Interaction Between *Uroplata girardi* (Coleoptera: Chrysomelidae) and *Ophiomyia camarae* (Diptera: Agromyzidae) on a Shared Host *Lantana camara* (Verbenaceae)

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ABSTRACT Multiple releases of insect agents intended to target a single plant pest species could result in competitive interactions that in turn might affect the community structure of the phytophagous insects. Two leaf-feeding biological control agents, *Uroplata girardi* Pic (Coleoptera: Chrysomelidae) and *Ophiomyia camarae* Spencer (Dipetera: Agromyzidae), were released against the weed *Lantana camara* L. (Verbenaceae) in South Africa in the 1970s and 2001, respectively. Since the population explosion of *O. camarae* in 2005, a decline of *U. girardi* populations had been observed in KwaZulu-Natal (KZN) humid coast, leading to speculation that negative interaction may be operating between the agents. The study therefore was conducted to determine the competitive effect of *O. camarae* on *U. girardi*. The study showed that 76% of *O. camarae* larval mines were formed on uninfested (clean) compared with only 24% formed on *U. girardi*-infested leaves, suggesting that the fly chose to lay more eggs on clean leaves. Almost the same number of *U. girardi* larval mines was formed on both *O. camarae*-infested and clean leaves, indicating that *U. girardi* females in this case oviposited indiscriminately on the two types of leaves. The survival of *U. girardi* was 53.8% when reared on clean leaves compared with only 14.6% survival on *O. camarae*-infested leaves. At the end of the sampling period, densities of *U. girardi* was over two times higher in single-species than in combined-species treatment. Releasing both agents together did not significantly affect *O. camarae* densities during the sampling period. In the field, *O. camarae* densities increased rapidly from spring to autumn, whereas those of *U. girardi* remained consistently low during the same period. The bias toward oviposition on clean leaves in *O. camarae* enables its larvae to avoid unfavorable encounters with *U. girardi* larvae, thus enhancing its development and survival. The apparent inability of *U. girardi* to distinguish between suitable and unsuitable leaves for oviposition could compromise the fitness of this beetle, and this could explain the suppression of *U. girardi* populations during summer when *O. camarae* populations begin to increase rapidly. This study provides evidence for an asymmetric interaction between two introduced agents, and therefore highlights the importance of conducting interaction studies on agents with extensive niche overlap before their release into the environment.

KEY WORDS multiple release, competitive interaction, host quality, population dynamics, biological control

Multiple releases of biological control agents have become a contentious issue in weed biological control worldwide, with results ranging from failure to success in controlling the target weed species (Julien and Griffiths 1998, Denoth et al. 2002). Although there are several cases where the success in biological control of an invasive alien weed is attributed to the combined effect of two or more agents (Hoffmann and Moran 1998, Hoffmann and Moran 1999, Anderson et al. 2000), some weeds have been successfully controlled by only one agent species (Denoth et al. 2002, Crowe and Bourchier 2006). The argument that using multiple agents may reduce the likelihood of success through the process of competitive exclusion (Ehler and Hall 1982) is largely based on intuition rather than empirical evidence. Critics of multiple release of agents in biological control systems have compared it to a lottery model that is based on the assumption that the more agents that are introduced, the more likely it is that the most effective agent will be among them (Myers 1985). However, it is also acknowledged that selecting effective candidates for quarantine evaluation and predicting agent performance in the new environment are some of the most difficult challenges in biological control of weeds.

Biological control of *Lantana camara* L. (Verbenaceae), commonly known as lantana, was initiated in South Africa in the 1960s (Oosthuizen 1964). *Lantana camara*, originally from Central and South America, is

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a thicket-forming shrub that has spread from gardens into pastures, woodlands and forests, where it competes for resources and reduces the productivity of pastures and forest plantations (Cilliers and Neser 1991, Baars and Neser 1999, Day and Neser 2000). Lantana is a threat to biodiversity in several countries such as Australia, India, the United States (Hawaii) and South Africa (Day and Neser 2000). In the subtropical humid coast of KwaZulu-Natal (KZN), South Africa, lantana often retains its leaves throughout the year, thus sustaining a number of leaf-feeding insects. Since the initiation of lantana biological control program, 24 different agent species have been released, aimed at imposing cumulative stress on the plant (Cilliers 1983, Denoth et al. 2002) in the hope that the combined effect of the agents would increase plant damage and result in better control of the weed (Cilliers and Neser 1991, Baars and Neser 1999, Day and Neser 2000, Simelane and Phenye 2005). So far twelve of the agent species have become established on *L. camara*, with eight of these feeding and developing on the same part of the plant, the leaves (Baars and Neser 1999, Baars 2003b, Simelane 2006). As the number of biological control agents that share the most similar resources increases, so does the chance that some interactions between them will be negative (Harris 1985, Julien and Griffiths 1998). It is argued that host plants constitute a common resource budget, and herbivores that are not spatially separated (i.e., sharing the same plant) will compete because one species will lower the availability of the resource for other species (McEvoy 2002, Blossey and Hunt-Joshi 2003). Taking into account that each introduced biological control agent creates a situation where negative interactions become possible, and that each agent poses a risk to nontarget plant species, restraint in introduction of weed biological control agents in succession is advised (McEvoy and Coombs 1999, Denoth et al. 2002, Crowe and Bourchier 2006).

The lantana hispid *Uroplata girardi* Pic (Coleoptera: Chrysomelidae) (Cilliers 1987a), and the leaf-mining fly *Ophiomyia camarae* Spencer (Diptera: Agromyzidae) (Simelane 2002) were among the suite of biological control agents released against lantana in South Africa in the 1970s and 2001, respectively. *Uroplata girardi* female inserts its egg into the leaf tissue, covering it with frass that remains visible on the leaf surface (Cilliers 1987b). On hatching, larva mines within the mesophyll tissue, forming a blotch on the leaf as the larva develops. The adult female of *O. camarae* inserts its eggs singly into the leaf tissue, often into a lateral vein. Upon hatching, *O. camarae* larva tunnels along the leaf veins, forming a herringbone pattern that often results in leaf chlorosis and premature abscission. The generation time for *U. girardi* is 41 d versus 30 for *O. camarae.*

Uroplata girardi was found to be abundant at several sites along KwaZulu-Natal (KZN) humid coast in 1998, with ≈50% of the leaves per plant infested with larvae during population peaks in March and April (Cilliers 1987a, Baars 2003a, Baars and Heystek 2003). Since its release in 2001, *O. camarae* has become abundant and widely distributed, particularly along the coastal regions of KZN (Simelane and Phenye 2004). Compared with the field surveys done in 1998 (Baars and Heystek 2003), the abundance of *U. girardi* had declined, whereas that of *O. camarae* had increased in the same region (Heystek 2006), indicating the possibility of a negative interaction between the two agents. In fact, both *O. camarae* and *U. girardi* were found to be abundant (≈50% leaves infested per plant) in Richards Bay during 2004–2005 (Heystek 2006). During 2006–2007, however, *U. girardi* was rarer (≈20% leaves infested per plant), whereas *O. camarae* remained abundant, averaging 50% of infested leaves per plant but peaking at 86% during March and April at several sites in KZN (Urban and Phenye 2005, April 2009). Since the populations of both species peak at the same time (March and April), attack the leaves of the same lantana variety in the same habitat and thus use the same resource, some form of interaction is expected, but the nature of this interaction is not yet understood.

It has been shown that in the case of at least nine species, leaf-mining insects use undamaged leaves more often than not and that survivorship in these species is significantly higher on undamaged than on damaged leaves (Faeth 1986). If *O. camarae* matches this trend, it will be more commonly associated with undamaged leaves that will consequently become degraded and drop prematurely, reducing the resource available to other lantana herbivores such as *U. girardi* that share the same feeding niche. This study therefore was carried out to determine: 1) the influence of leaf quality on use by both *U. girardi* and *O. camarae*, 2) the effect of coexistence on the population densities of the two biological control agents under semifield conditions, and 3) whether negative interactions between the two agents might have caused a decline in the abundance of *U. girardi* over time.

Materials and Methods

Study Organisms. Plants used in the study were propagated from a single *L. camara* mother plant of variety 021 Dark Pink collected at Kuswag Road, Amanzimtoti, KZN (30° 02′ 08″ S, 30° 53′ 42″ E). Variety 021 appears to be the most common in KZN, and the most used by both *U. girardi* and *O. camarae* (Simelane 2005, Heystek 2006). Forty eight shoot-tip cuttings of 7 cm in length were dipped in rooting hormone, planted in peat cylinders, transported to Pretoria and placed on a warm mist-bed in a glasshouse to induce rooting. Each rooted cutting initially was planted in a plastic nursery bag of 4.74 liters (150 by 125 by 300 mm), with a soil mix containing two parts compost, two parts vermiculite, and one part sand, before being transplanted into the ground at the experimental site. In September 2006, laboratory culture of *U. girardi* was established from field-collected adults while that of *O. camarae* was established from field-collected lantana leaves containing *O. camarae* pupae. Cultures of both agents were maintained and experiments were conducted in a glasshouse at Ri-

etondale Research Centre, Pretoria, South Africa. Temperature, ranging from 22 to 30°C, and 23–88% RH were maintained during rearing and laboratory studies. Flood lights (300 W) were also installed in the glasshouse, and a photoperiod of 12:12 (L:D) h was maintained throughout the studies.

Relationship Between the Number of Oviposition Marks and the Larval Mines of *U. girardi* and *O. camarae*. To confirm whether new larval mines are closely correlated with oviposition marks formed by either *U. girardi* or *O. camarae* females, an experiment was conducted in April 2010. Both *O. camarae* and *U. girardi* eggs are embedded in the plant tissues but females of both species leave visible oviposition marks on the leaf surface, and these were used to quantify levels of oviposition. *Uroplata girardi* females insert each egg into the leaf tissue, covering it with frass that remains visible on the leaf surface (Cilliers 1987b). *Ophiomyia camarae* females insert each egg into the leaf vein, often toward the apex of the leaf, leaving a visible oviposition scar on the surface of the leaf (Simelane 2002). To confirm whether new larval mines were closely correlated with numbers of eggs laid under the experimental condition of this study, 30 adults of both insect species were confined separately on potted *L. camara* plants in two separate gauze-covered cages (55 by 55 by 95 cm). After 12 d, 30 leaves from each plant were marked with a tag tied around the leaf petiole, and all of the oviposition marks on each of these leaves were counted and recorded. On becoming visible, new larval mines that were subsequently formed on the tagged leaves were counted, and the relationship between the number of oviposition marks and the number of larval mines was determined using linear regression analysis.

Influence of Leaf Quality on Utilization by *U. girardi and O. camarae*. A laboratory study was carried out to determine how utilization of *L. camara* leaves by either *U. girardi* or *O. camarae* was influenced by leaf quality (i.e., whether the leaf already hosted larvae of the other species). The study was conducted over a period of 2 mo (i.e., from 1 September 2008 until 31 October 2008). Six lantana plants in 10-liter pots were housed separately in gauze-covered cages (55 by 55 by 95 cm). Three of the plants were exposed to 30 unsexed *U. girardi* adults and the other three were exposed to 15 pairs of *O. camarae* adults. The insects were left in their respective cages until signs of larval mining were visible. At this stage the surviving adults were removed from the cages and a fresh (undamaged) potted lantana plant was placed close to the infested one. Thirty unsexed *U. girardi* adults were then confined for 12 d in each of the cages containing one plant infested by *O. camarae* and the other uninfested (clean) plant. Similarly, 30 adults of *O. camarae* were confined for the same period in each of the three cages containing *U. girardi*-infested and clean plants. After eight weeks, leaves were inspected and the new larval mines formed on both previously infested and clean leaves were counted. Comparison was made between the proportions of new larval mines of one insect species formed on clean leaves versus those formed on leaves previously infested by the other species.

Influence of Leaf Quality on Performance of *U. girardi*. To determine whether leaf quality (*O. camarae*-infested leaves) affects the performance (i.e., survival and body size) of *U. girardi*, a set of *U. girardi* larvae developing on either *O. camarae*-infested or clean leaves were monitored to determine their survival on each of the two treatments. Six lantana plants in 10-liter pots were infested separately with *O. camarae* adults in March 2010 as described in the previous experiment. When signs of larval mining by *O. camarae* were visible, the infested plants were exposed to 30 adults of *U. girardi* for a period of 12 d. After 8 wk, when the larval mines of *U. girardi* were also visible on the leaves, a set of 15 leaves that were infested with larvae of both insects were marked and each infested leaf was enclosed in a mesh gauze (10 by 8 by 4 cm) to recover the emerging *U. girardi* adults. Another set of 15 leaves infested with only *U. girardi* mines also were marked and enclosed with a mesh gauze to recover emerging *U. girardi* adults. Survival to adulthood and body lengths of *U. girardi* were compared between the beetles reared on *O. camarae*-infested leaves and those reared on clean leaves.

Population Dynamics of *U. girardi* and *O. camarae* Under Semifield Conditions. To determine whether the occurrence of either *U. girardi* or *O. camarae* on plants had an effect on the overall abundance of the other species, a set of measurements was made under semifield conditions during a 6-mo period, that is, from November 2006 to May 2007. Thirty rooted lantana cuttings were planted separately into 30-cm (diameter) by 50-cm (depth) holes dug in the field. The plants were watered at least three times per week and were allowed to grow up to a height of 50 cm before being exposed to insects. Mesh cages (1.8 by 1.8 by 1.8 m) were erected over the plants, and access to the cage was through a zip fastener. Each plant was inoculated either with 30 unsexed *U. girardi* adults alone, 15 pairs of *O. camarae* adults alone, or 30 adults of each insect species (*U. girardi* and *O. camarae*) together. The numbers of leaves with mines of each insect species on each plant were recorded every month for 6 mo, starting from summer (1 December 2006) to autumn (31 May 2007). On the basis of larval mines, the population density of each insect species in the cages where both species were initially released together was compared with that in which the same species was released alone.

Population Dynamics of *U. girardi and O. camarae* in the Field. Populations of the two insect species were monitored every 2 mo at five selected sites in KZN over a full calendar year from July 2006 and to June 2007. Three sites: Pahla (30° 02′28″ S, 30° 53′23″ E); Kuswag (30° 02′08″ S, 30° 53′42″ E); and Scottburgh (30° 16′11″ S, 30° 45′13″ E) were located on the south coast of KZN. The two other sites: Tongaat (28° 44′25″ S, 31° 55′08″ E) and Richards Bay (28° 46′08″ S, 32° 04′50″ E) were on the north coast of the province. All the sites were characterized by a warm and humid climate throughout the year. At each site, 10 branches

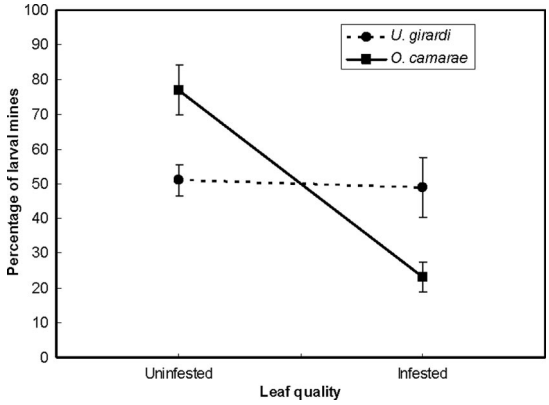

Fig. 1. Percentage (±SE) of larval mines formed by either *U. girardi* or *O. camarae* on either infested or uninfested (clean) leaves.

were selected at random from a tree consisting of several branches. On each lantana branch of ≈110 cm length (i.e., with ≈100 leaves), percentage of leaves infested by each insect species was calculated to determine its relative abundance in the site.

Statistical Analysis. Differences in preference of both insect species were compared between two treatments (infested and uninfested leaves) by using χ^2 (χ^2) tests (Statistica 2004). Differences in survival of *U. girardi* also were compared between two treatments (*O. camarae*-infested and clean leaves) by using χ^2. Student's *t*-tests were used to determine significant differences in abundance of an insect species between combined-species and single-species treatments under semifield conditions.

Results

Influence of Leaf Quality on Utilization by *U. girardi* and *O. camarae*. Although not all oviposition marks resulted in the formation of new larval mines, initial experiment showed that there were very strong positive correlations between the number of oviposition marks (x) and the number of new larval mines (y) for both *U. girardi* ($y = 0.738x + 0.08$; $r^2 = 0.83$; $P < 0.001$) and *O. camarae* ($y = 0.606x + 0.07$; $r^2 = 0.80$; $P < 0.001$). Therefore the proportion of larval mines formed on a leaf treatment was a reflection of oviposition choice by a female of each species.

The study showed that a significantly higher proportion of new larval mines of *O. camarae* was formed on clean rather than on *U. girardi*-infested leaves ($\chi^2 = 104.9$; df = 2; $P < 0.05$) (Fig. 1), suggesting that *O. camarae* females may have preferentially selected good-quality leaves for oviposition. Of the total number of mines formed by *O. camarae* larvae, 76% were formed on clean leaves compared with only 24% formed on leaves already infested with *U. girardi*. In contrast, almost the same number of larval mines of *U. girardi* were formed on both clean and *O. camarae*-infested leaves ($\chi^2 = 6.0$; df = 2; $P > 0.05$), suggesting that the *U. girardi* females may have oviposited indiscriminately on both leaf treatments. Of the total number of mines formed by *U. girardi* larvae, 52.7% were formed on clean leaves versus 47.3% formed on leaves already infested with *O. camarae*.

Influence of Leaf Quality on Performance of *U. girardi*. The survival of *U. girardi* to adulthood was significantly higher when reared on clean leaves than on *O. camarae*-infested leaves ($\chi^2 = 655.8$; df = 4; $P < 0.05$), averaging 53.8 ± 4.43% (mean ± SE) on clean leaves versus 14.6 ± 1.91% on infested leaves. However, the body sizes of *U. girardi* adults emerging from the two leaf treatments were almost the same ($t = -0.8$; df = 28; $P = 0.43$), averaging 4.01 ± 0.23 mm on infested leaves versus 4.12 ± 0.17 mm on clean leaves.

Population Dynamics of *U. girardi* and *O. camarae* Under Semifield Conditions. The results showed that co-infestation by both agents had a negative effect on population density of *U. girardi* during the 6-mo period (Fig. 2). During the 6- mo period, the percentage of leaves infested per plant by *U. girardi* was significantly higher when the beetle was released on its own than when released together with *O. camarae* ($t = 2.41$; df = 58; $P = 0.02$). When confined alone, *U. girardi* populations increased rapidly, reaching 34 and 25% of larval-mined leaves per plant in January and February, respectively, and then declined sharply from March to May. When *U. girardi* was released together with *O. camarae*, no *U. girardi* larval mines were recorded in December, whereas a few were recorded in the single species treatment during the same period. In the combined-species treatment, leaf infestation by *U. girardi* was substantially reduced, reaching 13 and 12% of larval-mined leaves per plant in January and February, respectively, and then declined sharply from March to May. Although the simultaneous release of both agents seemed to have affected *O. camarae* during the first 3 mo, the population density of *O. camarae* in single- and combined-species treatments during the 6-mo period did not differ significantly ($t = 1.42$; df = 58; $P = 0.168$) (Fig. 3). When *O. camarae* was released alone, its population density increased rapidly from December, reaching a peak of 63% of infested leaves per plant in April before declining to 5% in May. In the combined-species treatment, population density of *O. camarae* reached a peak of 48% of infested leaves per plant in April before declining sharply in May.

Population Dynamics of *U. girardi* and *O. camarae* in the Field. Although the relative abundance of the two insect species (*U. girardi* and *O. camarae*) varied considerably among the sites and between biological control agents, the general trend observed in four (Kuswag Road, Tongaat, Scottburgh, and Richards Bay) of the five sites was that the relative abundance of *U. girardi* was consistently lower than that of *O. camarae* during the sampling period (Fig. 4). At the Pahla site, however, the relative abundance of *U. girardi* was much higher than at the other four sites during the sampling period, and also often higher than that of *O. camarae* at that site. Across all sites, *U. girardi* populations were consistently lower throughout the year, with abundance levels ranging from 1 to 7.5% of infested leaves per plant. Although abun-

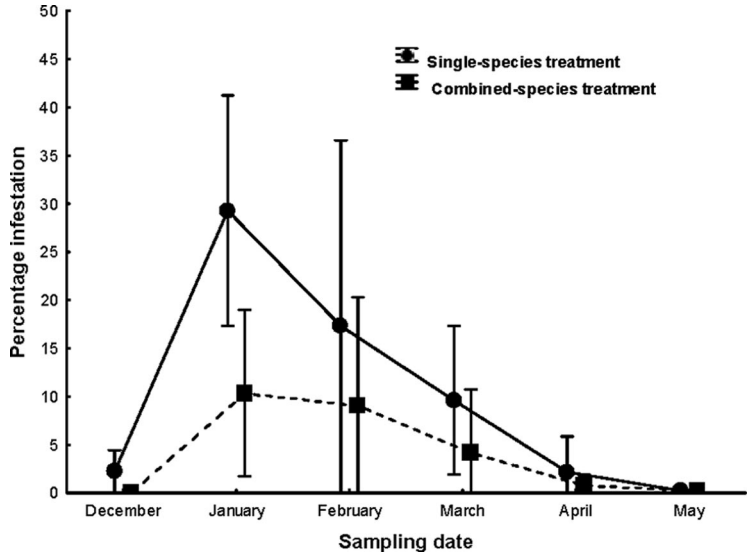

Fig. 2. Percentage (± SE) of leaves infested with *U. girardi* in single-species (bull5) and combined-species treatments (squlf) from December 2006 to May 2007).

dance levels of *O. camarae* were low during winter and spring across all sites, there was a sharp increase in abundance of the fly during summer and autumn, averaging 43% of infested leaves per plant across all sites in March.

Discussion

The results of the current study showed that a higher proportion of *O. camarae* larval mines were formed on clean than on *U. girardi*-infested leaves, and this is most likely attributable to oviposition choice by *O. camarae* females. In contrast, almost the same number of *U. girardi* larval mines was formed on both *O. camarae*-infested and clean leaves, indicating that the beetle may have oviposited indiscriminately on the available plant leaves. We argue that the ability of *O. camarae* females to correctly separate acceptable sites from nonacceptable ones influences the survival of its offspring. Thus, the avoidance of *U. girardi*-infested leaves by *O. camarae* may be increasing the fitness of this fly, thereby contributing to its competitive superiority in the introduced range, particularly in KZN humid coast. The indiscriminate egg-laying pattern displayed by *U. girardi* subjects almost half of its offspring (larvae) to suboptimal food resource (i.e., leaves infested previously with *O. camarae*) thus increasing its larval mortality and inhibiting

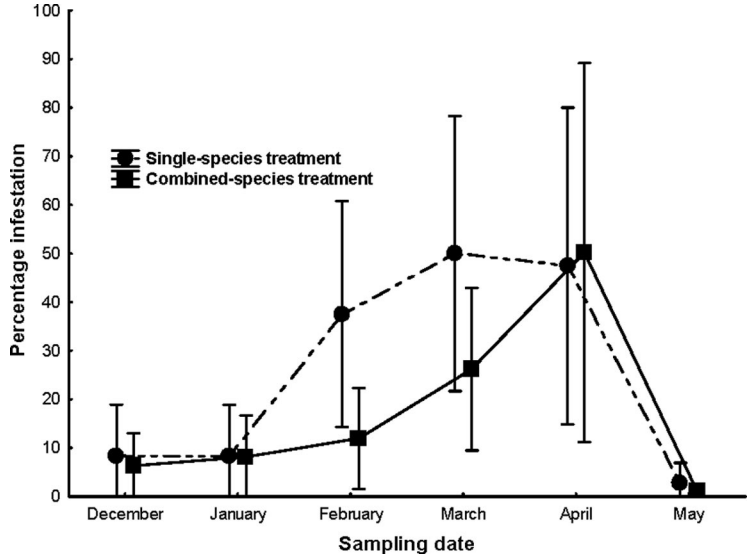

Fig. 3. Percentage (± SE) of leaves infested with *O. camarae* in single-species (bull5) and combined-species treatments (squlf) from December 2006 to January 2007.

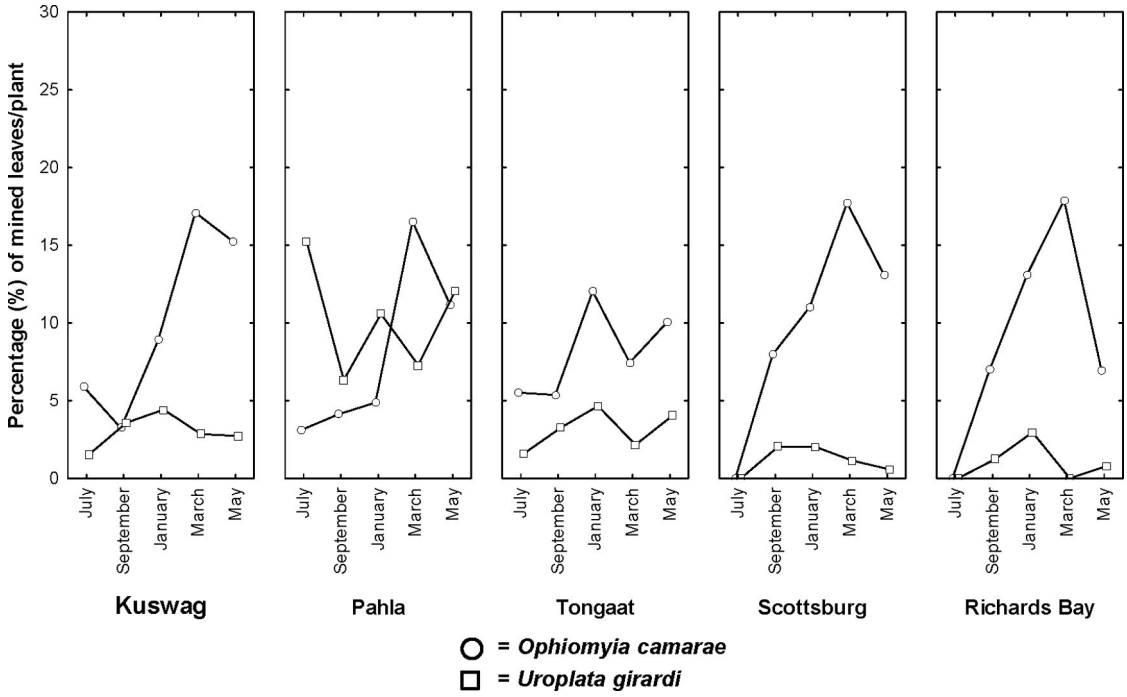

Fig. 4. Percentage (± SE) of leaves infested with *U. girardi* and *O. camarae* at different sites in KwaZulu-Natal.

population growth of this beetle. The mortality of *U. girardi* could be quite severe from late summer to autumn when *O. camarae* attack rate increases up to 86% of infested leaves per plant along the humid KZN coast (Urban and Phenye 2005). During the laboratory experiment, we also observed that leaves infested with either *O. camarae* or both agents often abscised prematurely, and this is likely to increase larval mortality of *U. girardi* more than that of *O. camarae* because of the longer development time required by the former (≈41-d as opposed to 30-d generation time). These factors combined influence the population dynamics of *U. girardi*, and could explain the population decline of this beetle after the establishment and population explosion of its competitor, *O. camarae* (Heystek 2006).

The oviposition behavior of *O. camarae* observed in the current study is consistent with previous studies that have demonstrated that oviposition site choice for insects constitutes a postfertilization investment in some insect species (Jaenike 1978, Leather et al. 1987, Leather 1994). A number of insect species in the leaf-mining guild, particularly agromyzid flies, have been found to prefer undamaged leaves, and that they often have significantly higher survivorship on undamaged than on damaged leaves (Faeth 1986, Quiring and McNeil 1987). The selection behavior of *O. camarae* appears to be very similar to that of *Agromyza frontella* Rondani (Diptera: Agromyzidae), which ranks plant leaves according to their infestation status, selecting unexploited leaves as desirable for oviposition, and this seems ideally suited for optimizing performance of the leafminer offspring (Quiring and McNeil 1987).

Under semifield conditions, the study showed that colonization of the host by both *U. girardi* and *O. camarae* impeded population density of *U. girardi*, with infestation level by the beetle averaging 9% per plant when confined with *O. camarae*, compared with ≈29% per plant when confined alone (Fig. 2). Although the initial establishment of both agents was delayed somewhat in the combined treatment, the population density of *O. camarae* increased rapidly from March to April, and by May the overall reproductive output of *O. camarae* in both treatments was almost the same (Fig. 3). The low population density of *U. girardi* in the combined-species treatment is not surprising as the laboratory study also has suggested that *U. girardi* accepts and uses both infested and clean leaves almost equally. As shown in the previous experiment, survival of *U. girardi* is substantially reduced when reared on *O. camarae*-infested leaves, and this explains the suppression of population growth of this beetle in combined-species treatment. Although *O. camarae* has a physiological advantage over *U. girardi* (e.g., ≈30-d generation time for *O. camarae* versus ≈41 d for *U. girardi*), our study showed that population densities of *U. girardi* were consistently lower when the beetle was confined with *O. camarae* than when released on its own. Although there is apparently no overall support for the belief that superior competitors undergo more generations per year than inferior competitors (Denno et al. 1995), the population explosion and biological control success of *O. camarae* in the KZN coastal region in recent years also can be explained by its very rapid rate of population increase: approximately treble that of *U. girardi* when

isolated under similar conditions (Figs. 2 & 3). The ability of *O. camarae* to select and use good quality leaves when occurring sympatrically with *U. girardi* (Fig. 1) may be enhancing its competitive superiority.

Although *U. girardi* and *O. camarae* population densities varied between sites in KZN, the pattern of population growth in four of the five sites was very similar (Fig. 4). Overall, our field survey conducted from 2006 to 2007 in KZN indicated lower *U. girardi* abundance levels, ranging between 2 and 7.5% of infested leaves per plant, whereas Baars and Heystek (2003) had reported much higher abundance levels of the beetle at some KZN sites before the release of *O. camarae.* According to Baars and Heystek (2003), relative abundance of *U. girardi* in 1998 ranged from occasional to highly abundant, translating into ≈25% and over 50% of infested leaves per plant, respectively. In the current study, *O. camarae* populations persisted at higher levels (up to 86% of infested leaves per plant during March and April) in at least four (Kuswag Road at Amanzimtoti, Tongaat, Scottburgh, and Richards Bay) of the five sites, whereas those of *U. girardi* were consistently lower (<10% of infested leaves per plant) throughout the year (Fig. 4). Heystek (2006) observed the same pattern in other sites within the same region during 2004. The population peak of *U. girardi*, which used to occur during March and April in the humid KZN coast (Cilliers 1987), apparently has been replaced by that of *O. camarae*, which occurs during the same months in the same region (Urban and Phenye 2005, April 2009). Therefore, the higher population densities of *O. camarae* during March and April is most likely to be detrimental to the population growth of *U. girardi*, and this could explain the demise of this beetle in the region.

Overall, other lantana biocontrol agents are scarce in South Africa, and are less likely to influence the population dynamics of *O. camarae* and *U. girardi* in KZN humid coast. Although lantana biocontrol agents such as *Telionemia scrupulosa* Stål (Heteroptera: Tingidae) and *Octotoma scabripennis* Guérin (Coleoptera: Chrysomelidae) occasionally defoliate whole stands of lantana, their impact, though striking, is only sporadic, and the plants soon recover (Baars and Neser 1999).

At Pahla site, however, *U. girardi* abundance initially was high, but began to decline in March, whereas that of *O. camarae* increased. By May, the *U. girardi* population had increased again, whereas that of *O. camarae* had not recovered. Pahla site was located near the railway line where herbicides were sprayed periodically onto the weeds. It is likely that herbicides selectively reduced the survival of *O. camarae* and the parasitoids of *U. girardi*, because they are smaller, with a thinner integument and more active, thus favoring proliferation of *U. girardi* at that site.

Our study provides evidence for negative interaction between two introduced biological control agents, and therefore highlights the desirability of conducting interaction studies on herbivorous insects using the same host plant, particularly those with extensive niche overlap, before they are released into the environment. This could limit the chances of introducing agents that would either hamper the effectiveness of superior agents or increase the risk to nontarget plant species.

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