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### What lies beneath?

*Linking litter and canopy food webs to protect ornamental crops*

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## Generalist red velvet mite predator (*Balaustium leanderi*) performs better on a mixed diet

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Generalist predators have the potential advantage to control more than one pest and to be more persistent than specialist predators because they can survive on different foods. Moreover, their population growth rate may be elevated when offered a mixture of prey species. We studied a generalist predatory mite *Balaustium leanderi* that shows promise for biological control of thrips and whiteflies in protected rose cultures in Colombia. Although starting its life in the soil, this predator makes excursions onto plants where it feeds on various arthropods. We quantified life history parameters of the predator, offering high densities of three pest species: first-instar larvae of *Frankliniella occidentalis*, eggs of *Trialeurodes vaporariorum* and *Tetranychus urticae*, either alone or in combination. The predators completed their life cycle on each diet. The egg-to-egg period was c. 2 months. All eggs were laid in one batch in 1-2 days, indicating a pronounced semelparous reproduction pattern. In general, females reproduced earlier and laid more eggs on mixed diets, and these early reproducers consequently had higher population growth rates than late reproducers. The best diet in terms of egg-to-egg period and juvenile survival was the combination of eggs from whiteflies and spider mites. Spider mite eggs alone and western flower thrips larvae alone were the worst diets. It remains to be investigated whether mixed diets promote the population growth rate of *Balaustium leanderi* sufficiently for biocontrol of whiteflies and thrips in the presence of alternative prey, such as spider mites, to become effective.

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## Introduction

Whether to use generalist or specialist predators for biological control of crop pests is an important and hotly debated topic (Symondson et al. 2002). Most attention has been paid to specialist biocontrol agents, because their dynamics are tightly linked to that of the prey and because of the lower risk of side effects on populations of non-target organisms (Murdoch et al. 1984, 1985; Hassell & May 1986; Murdoch 1994). However, generalist predators are increasingly used for biocontrol (Chiverton 1986; Rosenheim et al. 1993; Settle et al. 1996; Chang & Kareiva 1999; Symondson et al. 2002; Messelink et al. 2012). This also applies to generalist phytoseiid mites that live on plants and feed on various arthropod herbivores (Nomikou et al. 2001; Messelink et al. 2008, 2010, 2012), as well as on plant food such as pollen (Nomikou et al. 2002; van Rijn et al. 2002) and on plant fungi, such as spores of mildew (Pozzebon & Duso 2008). Compared to specialist natural enemies, the advantage of using generalist predators is that they can feed on other prey than the target pest, thereby enabling persistence of their populations at high densities, even in periods of low pest density. A disadvantage of using generalist predators is that they may also attack non-target prey or even other predators (intraguild predation or higher-order predation; Rosenheim et al. 1995; Rosenheim 1998). Although this could potentially disrupt biological control, this is often not the case for intraguild predation (Janssen et al. 2006), but can occur in the case of higher-order predation (Messelink et al. 2011).

Generalist predators may be present on the plants, but they may also live in the soil, yet make foraging excursions onto the plants. In this case, their population size depends on the community of arthropod decomposers and predators in the soil or litter (Settle et al. 1996; Scheu 2001), as well as on the community of arthropod herbivores on the plant canopy. Some species in the genus *Balaustium* (Acari: Erythraeidae) are good examples of species that occur in the litter and on plants (Putman 1969; Childers & Rock 1981; Welbourn 1983; Welbourn & Jennings 1991). Moreover, these species prey on a range of species on plants; they have been observed to feed on fruit-tree red spider mites, *Panonychus ulmi* (Acari: Tetranychidae) (Putman 1969; Cadogan & Laing 1977), eggs and larvae of Lepidoptera and Diptera, aphids and pollen (Hayes 1985). Muñoz et al. (2009) observed that an undescribed species of *Balaustium* (C. Welbourn, pers. comm. 2008) feeds preferentially on immatures of three plant pests: two-spotted spider mites *Tetranychus urticae* (Acari: Tetranychidae), western flower thrips *Frankliniella occidentalis* (Thysanoptera: Thripidae) and greenhouse whiteflies, *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae). The same species was used in this study. These predatory mites are found in the vegetation outside greenhouses of flower cultures on the Bogotá Plateau in Colombia (Torrado et al. 2001) in cold as well as temperate zones (Getiva & Acosta 2004). Provided pesticides are not applied, they can be

abundant and they are considered as candidate predators for control of several pest species (Muñoz et al. 2009).

In this article, we assess the potential of *Balaustium leanderi* (Fuentes et al. 2014) to feed and reproduce on a diet of spider mites, thrips and whiteflies. We measured prey mortality when exposed to mobile life stages of this predator and we determined the life table parameters on a diet of each of these pest species as well as all possible mixtures. The mixtures were offered because several generalist predatory mites have been shown to reproduce better on mixtures of prey species than on each prey species alone (Oelbermann & Scheu 2002; Messelink et al. 2008), which further increases their capacity for pest control (Messelink et al. 2008, 2010). This research may pave the way for future research on the efficacy of *B. leanderi* as a biocontrol agent and on the role of soil-inhabiting prey (e.g. fungivorous mites) to boost their populations and thereby improve pest control.

## Materials and methods

### Predator and prey cultures

Predators and prey were reared under local greenhouse conditions with a daily maximum and minimum temperature of  $31.7 \pm 3.5$  and  $11.1 \pm 2$  °C (mean  $\pm$  s.d.). The whitefly *T. vaporariorum* was reared on tomato plants (*Solanum lycopersicum*), whereas the thrips *F. occidentalis* was reared on *Pelargonium grandiflorum* flowers in plastic containers (30 × 16 × 12 cm) with moist paper towels on the bottom to promote humidity. The spider mite *T. urticae* was reared on bean plants. The tomato and bean plants were 2 weeks old at infestation; *P. grandiflorum* flowers were bought weekly from a commercial producer, which sprayed minimal levels of pesticides. The cultures of whiteflies and spider mites were kept in separate compartments in a greenhouse inside cages to avoid contamination.

Predator rearing units consisted of closed plastic containers (18 cm diameter, 20 cm height) with an opening (10 cm diameter) covered with a mite-proof steel mesh for ventilation. To provide a suitable substrate for juvenile development, the bottom of the container was covered with a layer of moist peat (c. 3 cm deep). A disc of paper towel (17 cm diameter) was placed on top of the layer to maintain moisture. A total of 15 adult predator individuals were placed in the container and they were provided with plant material infested with all stages of whiteflies, thrips and spider mites twice per week.

To obtain a cohort of *B. leanderi* eggs, we offered individual young adult females a mixture of the three prey species (Muñoz et al. 2009). To this end, *B. leanderi* adults were placed individually in an arena consisting of a rose leaflet on top of an inverted Petri dish (3 cm diameter), which was used as a base for the leaflet; the petiole was inserted in a water-filled plastic tube (6 cm long, 2 cm diameter) to provide water to the leaflet. Mites were kept on the leaflet inside a ring consisting of an opaque PVC tube

(1 cm high, 2 cm diameter), with a hole in its wall, closed by a piece of cork underneath which the mites preferred to lay eggs. The ring was closed with plastic wrap (Vinipel) (see SUPPLEMENTARY MATERIAL 1.1). After 7-10 days, they had laid at least 50 eggs, these egg batches were transferred to a Petri dish with wet cotton wool (Cadogan & Laing 1977). As soon as the pre-larvae had hatched from the eggs, they were transferred each to a separate arena (the same as described above but now without a hole). In this way, batches of 50 individuals at the onset of the pre-larval stage were obtained. For details of culture methods please see SUPPLEMENTARY MATERIAL 1.1.

### Developmental stages, survival and reproduction

Preliminary observations (K. Muñoz-Cárdenas, pers. obs., 2008) showed that *B. leanderi* reproduces by thelytoky, as is the case in a related species (*B. murorum*, Halliday 2005; *B. nr. putmani*, Hedges et al. 2012). We therefore studied the life cycle of *B. leanderi* with individuals kept singly in an arena (as described above) throughout their life span.

There were seven treatments, three of which involved a daily supply with one of the three prey species, offered in sufficient numbers to prevent prey depletion: 80 spider mite eggs, 80 whitefly eggs or 20 first-instar thrips. Predator larvae were offered half these amounts because of their lower prey requirements. Each treatment was replicated with c. 50 *B. leanderi* individuals, each in a separate experimental unit. We also carried out four treatments involving the following prey combinations based on a replacement design (i.e. half or a third of the amounts of prey offered in the monocultures): (1) 40 eggs of *T. urticae* and of *T. vaporariorum*, (2) 40 eggs of *T. vaporariorum* and 10 larvae of *F. occidentalis*, (3) 40 eggs of *T. urticae*, 10 larvae of *F. occidentalis*, and (4) 30 eggs of *T. urticae*, 30 eggs of *T. vaporariorum* and six larvae of *F. occidentalis*. Each of these treatments was replicated with 15 *B. leanderi* individuals. Predator larvae again received half the amount of prey. Prey mortality was measured to verify that enough prey was offered to the predatory mites (see SUPPLEMENTARY MATERIAL 1.2 for results).

Spider mite eggs and thrips larvae were replaced daily with fresh prey from the cultures, using a fine paintbrush. Thus, spider-mite eggs were offered free of the silken web produced by *T. urticae*. Whitefly eggs were replaced once per week as follows. Three whitefly females were allowed to lay eggs on rose leaflets in a clip cage in the presence of males for a period of 3 days. The leaflets with eggs were subsequently used as arenas for predatory mites. Excesses of whitefly eggs and honeydew were removed with a small wet cotton swab. We registered the number of days of every stage, the day at which every *B. leanderi* female laid eggs and the day they died.

Effects of diet on life span and pre-oviposition period were analysed using generalized linear models (GLM) with a Poisson error distribution. For fecundity, a quasi-

Poisson error distribution was used to correct for overdispersion. The effect of diet on survivorship was analyzed using a Cox proportional hazards model (Hosmer & Lemeshow 1999; Crawley 2007). To test the effect of diet on the percentage of non-reproductive predatory mites, we performed a GLM with a quasi-binomial error distribution to correct for overdispersion. Treatments were compared using the mult-comp package (Hothorn et al. 2008).

### Life table parameters

As shown below, the reproduction of *B. leanderi* represents a special type of semelparity (Stearns 1976, 1992; Roff 1992), appropriately referred to as 'pronounced' semelparity (Hautekeete et al. 2001): all eggs are deposited within a very short time span (also called 'big-bang reproduction'; Diamond 1982; Zeineddine & Jansen 2009). Under big-bang reproduction and thelytoky, the life history can be summarized by the following variables: (1) the egg-to-egg developmental time, which then equals the generation time  $T$ ; (2) the number of eggs produced per reproductive female at age  $T$  ( $m_T$ ); (3) the survival from egg deposition until reproducing adult ( $l_T$ ). The latter variable is the product of the survival until adulthood ( $l_A$ ) and the proportion of adults that reproduces ( $s_T$ ). Based on these life table parameters, we calculated the net reproduction rate ( $R_0 = l_T m_T$ ) and the intrinsic rate of increase ( $r_m$ ), which for the special case of big-bang reproduction equals (Carey 1993):

$$r_m = \ln(R_0)/(T + 1). \quad (1)$$

Under big bang reproduction, the variables  $T$  and  $m_T$  can be quantified for each individual separately. Such an individual-based assessment is obviously not possible for the survival probability until becoming a reproducing adult ( $l_T$ ). We therefore provisionally used population estimates of  $l_T$  when estimating the  $r_m$  for each individual, which enabled us to estimate the mean and the variance of  $r_m$ .

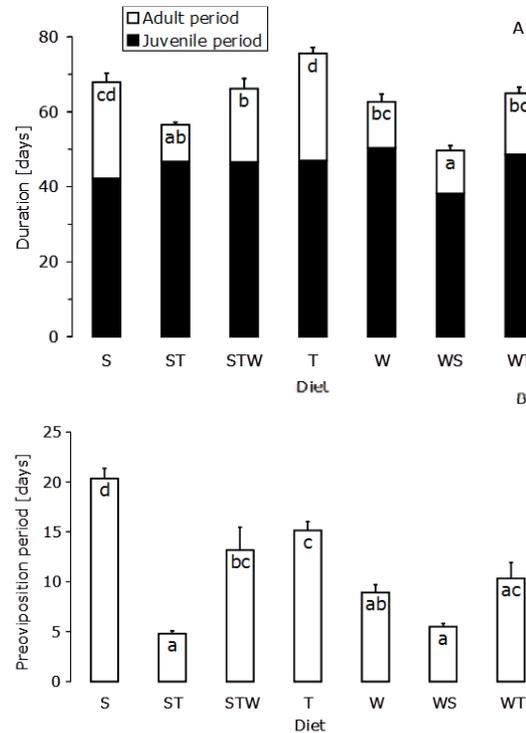
To explore trade-offs between the net reproduction and the egg-to-egg period, we carried out a regression analysis of individual  $R_0$  against individual  $T$  and individual  $r_m$  against individual  $T$ . To help exploring how the trade-off between individual  $R_0$  and individual  $T$  influences the relation between individual  $r_m$  and individual  $T$ , we plotted  $r_m$  based on the overall mean of  $R_0$  and  $T$  in relation to  $T$  (necessarily leading to a hyperbolic relation because  $R_0$  is constant).

The effect of diet on intrinsic rate of population increase was analysed with a GLM with a Gaussian error distribution. To detect trade-offs and possibly other trends in the intrinsic rate of population increase and the net reproduction, these parameters were plotted against the egg-to-egg developmental time. All the statistical tests were done using the software R (2.15.1).

## Results

### Developmental stages

We observed seven developmental stages (see SUPPLEMENTARY MATERIAL 1.1), comparable to the related species *B. putmani* (Putman 1969; Cadogan & Laing 1977) and *B. hernandezii* (Makol et al. 2012): (1) the spherical egg (c. 0.16 mm diameter), initially red but turning dark red later; (2) the red oval prelarva with an orange band (c. 0.2 mm wide, c. 0.3 mm long); (3) the orange-red, six-legged larva; (4) the scarlet, oval and quiescent (legless and sessile) protonymph; (5) the scarlet, oval and eight-legged



**FIGURE 1.1.** The effect of single prey species and mixtures of species on the life span of *Balaustium leanderi*. Diets consisted of whitefly eggs (W), thrips larvae (T), spider-mite eggs (S), or combinations of these prey. **(A)** Mean (+ s.e.) life span, including the mean duration of the immature phase indicated by the black bars and the adult longevity indicated by the white bars. **(B)** Mean (+ s.e.) pre-oviposition period. Different letters indicate significant differences among diets for the total life span (A, white + black bars) and for the pre-oviposition period (B).

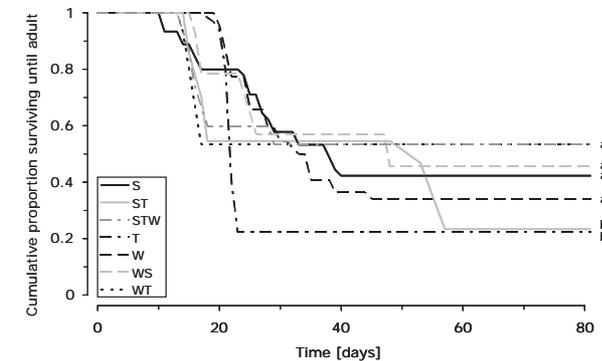
deutonymph showing three distinctive parallel white dorsal lines; (6) the orange-red tritonymphs (morphologically similar but larger than the protonymph); (7) the bright-red to dark-red adults with four pairs of legs and three white lines on the dorsum (like the deutonymph) (1 mm wide, 1.5 mm long). We found only females, as in *B. murosorum* (Halliday 2005).

The overall life span varied significantly with diet (FIGURE 1.1A; GLM, deviance = 67.7, d.f. = 6,73,  $P < 0.0001$ ). The shortest mean life span was found on a mixed diet of eggs of whiteflies and spider mites, the longest when offered thrips larvae. Most of the variation in overall life span was due to differences in the longevity of the adults (FIGURE 1.1A).

The time from emergence as an adult to the first egg laid (the pre-oviposition period) also varied significantly with the diet offered (FIGURE 1.1B; GLM, deviance = 123.7, d.f. = 6,47,  $P < 0.0001$ ). It was shortest on a mixed diet of whiteflies and spider mites and on a diet of spider mites and thrips, and longest on a diet of thrips or spider mites alone, thrips alone and the combination of all three prey species.

### Survival

Survival varied significantly with diet (FIGURE 1.2; Log rank test = 13.36, d.f. = 6,  $P = 0.038$ ). The predatory mites fed with thrips alone or in combination with spider mites showed significantly more mortality compared to the predatory mites fed with the other diets. In general, most mortality occurred during the development from pre-larvae to larvae, which occurs from days 15-30 (FIGURE 1.2).

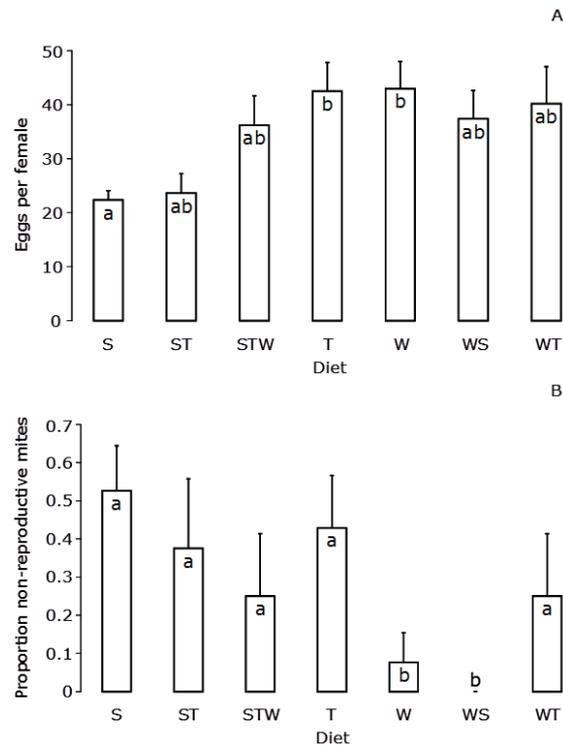


**FIGURE 1.2.** Cumulative survivorship of *Balaustium leanderi* predators on different diets. S refers to spider-mite eggs, T to thrips larvae and W to whitefly eggs. Different letters next to the survivorship curves indicate significant differences.

## Reproduction

Oviposition occurred within 1 or 2 days, implying big-bang reproduction. Thus, to characterize reproductive effort, it suffices to focus on fecundity per reproductive female (FIGURE 1.3A). Fecundity varied significantly with diet (GLM,  $F_{6,46} = 3.34$ ,  $P = 0.008$ ). In particular, fecundity on a diet of spider mite eggs was significantly lower than that on a diet of whitefly eggs or of thrips larvae.

The percentage of non-reproductive predatory mites ( $s_T$ ) also varied with diet (FIGURE 1.3B; GLM,  $F_{6,71} = 2.58$ ,  $P = 0.026$ ). On a diet of whitefly eggs either with or without spider mites, fewer than 10% of the adult predators did not oviposit, whereas on the other diets this was 25% or more. The proportion of non-reproductive preda-



**FIGURE 1.3.** The effect of diet on the average (+ s.e.) (A) total number of eggs laid by reproductive adult females of *Balaustium leanderi* and (B) proportion of non-reproductive *B. leanderi* females. Different letters indicate significant differences. S refers to spider-mite eggs, T to thrips larvae and W to whitefly eggs.

tors fed on the mixed diet of eggs of whiteflies and spider mites and that fed on a diet of whiteflies alone was significantly lower than in the other treatments (FIGURE 1.3B).

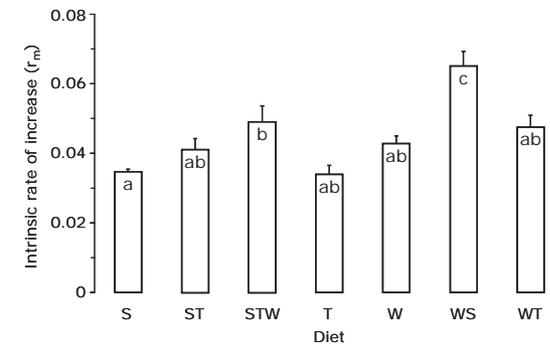
## Life table parameters

Using the individual estimates of  $T$  and  $m_T$  and the population estimates of  $l_T$ , we calculated 'individual'  $r_m$ , their mean and standard error for each diet (FIGURE 1.4) and found significant dietary effects on  $r_m$  (GLM,  $F_{8,47} = 12.88$ ,  $P < 0.0001$ ). Clearly, a mixed diet of whitefly and spider mite eggs together gave the highest value of  $r_m$  and a diet of exclusively thrips larvae or spider mites resulted in the lowest values.

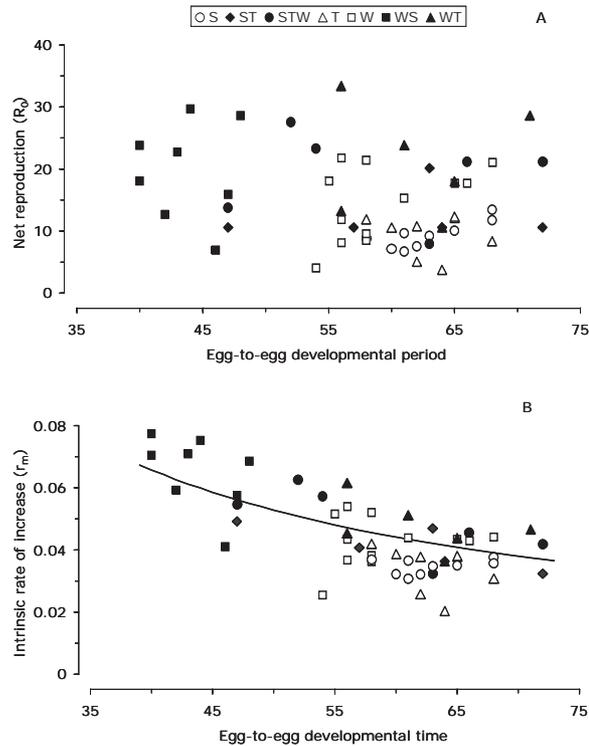
The effect of diet on  $R_0$  was not tested separately because it essentially converges to analyzing the effect on fecundity ( $l_T$  being a population estimate). We found a non-significant negative correlation between the generation time  $T$  and the net reproductive rate  $R_0 = l_T m_T$  (FIGURE 1.5A; linear regression, d.f. = 1, 52,  $R^2 = 0.045$ ,  $P = 0.12$ ).

Regressing  $r_m$  against  $T$  is not very informative: because  $T$  was used to calculate  $r_m$ , it results in a spurious correlation. Instead, it was thought to be more instructive to see how  $r_m$  declines with  $T$  when  $r_m$  is calculated following expression (1), using each individual developmental time  $T$  (points in FIGURE 1.5B) and the overall mean  $R_0$  (drawn line in FIGURE 1.5B). Clearly, the data points tend to be above the line for low values of  $T$  and below the line for higher values of  $T$ . This demonstrates the extent to which the  $R_0$ - $T$  relation determines the individual  $r_m$ .

FIGURE 1.5 illustrates the main points of our life history assessment. First, a diet of thrips larvae or spider mites is the least profitable food in terms of  $R_0$  and  $r_m$  (the data points cluster at the lower right end of the plot). Second, the mixture of eggs of whiteflies and spider mites tend to be the most profitable food source, especially when looking at  $r_m$  (all data point cluster at the higher left end of the plot; FIGURE 1.5B).



**FIGURE 1.4.** The effect of different diets on the intrinsic rate of population increase ( $r_m$  + s.e.) of *Balaustium leanderi*. Different letters indicate significant differences. S refers to spider-mite eggs, T to thrips larvae and W to whitefly eggs.



**FIGURE 1.5.** Relation of (A) net reproduction ( $R_0$ ) and (B) the intrinsic rate of population increase ( $r_m$ ) to egg-to-egg developmental period ( $T$ ) of *Balaustium leanderi* on different diets. Panel B only serves for visual inspection and was not used for a regression analysis because it would yield spurious correlations. The interpretation of this figure is facilitated by including a line expressing  $r_m$  as a function of  $T$  (see text). The deviation of the data from this line shows the extent to which the relation between  $R_0$  and  $T$  (Panel A) affects the value of  $r_m$ .

## Discussion

### Pronounced semelparity

We show that *B. leanderi* exhibits big-bang reproduction or ‘pronounced semelparity’ (Stearns 1976, 1992; Roff 1992; Hautekeete et al. 2001): they lay all their eggs in 1 or 2 days after a long period of development and die soon thereafter. Big-bang reproduction is widespread among the hard ticks (Acari: Ixodidae), whereas iteroparous reproduction prevails among the soft ticks (Acari: Argasidae) (Sonnen-

shine 1991). On a continuous scale from ‘pronounced semelparity’ to ‘pronounced iteroparity’ (Hautekeete et al. 2001), many fast-reproducing mites exhibit semelparous reproduction; examples are physogastric heterostigmatic mites (Bruce & Wrensch 1990; Kaliszewski et al. 1995), prostigmatic mites such as eriophyoids (Sabelis & Bruin 1996) and tetranychoid mites (Sabelis 1991), and mesostigmatic mites such as phytoseiids (Sabelis & Janssen 1994). However, all these mites require a few weeks to produce all offspring and do not immediately die after reproducing (Blommers & van Arendonk 1979). Hence, they do not even come close to the phenomenon of big-bang reproduction as described here for *B. leanderi* and elsewhere for *B. hernandezii* (Makol et al. 2012). Theory on semelparous and iteroparous reproduction predicts that big-bang reproduction is favoured by natural selection when adult survival (up to the next reproductive bout) is predictably very low relative to juvenile survival (Cole 1954; Charnov & Schaffer 1973; Young 1981; Ranta et al. 2002; Zeineddine & Jansen 2009). However, which ecological factors determine predictably low survival in adults of erythraeid predators remains to be elucidated. High soil surface temperatures may cause dramatic mortality, but at least some *Balaustium* spp. seem to resist temperatures up to 48–52 °C and have a high dehydration tolerance (Hedges et al. 2012). Critical factors determining survival of *B. leanderi* clearly need to be investigated.

### Effect of diet on life table parameters

In the case of big-bang reproduction, life-history theory predicts the existence of a switch point in the relative importance of net reproduction ( $R_0$ ) and the generation time ( $T$ ) (Caswell 1982). Here, we investigate the existence of such a switch point in *B. leanderi*. The relative contribution of  $R_0$  and  $T$  to  $r_m$  can be assessed from the ratio of  $r$ -values obtained after a fixed proportional increase ( $a$ ) in  $R_0$  [referred to as  $r(R_0)$ ] and in  $1/T$  [referred to as  $r(T)$ ]:

$$r(R_0)/r(T) = [\ln(aR_0)/(T+1)]/[a\ln(R_0)/(T+1)] = \ln(aR_0)/a\ln(R_0). \quad (2)$$

In order to study the relative importance of  $R_0$  and  $T$  for the population growth rate of *B. leanderi*, we assessed the change of  $r_m$  as a result of changing from feeding and developing on one diet to another diet. Because the change from diet  $j$  to diet  $i$  and the change from diet  $i$  to  $j$  would result in the same absolute value of the change in  $r_m$ , we took the subset of changes from an inferior diet to a superior diet. Hence, each combination of diets was represented once.

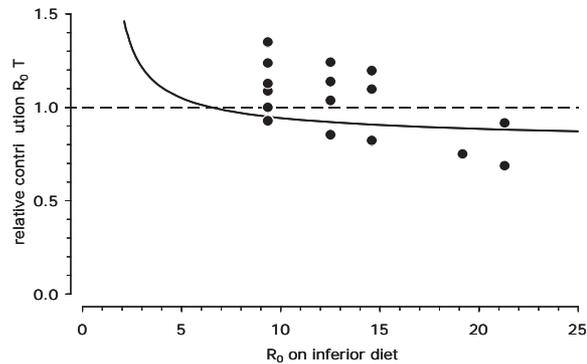
Expression (2) can be used to calculate the relative contribution of  $R_0$  and  $T$  to  $r_m$  as a function of  $R_0$  for equal proportional changes ( $a$ ) in both parameters. However, the changes in  $R_0$  and  $T$  were not equal in our data set. The  $R_0$  on the best diet

(whiteflies plus thrips) was 21.29 and on the worst diet (thrips) 9.35. Hence, the maximum proportional change in  $R_0$  was  $a = 2.277 (= 21.29/9.35)$ . Likewise,  $T$  on the best diet (whiteflies plus spider mites) was 43.75, and on the worst diet (thrips) it was 63.0, resulting in a proportional change of  $b = 1.44 (= 63.0/43.75)$ . We used these values to calculate the relative contribution of  $R_0$  and  $T$  to  $r_m$  as a function of  $R_0$  using:

$$r(R_0)/r(T) = \ln(aR_0)/b\ln(R_0). \quad (3)$$

The curve resulting from this (FIGURE 1.6) shows that  $R_0$  contributes more to increases of  $r_m$  for values of  $R_0 < 7$ , whereas  $T$  is more important for higher values. Hence, there is indeed a switch point from  $R_0$  being more important to  $T$  being more important for realistic values of these parameters.

We subsequently considered all possible diet changes of *B. leanderi* that resulted in an increase of the intrinsic growth rate (hence, changing to a better diet) and calculated the contribution of  $R_0$  and  $T$  to the increase in  $r_m$  using expression (3), using the relative changes in  $R_0$  and  $T$  for this particular diet shift as estimates of  $a$  and  $b$ . The results are shown as points in FIGURE 1.6. Our data indeed show that the contribution of  $T$  to  $r_m$  is higher than that of  $R_0$  for higher values of  $R_0$ , whereas the opposite is true for low values of  $R_0$  (FIGURE 1.6). However, the switch point seems to occur for somewhat higher values of the  $R_0$  on the inferior diet than predicted (cf. points and curve in FIGURE 1.6). The existence of such a switch point has interesting consequences for the evolution of the life-history of *B. leanderi*, which will experience



**FIGURE 1.6.** The relative contribution of  $R_0$  and  $T$  to changes in intrinsic growth rate as a result of changing from an inferior diet to a superior diet. Above the interrupted line, the contribution of  $R_0$  to an increase in  $r_m$  as a result from the switch from an inferior diet to a superior diet is more important, below this line, the contribution of  $T$  is larger. The curve is calculated using expression (3) (see text), points were calculated from the data of each possible shift from an inferior to a superior diet.

stronger selection for higher net reproduction than for a shorter developmental period on some diets, and the reverse on other diets. This could be verified by setting up an experimental evolution approach with samples from the same population of this predator on different diets.

### Thrips and spider mites as inferior prey

To explain the low performance on a diet of thrips larvae only, the above analysis indicates that we should focus on the factors that decrease net reproduction of the erythraeid predator ( $R_0$ ). Thrips are known to counter-attack predatory mites, especially their eggs (Faraji et al. 2002a,b; Janssen et al. 2002; Magalhães et al. 2005), and this may offer explanations for the low numbers of eggs found for predators on a diet of thrips. Firstly, the female predators may oviposit normally on a diet of thrips larvae, but counterattacks by the thrips may have resulted in egg mortality, thus falsely giving the impression that the oviposition rate of the predators was low. Second, it is known that predators may retain eggs when eggs run the risk of being preyed upon (Montserrat et al. 2007), and this may have occurred here. Third, it is possible that thrips also injure adult predators, which are therefore unable to produce eggs (for such effects on phytoseiid predators, see Bakker & Sabelis 1989). Furthermore, the low juvenile survival on a diet of thrips larvae (FIGURE 1.2) may directly result from attacks on predator larvae by thrips larvae. In particular, the larvae of the erythraeid predator are vulnerable because they are similar in size to thrips larvae. The deutonymphs, however, are larger and therefore suffer less from counterattack by thrips larvae. All these possible effects warrant a more detailed study of counterattacking behaviour of the thrips and the impact on the predatory mites.

On the other hand, the decreased performance on a diet of spider mites which led to a  $r_m$  as low as the one obtained for the predators fed on thrips (FIGURE 1.4) was not due to low survival (FIGURE 1.2) but to the long generation and pre-oviposition time, the low oviposition, and the high number of individuals that did not reproduce. This could indicate that there is a deficiency in the nutrients found in the spider mite eggs: this possible lack of nutrients may have affected the development and reproduction of *B. leanderi*.

### The benefit of a mixed diet

The major outcome of our study is that the intrinsic rate of population increase was significantly higher when the predators fed on a mixture of whitefly eggs and spider-mite eggs compared to other diets. Such effects of mixed diets have been reported before (Toft & Wise 1999; Oelbermann & Scheu 2002; Messelink et al. 2008; Harwood et al. 2009). Because we used a replacement design for the number of each prey species in the mixtures and because spider-mite eggs are smaller than whitefly eggs

(thus containing less food), the higher reproductive capacity must be due to the nutritional composition of the mixed diet and not due to an increased availability of food. However, the quality of the diet is probably not only determined by nutritional content, but also by interference among the prey species, i.e. intraguild predation by thrips larvae, and by prey defences, such as the web of spider mites which protects the eggs, but can also be used as a refuge by thrips larvae. These latter factors were not taken into account in our experiments (since the web was removed) and therefore need to be considered in future experiments.

Clearly, the role of mixed diets for predatory arthropods that are used as biological control agents needs more attention. Mixed diets may boost populations of predators, thereby increasing their impact on pest populations (see also Messelink et al. 2008), even on pests that are difficult to attack by the predators (Messelink et al. 2010). We therefore advocate elaborate testing of dietary effects of all arthropods that are sufficiently abundant in the litter and on the plant and may serve as prey for biological control agents. Moreover, it would be worthwhile to investigate which alternative foods/prey can be manipulated to boost predator populations in the litter layer, thereby increasing their impact on pests in the crop.

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## SUPPLEMENTARY MATERIAL 1.1 – Details of culture methods

Generalist red velvet mite predator (*Balaustium leanderi*) performs better on a mixed diet



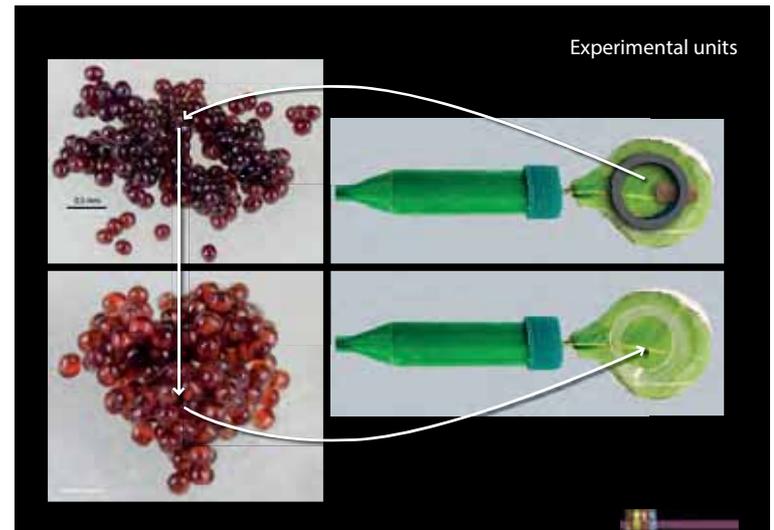
Karen Muñoz<sup>1,3</sup>  
Luz Fuentes<sup>2</sup>  
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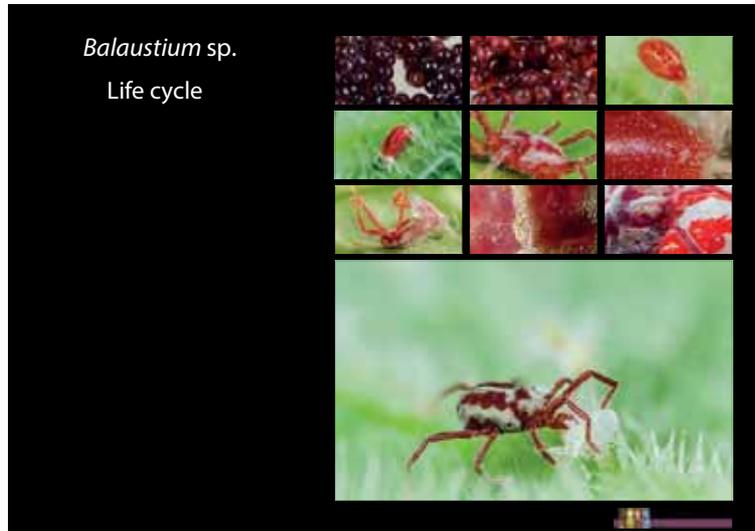
Photography: Jan van Arkel<sup>1</sup>



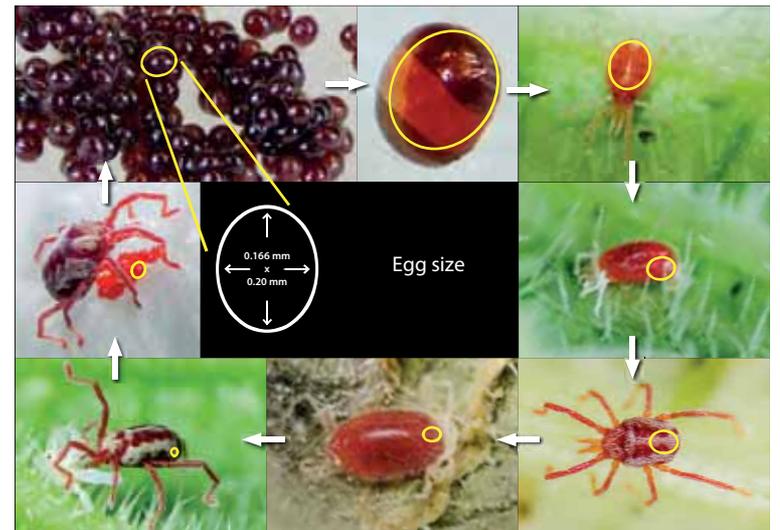
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## SUPPLEMENTARY MATERIAL 1.2 – Prey mortality

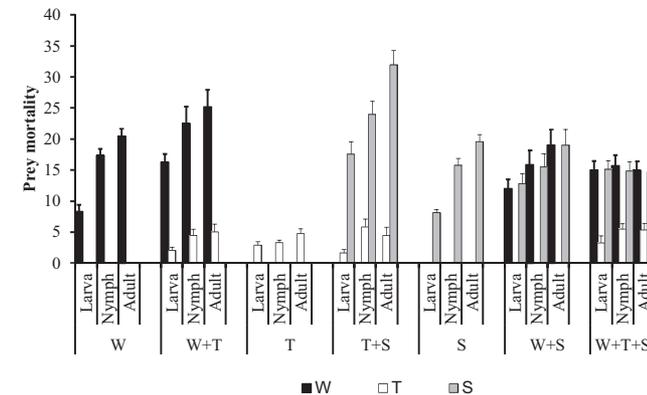
### Methods

As explained in the Methods section of the main text, we provided sufficient amounts of each prey species and stage to allow for maximum predation rates. Each day, the number of surviving prey individuals was assessed per arena. Mortality rates per prey species were first averaged per predator individual per stage and were compared among stages with a mixed effects model with the individual predator as random factor (LME of the nlme package of R). For these comparisons, only the single diets (so not the mixed diets) were used.

### Results

All mobile stages of the predator consumed prey. Prey mortality rates increased with the developmental stage of predator, irrespective of the prey offered (FIGURE S1.2.1; TABLE S1.2.1a).

Because we supplied sufficient amounts of prey, we expected consumption of each prey species in a prey mixture to be lower than with single prey diets due to predator satiation. This was indeed the case for the mixed diet of eggs of whiteflies and of spider mites (FIGURE S1.2.1), but more eggs of spider mites and more eggs of whiteflies were killed in the presence of thrips larvae than when these eggs were offered alone (FIGURE S1.2.1; TABLE S1.2.1b). This may have been caused by thrips larvae acting as intraguild predators on the eggs of whiteflies and spider mites, there-



**FIGURE S1.2.1.** Average (+ s.e.) prey mortality (prey/predator/day) in the presence of different developmental stages (larva, deutonymph, adult) of *Balaustium leanderi* when offered single or mixed diets of whitefly eggs (W), thrips larvae (T) and spider-mite eggs (S).

by increasing overall levels of mortality of these latter two prey. Therefore, we refer to prey mortality rates instead of predation rates throughout the manuscript.

**TABLE S1.2.1a.** Comparisons among the number of prey consumed by different stages of *Balaustium leanderi* (mixed effects model with repeated measures).

Prey	Overall effect and comparisons	df	Likelihood ratio	P
Whitefly eggs	Overall	2	109.0	<0.0001
	Larvae-Nymphs	1	77.7	<0.0001
	Nymphs-Adults	1	24.4	<0.0001
	Adults-Larvae	1	105.5	<0.0001
Thrips larvae	Overall	2	30.2	<0.0001
	Larvae-Nymphs	1	1.11	0.29
	Nymphs-Adults	1	20.7	<0.0001
	Adults-Larvae	1	27.3	<0.0001
Spider mite eggs	Overall	2	187.8	<0.0001
	Larvae-Nymphs	1	135.7	<0.0001
	Nymphs-Adults	1	56.9	<0.0001
	Adults-Larvae	1	181.5	<0.0001

**TABLE S1.2.1b.** Comparison of the prey mortality in treatments with whitefly eggs (W) or spider mite eggs (S) alone and in combination with western flower thrips (T) (linear mixed effects model with repeated measures).

Predator stage	Prey	Comparison	df	Likelihood ratio	P
Larva	Whitefly eggs	W vs. W+T	1	46.9	<0.0001
	Spider mite eggs	S vs. S+T	1	77.2	<0.0001
Nymph	Whitefly eggs	W vs. W+T	1	15.9	<0.0001
	Spider mite eggs	S vs. S+T	1	44.9	<0.0001
Adult	Whitefly eggs	W vs. W+T	1	14.4	<0.0001
	Spider mite eggs	S vs. S+T	1	63.1	<0.0001

