*-test for dependent samples, $P < 0.05$). Different upper case letters indicate significant differences among treatments inside the chamber (ANOVA, post hoc Bonferroni, $P < 0.05$)
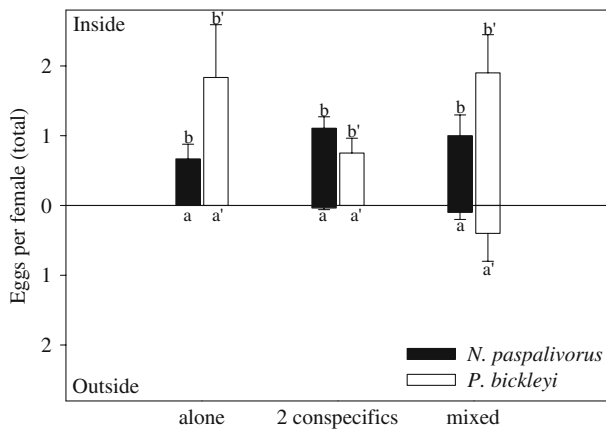

Fig. 2 Oviposition site preference of adult females of *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi* when alone, with a conspecific female or with a heterospecific female (mixed). Different letters on top of bars indicate significant differences between sites within treatments (*T*-test for dependent samples, $P < 0.05$)

Treatment did not affect the survival rate of either species (Logistic regression; Wald = 1.49, $P = 0.222$ and Wald = 2.06, $P = 0.151$ for *N. paspalivorus* and *P. bickleyi*, respectively). About 93% *N. paspalivorus* females (i.e., 63 individuals) and 85% *P. bickleyi* females (i.e., 50 individuals) survived until the end of the experiment across treatments.

Experiment 2: intraguild predation by adult females on larvae

Daily prey loss and oviposition did not differ between *N. paspalivorus* and *P. bickleyi* (Table 1). Treatment (with and without prey) did not affect survival of *N. paspalivorus* females (chance and time combined) (Cox regression; Wald = 0.12, $P = 0.726$). In both
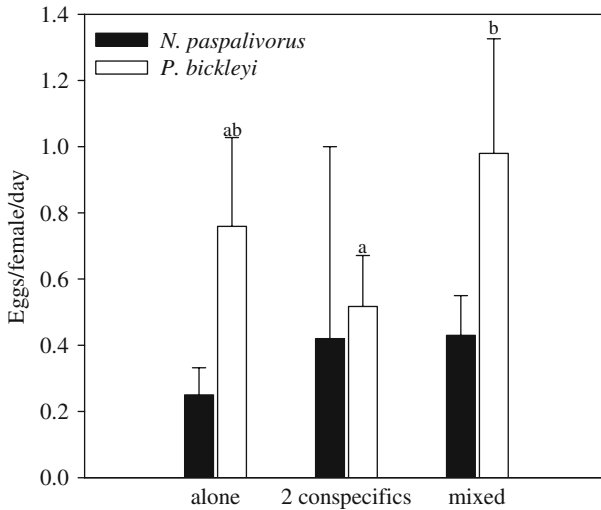
Fig. 3 Daily oviposition (mean ± SE) of *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi* inside the chamber when alone, with a conspecific female or with a heterospecific female (mixed). Different letters on top of bars indicate significant differences within species among treatments (ANOVA, post hoc Bonferroni, $P < 0.05$)

Table 1 Daily prey loss and oviposition rate of *Neoseiulus paspalivorus* and *Proctolaelaps bickleyi* held singly with heterospecific larvae for 10 days at $25 \pm 1°C$, $60 \pm 5\%$ RH and 16:8 h L:D photoperiod

Source of variation	Female	N	Mean ± SE	T^a	df	P
Prey loss	*N. paspalivorus*	14	1.35 ± 0.23	0.17	25	0.869
	P. bickleyi	13	1.28 ± 0.34			
Oviposition	*N. paspalivorus*	14	0.04 ± 0.08	1.81	25	0.082
	P. bickleyi	13	0.00 ± 0.00			

[a] *T*-tests for independent samples

treatments, more than 70% (i.e., 22 individuals) of *N. paspalivorus* females survived until the end of the experiment (Fig. 4a). As opposed to *N. paspalivorus*, survival (chance and time combined) of *P. bickleyi* females was significantly affected by treatment (Cox regression; Wald = 15.35, $P = 0.001$). No *P. bickleyi* female survived until the end of the experiment when offered heterospecific larvae with extremely high mortality (~40%) occurring between days 1 and 3. About 30% (i.e., nine individuals) survived until the end of the experiment when held without prey (Fig. 4b).

Experiment 3: aggressiveness of adult females against heterospecific larvae

Aggressiveness against heterospecific larvae (chance and latency to attack) did not differ between the two predator species (Cox regression; Wald = 0.641, $P = 0.423$). For those females that successfully attacked heterospecific larvae, the mean (min, ±SE) latency to attack was significantly shorter in *P. bickleyi* (92.5 ± 17) than in *N. paspalivorus* (157.5 ± 18) (*T*-test for independent samples; $T_{14} = 2.66$, $P = 0.018$). Only about 25% *N. paspalivorus* and 35% *P. bickleyi* females launched a successful attack on the heterospecific larva within the 6 h experimental period (Fig. 5).
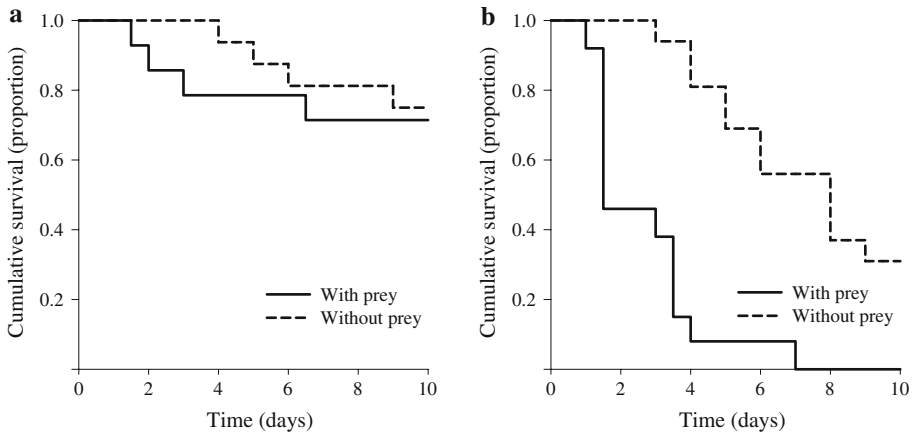
Fig. 4 Survival functions of adult *Neoseiulus paspalivorus* (**a**) and *Proctolaelaps bickleyi* (**b**) females caged singly with and without heterospecific larvae
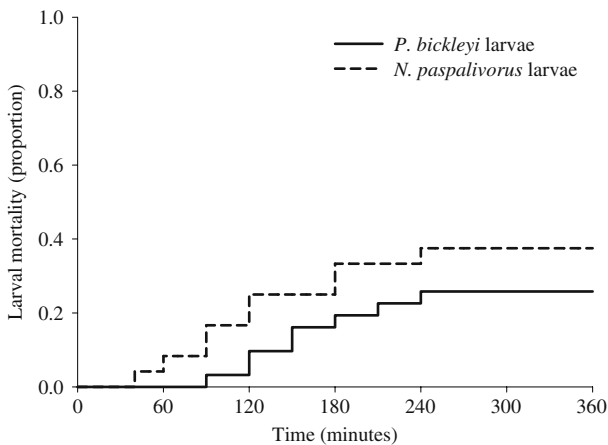

Fig. 5 Survival functions of larvae of *Proctolaelaps bickleyi* and *Neoseiulus paspalivorus* caged singly with a heterospecific female for 6 h

Discussion

Both *N. paspalivorus* and *P. bickleyi* preferentially resided and oviposited inside the tight artificial chamber, which mimicked the area under the perianth of coconut fruits, as compared to the uncovered surface area. Intraspecific interactions in spatial niche use were evident in reduced oviposition of *P. bickleyi* and reduced residence time inside the chamber of *N. paspalivorus* in the presence of a conspecific female. Residence inside the chamber of *N. paspalivorus* seemed also influenced by the presence of *P. bickleyi*. Both *N. paspalivorus* and *P. bickleyi* preyed upon each other with moderate IG predation rates of adult females on larvae as compared to other phytoseiid IG predator–prey combinations (e.g., Croft et al.

1996; Schausberger 1997). Neither species yielded nutritional benefits from IGP in terms of adult survival and oviposition.

Proximate reasons for the microhabitat preference of *N. paspalivorus* and *P. bickleyi* involve positive thigmotaxis and preference for elevated relative humidity, which was probably close to saturation inside the artificial chamber. Positive thigmotaxis has been suggested for several plant-inhabiting generalist predatory mites such as *Typhlodromus pyri* Scheuten and *Kampimodromus aberrans* (Oudemans) (both Phytoseiidae), which preferentially reside in the angles between leaf veins and leaf blade or between leaf hairs (e.g., Roda et al. 2000; Kreiter et al. 2002; Seelmann et al. 2007). Regarding humidity *P. bickleyi* seems to be more sensitive to dry conditions and deprivation of free water than *N. paspalivorus* (Lawson-Balagbo personal observation). The overall ambient humidity in the climatic chamber used to store the experimental units (∼60%) was apparently not very suitable for *P. bickleyi* for which we registered overall high mortality. Humidity susceptibility of predatory mites is often related to the prevailing ambient humidity regime of their respective geographic areas of origin and/or the host plant and/or part of it they inhabit (McMurtry et al. 1976; Sabelis 1985; Van Dinh et al. 1988; Bakker et al. 1993; Walzer et al. 2007). *Neoseiulus paspalivorus* is usually found in buds and sheaths of herbaceous plants such as *Paspalum* sp., Poaceae (DeLeon 1957; de Moraes et al. 2004a, b; Kreiter et al. 2005) and on coconut fruits in regions characterized by a long drought period (Lawson-Balagbo et al. 2008). Ascid mites in general inhabit the upper soil surface but are also found on plants under warm and humid conditions as well as in protected man-made environments such as food stores, and mushroom-growing facilities (Halliday et al. 1998; Gerson et al. 2003). Although *P. bickleyi* and *N. paspalivorus* are frequently found on coconut palms, these two species have never been reported from its leaflets (Lawson-Balagbo et al. 2008). *Proctolaelaps bickleyi* is a pan-tropical species and rather frequent on dropped or decaying coconut fruits and plant detritus in association with fungi growing in humid environments (Halliday et al. 1998; Gerson et al. 2003; Lawson-Balagbo et al. 2008).

Both predatory mites engaged in IGP. Aggressiveness (chance and latency to attack) and predation rates were moderate in comparison to other phytoseiid species (e.g., Croft et al. 1996; Schausberger 1997; Walzer and Schausberger 1999b; Schausberger and Croft 2000; Zannou et al. 2005) with shorter latency to attack for *P. bickleyi* than *N. paspalivorus*. However, provision of free water in our experiments may have considerably reduced the propensity to IGP (Schausberger 1997). Lack of any nutritional benefits of IGP in terms of survival and oviposition for either species suggests rather elimination of food competitors than food acquisition as ultimate reason for IGP. Interestingly, adult *P. bickleyi* females survived longer without prey than when confined with heterospecific larvae as IG prey. They killed heterospecific larvae but were negatively affected by their presence. Possible reasons or combinations thereof include (1) toxicity of *N. paspalivorus* larvae to *P. bickleyi*, (2) physical impediment of *P. bickleyi* females to access free water by the larvae of *N. paspalivorus,* which aggregated mostly at the lower rim of the cavities in contact with the moist tissue paper, (3) energy costs of competitor elimination exceeding the nutritional benefits received, and/or (4) energy loss due to trait-mediated interactions between IG predator and prey. Regarding the latter, the presence of heterospecific larvae could have lead to increased activity and with that increased energy expenditure of *P. bickleyi* as is known from classical predator–prey interactions (Bolker et al. 2003; Luttbeg and Kirby 2005) reducing survival times.

Our study reasserts that the coconut perianth and its tightness to the fruit surface is a key factor for the occurrence of natural enemies of *A. guerreronis* and potential predator–predator interactions on the fruits (Howard and Abreu-Rodriguez 1991; Aratchige 2007;

Aratchige et al. 2007; Lawson-Balagbo et al. 2007b). It is known that the complexity of the habitat of a given herbivorous prey may influence IGP between co-occurring predators and the ability of the predators to elicit trophic cascades (e.g., Dyer and Gentry 1999; Roda et al. 2000; Gross et al. 2005; Finke and Denno 2006; Janssen et al. 2007; Seelmann et al. 2007). As such, IGP would occur to a greater extent in structurally simple habitats as opposed to the more complex habitat provided by the coconut fruit with the open surface area and the concealed area under the perianth. The latter may well provide a spatial refuge to predatory mites from IGP by larger insects (Berryman and Hawkins 2006; Lawson-Balagbo et al. 2007b). Moreover, if the perianth remains tight to the fruit surface and the entrance points are small only *N. paspalivorus* would gain access leaving *P. bickleyi* outside. This would reduce the encounter rate of the two predators and limit IGP. However, if the access points to the area under the perianth are wide enough, *P. bickleyi* is expected to invade, build up its populations by feeding on *A. guerreronis* and may then also engage in IGP (Finke and Denno 2006; Aratchige 2007; Aratchige et al. 2007). Our study suggests that such a situation may influence residence of *N. paspalivorus* under the perianth and possibly trigger earlier dispersal out of this area. Nevertheless, regarding suppression of *A. guerreronis* the voracity of *P. bickleyi* (Lawson-Balagbo personal observation) should more than compensate premature dispersal of *N. paspalivorus*.

In summary, we found some indications for negative interactions between *N. paspalivorus* and *P. bickleyi* in IGP and spatial niche use but these interactions were relatively moderate. We therefore tentatively conclude that these interactions should not compromise the compatibility of the two natural enemies and should not preclude their combined use against *A. guerreronis* on coconut fruits. However, we only studied a small sub-system of the arthropod community occurring on coconut fruits and only looked at a few possible interactions. The unexpected response of adult *P. bickleyi* females to *N. paspalivorus* larvae is interesting and deserves further attention. Besides characterizing the attributes of either species (Lawson-Balagbo et al. 2007a, b), more comprehensive understanding of their intra- and interspecific interactions is needed. In general, synergistic effects in the combined use of *N. paspalivorus* and *P. bickleyi* in controlling *A. guerreronis* would be desirable (e.g., Losey and Denno 1998). Such effects could occur if the former predator induces premature dispersal of *A. guerreronis* out of the protected area under the bracts enhancing predation of *A. guerreronis* by *P. bickleyi* on the open coconut fruit surface (Lawson-Balagbo et al. 2007b). This seems a plausible scenario to be scrutinized as potential control strategy. Ultimately, studies on augmentative biological control of both predators at larger spatial scales, e.g., on whole detached coconut fruits or coconut palms, should be conducted.

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