INTRODUCTION

The Mediterranean region is considered one of the most vulnerable areas to climate change worldwide (IPCC, 2014). Temperature increases between 1.5 and 2.0°C in winter and summer, respectively, coupled with a 5% decrease in rainfall are forecasted for the mid 21st century (Giorgi & Lionello, 2008; Gualdi et al., 2012; IPCC, 2018; Navarra & Tubiana, 2013). This increase, together with increasingly frequent extreme events (IPCC, 2018) such as drought and heatwaves (Hansen et al., 2012), can have detrimental effects on ecosystem dynamics (Ummenhofer & Meehl, 2017). Many authors have analysed, designed, categorized and represented the growing risks of this weather phenomenon (Beck & Mahony, 2017; O’Neill et al., 2017), which can trigger disruptions of natural control (Aguilar-Fenollosa & Jacas, 2014; Montserrat et al., 2013a) and failure of biological control (Montserrat et al., 2013; Roy et al., 2003;}

Effect of pollen provision on life-history parameters of phytoseiid predators under hot and dry environmental conditions

Pablo Urbaneja-Bernat | Josep A. Jaques

Departament de Ciències Agràries i del Medi Natural, Unitat Associada d’Entomologia UJI-IVIA, Universitat Jaume I, UJI, Castelló de la Plana, Spain

Correspondence
Pablo Urbaneja-Bernat, Departament de Ciències Agràries i del Medi Natural, Unitat Associada d’Entomologia UJI-IVIA, Universitat Jaume I, UJI, Campus del Riu Sec, 12071-Castelló de la Plana, Spain.
Email: paurbaneja@gmail.com

Funding information
Predoctoral grant from MCINN, Grant/Award Number: (EEBB-I-14-08555)

Abstract

Biological control can be severely disrupted under climate change conditions. This is the case of the spider mite *Tetranychus urticae* in Spanish citrus orchards, where the omnivorous phytoseiid *Euseius stipulatus*, the most abundant predator in the system, was highly impacted by hot and dry conditions mimicking future warmer summers. Such a situation can often be compensated by the provision of alternative food to support generalist predators. As a first step to studying whether such a technique could be applied in this case, we studied at laboratory conditions whether pollen could mitigate the negative effects of hotter and drier conditions derived of climate change on three phytoseiids with different diet specializations. In addition to *E. stipulatus*, these predators, which all together, are considered key for the biological control of *T. urticae* in citrus, are *Neoseiulus californicus* and *Phytoseiulus persimilis*. Our results confirm the extremely fine-tuning of *T. urticae* to hot–dry conditions. They also provide evidence of the poor performance of *E. stipulatus*, especially in terms of reproduction, compared to the other two phytoseiids at these conditions, even when high-quality pollen was available. Moreover, access to pollen in combination with *T. urticae* eggs enhanced survival but reduced predation and oviposition relative to a *T. urticae*-only diet for *N. californicus* and *P. persimilis*. Therefore, whether the overall effect of pollen would justify its use in citrus to counteract the deleterious effects of a hotter and drier climate on the natural regulation of *T. urticae* is still controversial.

KEYWORDS
alternative food, biological control, *Euseius stipulatus*, global warming, *Neoseiulus californicus*, *Phytoseiulus persimilis*
Stavrinides et al., 2010). This is the case for spider mites (Prostigmata: Tetranychidae), where outbreaks can follow droughts (English-loeb, 1990) and heatwaves (Montserrat, Guzman, et al., 2013). Contrary to the progressive increase in average temperature, which is a long-term process, extreme climatic events, such as heatwaves, can induce immediate consequences for poikilothermic animals as mites with further effects at higher organizational levels (i.e. population, communities) (Bannerman et al., 2011; Ciais et al., 2005; De Boeck et al., 2010; Gillespie et al., 2012; Jentsch et al., 2007; Sentis et al., 2013; Smith, 2011).

In the Mediterranean basin, the two-spotted spider mite, *Tetranychus urticae* Koch, is a key pest of clementine mandarins, *Citrus clementina* Tanaka (Rutaceae) (Aguilar-Fenollosa et al., 2011; Martínez-Ferrero et al., 2006; Pascual-Ruiz et al., 2014). Its main natural enemies are different phytoseiid predatory mite species (Mesostigmata: Phytoseiidae), which are present in this system and have different diet specializations (McMurtry & Croft, 1997; McMurtry et al., 2013). The most abundant phytoseiid in Spanish citrus orchards, irrespective of the citrus cultivar and management practices used, is the omnivorous *Euseius stipulatus* (Athias-Henriot; Abad-Moyano et al., 2009a; Aguilar-Fenollosa et al., 2011b; Vela et al., 2017). However, this phytoseiid is not the most effective predator of *T. urticae*. This role is played by the *T. urticae*-specialist *Phytoseiulus persimilis* (Athias-Henriot), which preys on this herbivore almost five times more frequently than *E. stipulatus* (Pérez-Sayas et al., 2015). The Tetranychidae-specialist *Neoseiulus californicus* (McGregor) is also commonly found in these citrus orchards (Abad-Moyano, Pina, Dembilio, et al., 2009; Aguilar-Fenollosa et al., 2011b; Vela et al., 2017). These specialists are consistently found in clementine orchards grown in association with a grass cover, where the abundance of *E. stipulatus* relative to other ground covers diminishes (Aguilar-Fenollosa et al., 2011c), resulting in enhanced biological control of *T. urticae* (Aguilar-Fenollosa et al., 2011b).

Urbaneya-Bernat et al., (2019) showed under semi-field conditions representative of hotter and drier environmental conditions in the Mediterranean basin that the regulation of *T. urticae* in clementine trees provided by *E. stipulatus, N. californicus* and *P. persimilis* could be seriously disrupted. The dynamics of *T. urticae* in simple trophic chain modules (Bascompte & Mélian, 2005) including these predators were species-specific and did not follow the same patterns in spring and summer. This study showed that these predators provided similar control levels of *T. urticae* when released singly in conditions mimicking spring climate change conditions. Although it is generally acknowledged that species with the highest specializations in lifestyle or habitat are typically most threatened by climate change (Aguilar-Fenollosa & Jacas, 2014), the omnivorous *E. stipulatus* provided no control at hotter and drier summer conditions representative of climate change, whereas the other two prey-specialized species were even more effective in summer than in spring. These unexpected results suggest that future warmer and drier summers could result in a deficient control of *T. urticae* in citrus orchards because of the high impact on most abundant *E. stipulatus*. However, this could be compensated by (a) a better performance of less abundant but more efficient *T. urticae*-specialists *P. persimilis* and *N. californicus*, which could reverse the situation (Urbaneya-Bernat et al., 2019) and/or (b) the addition of supplementary food to the system, as the importance of such a supply to support generalist predatory mite populations, like *E. stipulatus*, has been widely recognized (González-Fernández et al., 2009; Janssen & Sabelis, 2015; Khanamani et al., 2017; Maoz et al., 2011; McMurtry et al., 2013; Pozzebon et al., 2009). Indeed, *E. stipulatus* and *N. californicus* can persist in citrus when *T. urticae* is scarce, feeding on other food sources including pollen (Pina et al., 2012). Moreover, Beltrà et al. (2017) demonstrated that the provisioning of pollen and sugars in Spanish citrus orchards could boost phytoseiid natural populations in spring and fall. However, this supply had no effect from June to September. Therefore, there are doubts on whether pollen supply could be an effective measure to mitigate the effects of climate change in this system.

To challenge the hypotheses that (a) the specialist predators *N. californicus* and *E. stipulatus* can do better than the generalist omnivore *E. stipulatus* at hotter and drier conditions and (b) pollen supply can compensate the adverse effects of these conditions on these natural enemies, we performed a series of short-term experiments under laboratory conditions. This type of assays, which are commonly used to assess the effect of extreme climatic events such as heatwaves (Bannerman et al., 2011; Ciais et al., 2005; De Boeck et al., 2010; Gillespie et al., 2012; Jentsch et al., 2007; Sentis et al., 2013; Smith, 2011), allowed us to explore how different combinations of temperature (‘T’) and relative humidity (‘RH’), including those typical of hotter and drier abiotic conditions associated with climate change, affect the key biological parameters (i.e. survival, oviposition and predation) of *T. urticae* and its predators *E. stipulatus, N. californicus* and *P. persimilis* with and without provision of pollen as a supplementary food. The results of this work should help to explain the semi-field results observed (Urbaneya-Bernat et al., 2019) and provide evidence of whether pollen supply could be a tactic allowing the conservation of these natural enemies in a rapidly approaching warmer future.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant material

Two-year-old clementine plants (*Citrus clementina* Tanaka cv. Clementina de Nules (Rutaceae) grafted on citrange Carrizo) were used as a source of leaves for the assays. Fifty days before the beginning of each assay, 25 plants were defoliated and kept in a greenhouse at Universitat Jaume I (UTM: 39° 59'10.883 “N 0°3'4.769”W) set at 22 ± 2°C, 55 ± 10% relative humidity, and natural photoperiod. These plants were grown on vermiculite and peat (1:3; vol: vol) in 320 ml pots, were fertilized twice per week using a modified Hoagland’s solution (Bañuls et al., 1997) and received no pesticide treatments. When necessary for the rearing of mites, bean leaves (*Phaseolus vulgaris* L. (Fabaceae)), lemon fruits (*Citrus lemon* Burm.
f. (Rutaceae)) and *Carpobrotus edulis* (L.) (Aizoaceae) pollen (dried at 37°C, sieved and frozen until use) obtained from pesticide-free plants were used. This pollen is considered as high quality for phytoseiid mites. At laboratory conditions, it can sustain and even boost populations of *N. californicus* and *E. stipulatus*, respectively (Pina et al., 2012).

### 2.2 Mite stock colonies

Four different mite species were used in our studies: the two-spotted spider mite *T. urticae*, and the Phytoseiidae *E. stipulatus*, *N. californicus*, and *P. persimilis*. These colonies were maintained in separate climatic chambers set at 25 ± 1°C, 65 ± 5% ‘RH’ and a 16-hr light photoperiod.

Spider mites were collected in a Clementina de Nules orchard at Les Alqueries (UTM: 39°59’15.1"N 0°3’02.0”W) in 2010. This colony has been maintained every since using standard procedures on detached leaves of clementine mandarins (Aguilar-Fenollosa et al., 2012) and, in some cases (see below), on pesticide-free lemon fruits (Abad-Moyano et al., 2010). Spider mites were used to either feed the Phytoseiidae stock colonies or to start new cohorts for our assays. When used to feed phytoseiids, bean leaflets were infested by exposure to lemon fruit colonies. New cohorts were established by transferring 100 females to new rearing arenas on clementine leaves. Females were removed one day later, and these units containing less than 24-hr old eggs were held separately in a climatic chamber (25 ± 1°C, 65 ± 5% ‘RH’) and constituted the cohorts used in our assays.

Individuals of *N. californicus* were obtained from Koppert Biological Systems (SPICAL®) to initiate a laboratory colony. Contrarily, *P. persimilis* and *E. stipulatus* were collected in 2012 in two clementine orchards in Les Alqueries (same location as *T. urticae*) and Montcada (UTM: 39°32’42.906”N 0°23’45.699”W), respectively. Phytoseiid stock colonies were maintained on detached leaf arenas. These arenas consisted of single bean leaflets placed upside down on moistened filter paper placed on top of a water-saturated foam cube (3–4 cm thick) in an open plastic box half-filled with water. Phytoseiid colonies received twice a week detached bean leaflets infested with *T. urticae* and *C. edulis* pollen as food.

### 2.3 Experimental arenas

Arenas consisted of a petri dish (5 cm in diameter) with a 3 cm in diameter hole in the cover. The base of the dish was filled with bacteriological agar (2.5% weight). As soon as agar was cold and solid enough, a fully expanded clementine leaf was placed upside down on top of the agar to maintain its turgor. The cover was subsequently put in place so that the leaf substrate formed a 3 cm in diameter exposed area. The upper and lower parts of the dishes were sealed with a strip Parafilm® (Pechiney Plastic Packaging, Menasha, WI, USA). Finally, to prevent mite escape from the arena, permanent glue (Tree Tanglefoot®, Grand Rapids, MI, USA) was applied along the rim of the cover hole (Guzmán et al., 2016).

### 2.4 Effect of temperature and relative humidity on *T. urticae* performance: survival and oviposition

Less than 24 hr old presumably mated females (i.e. those reaching the adult stage immediately after the quiescent teliochrysalis stage) were selected and individually moved into a clean experimental arena. Survival (i.e. alive, dead specimens and escapees) and oviposition (number of eggs laid during the experiment) were assessed under a binocular microscope 24 hr after the onset of the assay.

Different ‘T’ (10–40°C in 5°C steps) and ‘RH’ values (30, 50 and 70%) were combined in our assays. Constant ‘RH’ values were obtained by using different salt solutions (Winston & Bates, 1960) in desiccators kept inside environmental chambers (Sanyo Electric Co., Ltd., Japan) set at a photoperiod of 16:8 hr L:D and the different target temperatures. We performed five replicates of six arenas per environmental condition (i.e. a total of 30 replicates per environmental condition).

### 2.5 Effect of temperature and relative humidity on phytoseiid performance: survival, predation and oviposition

A fully expanded healthy clementine leaf was introduced into a *T. urticae*-infested lemon stock colony. Twenty-four hours later, the infested leaf was moved into a phytoseiid colony and left there for an additional 24-hr period. Then, leaves were inspected under a binocular microscope to remove all motile stages. A separate phytoseiid colony was started with every single leaf, and they constituted the cohorts used in our assays. As this method did not work for *E. stipulatus*, the eggs of this species were obtained by exposing a few cotton threads to an existing colony. Twenty-four hours later, all motile forms on these threads were removed, and the remaining eggs were used to start a new cohort. Phytoseiids were reared up to the adult stage following the same procedure as for the stock colonies.

In our assays, we used gravid adult phytoseiid females at their peak oviposition rate (12–14 days from egg hatching; Aucejo-Romero et al., 2004; Janssen & Sabelis, 1992). To ensure the same level of starvation in all females tested, these were randomly selected from a cohort and individualized in plastic arenas (same as for the stock colonies but substituting the plant material by a plastic board) placed on top of a sponge in a water-containing tray where they starved for 24 hr. The edges of these plastic boards were covered with tissue paper in contact with the sponge and the water, which served as both a barrier and a water source for mites.

Experimental arenas received 15 *T. urticae* females, which fed, laid eggs, and produced a web for 48 hr. At that time, we removed all mobile forms of *T. urticae*, and only ≤ 48 hr of old eggs were left. The mean number of *T. urticae* eggs per arena was ∼75. Immediately
after, a starved phytoseiid female was introduced into the arena. These units were then transferred to a desiccator, where the desired 'RH' was achieved as above. Likewise, these desiccators were introduced into an environmental chamber set at the target temperature (same 'T' and 'RH' combinations as for *T. urticae*). Arenas were checked 24 hr after the onset of the assay (i.e. 48 hr after the onset of the starvation period for adult phytoseiid females) under a binocular microscope. This period was selected because *T. urticae* eggs used in the arenas could start hatching in 48 hr, especially at high temperatures (>30°C). Survival, oviposition and predation (number of *T. urticae* eggs eaten) were scored. Same as with *T. urticae*, we performed five replicates of six arenas per environmental condition and mite species.

2.6 | Effect of alternative food on phytoseiid performance: survival, predation and oviposition

In addition to arenas containing ≤ 48 hr old *T. urticae* eggs, two more diets were considered: (a) pollen of *C. edulis*, and (b) a combination of the former two. Arenas containing ≤ 48 hr of old eggs were obtained as before. Arenas containing pollen were prepared by adding *C. edulis* pollen ad libitum in a single point in the centre of the arena. As soon as the arenas were ready, one starved phytoseiid female was introduced. As before, the arenas were checked 24 hr later when survival, oviposition and predation were scored. In this assay, the combination of three 'T' (15, 25 and 30°C) and three 'RH' (30, 50 and 70%) was considered. We performed a total of 15 replicates per environmental condition, diet and phytoseiid species.

2.7 | Statistical methods

To study the effects of the 'T' and 'RH' on *T. urticae* and phytoseiid performance, we used general linear models (GLM) and separately analysed *T. urticae* and phytoseiids. In the case of survival, which had three different possible outputs (i.e. live and dead specimens and escapees), we used a GLM with a multinomial distribution of the error and a generalized logit link function. For predation (only for phytoseiids) and oviposition, we used a GLM with a Poisson distribution of the error and a logistic link function. The factors 'species', 'T' and 'RH' were used as fixed effects in all cases. As one of our main goals was to identify phytoseiid species-specific differences, in the case of predators, we started our analyses by considering all combinations, including 'species' as a factor. Once the statistical significance of the 'species' factor was clear, we similarly continued the analyses of survival, predation and oviposition by studying the effect of 'T', 'RH' and their interaction. We included the factor 'replicate' (1–5) as a random factor.

To study the effects of alternative food on the performance of phytoseiids, we used the same general linear models (GLM) as above. For survival, oviposition and predation, the factors 'species', 'diet', 'T' and 'RH' were used as fixed factors. As our main goal was to identify species-specific patterns of response, same as above, we started our analyses by considering all combinations, including the 'species' factor. Then, we studied the effect of 'diet'. Eventually, we separately analysed for each species and diet, the effects of 'T', 'RH', and their interaction. The factor 'replicate' (1–3) was included in our analyses as a random factor. In both cases, when necessary, we used the Bonferroni post hoc test for mean separation at \( p < .05 \). All data were analysed using SPSS 23.0 software.

3 | RESULTS

3.1 | Effect of temperature and relative humidity on *T. urticae* performance: survival and oviposition

The factor 'T' and the interaction 'T' * RH' significantly affected survival and oviposition (Table 1). The absolute highest survival (i.e. the percentage of live specimens) was observed at 25°C and 30% relative humidity (100% survival) (Figure 1a). Survival was always above 60%, even at the extreme temperatures tested (10 and 40°C) during the experiment.

Oviposition (eggs/day) was significantly affected by 'T', 'RH' and their interaction (Table 1), with minimum values observed at 10 and 40°C (0.3 ± 0.1 and 0.4 ± 0.1 eggs, respectively; Figure 1b). Between these temperatures, oviposition increased with no clear trends for relative humidity. Indeed, at 35°C maximum oviposition rates were attained independently of 'RH' (mean of 7.4 ± 0.9 eggs per female).

3.2 | Effect of temperature and relative humidity on phytoseiid performance: survival, predation and oviposition when preying on *T. urticae*

We observed significant differences \( p < .05 \) between phytoseiid species for all parameters considered (survival, predation and oviposition; Table S1). Consequently, we analysed the effect of 'T' and 'RH' for each phytoseiid species separately.

The GLM to analyse the survival 24 hr after the onset of the assay for the three predators (Figure 2) included 'T' and 'RH'. For *E. stipulatus*, 'T' and its interaction with 'RH' were significant (Table 2). This species could not survive temperatures above 30°C. Below this threshold, survival usually increased with 'RH'. However, the percentage of escapees
was around 50% in all combinations of ‘T’ and ‘RH’ considered except at 25°C and either 50 or 75% ‘RH’, when more than 60% of the specimens tested escaped from the arenas. For *N. californicus*, only the interaction between ‘T’ and ‘RH’ was significant (Table 2). This species could not survive 40°C at any of the three ‘RH’ values considered. Same as *E. stipulatus*, around half of the individuals tried to escape from the experimental setup at this temperature. However, for the remaining conditions, survival was similar and relatively high (Figure 2). At 25°C and 70%, relative humidity survival was 100%. For *P. persimilis*, ‘RH’ and the interaction ‘T’*‘RH’ significantly affected survival (Table 2). Like *N. californicus*, this species did not survive 40°C, and in line with the previous species, almost half of these individuals tried to escape and seek refuge elsewhere. For the remaining conditions, maximal survival was observed in the range 15–20°C. Compared to the other two species, in this case, survival at 35°C was maximal at the lowest relative humidity tested (Figure 2).

The number of eggs preyed was significantly affected by ‘T’, ‘RH’ and their interaction for the three phytoseiid species (Table 2). In the case of *E. stipulatus*, the lowest predation rates were observed at 10°C irrespective of relative humidity (Figure 2). Above this temperature and up to 25°C, predation increased, and maximum rates were usually associated with 70% relative humidity. A maximum of 15.6 ± 1.9 eggs eaten per female was observed at 15 and 25°C at this relative humidity. Beyond 30°C, there was no survival and so no predation was observed. Predation rates for *N. californicus* (Figure 2) were minimal at 10°C irrespective of relative humidity. Above this temperature, they increased up to 25–30°C, then decreased at 35°C and were zero at 40°C because of no survival at this temperature. Interestingly, at 15 and 35°C, predation was maximal at 50% relative humidity, whereas, at 25 and 30°C, the highest predation rates were associated with the highest relative humidity values tested, with a mean of 21.6 ± 1.2 *T.urticae* eggs eaten per female. *Phytoseiulus persimilis* was the most voracious mite at any of the temperatures and relative humidity combinations tested and presented a trend closely matching what we observed for *N. californicus* (Figure 2). In this case, maximum predation rates were reached at 30°C independent of relative humidity and at 25°C with 70% relative humidity with a mean of 39.3 ± 2.5 eggs per female. The number of eggs consumed per female decreased dramatically to 16.3 ± 2.5 eggs at 35°C, but these values were still higher than those observed at 10°C.

During the first 24 hr of the assay, the number of eggs laid was affected both by ‘T’ and ‘RH’ in *N. californicus*, by ‘T’ and the interaction of this factor with ‘RH’ for *P. persimilis*, and it was independent of these factors for *E. stipulatus* (Table 2). This independence could be attributed to the meagre oviposition rates observed for this phytoseiid at all combinations tested (0 to 0.2 eggs per female and day;
The oviposition rate of *N. californicus* (Figure 2) increased from about 0.1 to 2.5 eggs per female between 15 and 30°C with the absolute maximum number of eggs laid per female at 30°C and 50% relative humidity (3.2 ± 0.1 eggs). Below 20 and above 30°C, oviposition was minimal, and at 10°C, only a few eggs could be collected in the arenas kept at 70% relative humidity. Intriguingly, oviposition at 20°C and 70% relative humidity was as low as the reported minimum values. A similar trend was observed for the response of *P. persimilis* to temperature (Figure 2). In this case, oviposition increased from about 0.7 to around 4.1 eggs per female between 10 and 30°C. However, in this case, the effect of relative humidity changed direction depending on the temperature. Maximum oviposition rates at 25 and 30°C were associated with lowest and intermediate relative humidity values (around 4.2 ± 0.2 eggs per female).

### 3.3 Effect of alternative food on phytoseiid performance: survival, predation and oviposition

There were significant differences between the three phytoseiids for survival (Table S2). Consequently, we further analysed the influence of the factor ‘diet’ for each species separately (Table S3). We found that this factor was significant (*p* < .001) in all cases. Consequently, these results led us to eventually analyse the influence of ‘T’, ‘RH’, and their interaction for each mite species and diet separately.

For the omnivorous *E. stipulatus*, survival was highest when it had access to the pollen only diet (means of 77.1 versus 49.3 and 33.8% for pollen only, mixed, and *T. urticae* eggs only diets, respectively) (Figure 3). The pollen (either alone or with *T. urticae* eggs) made survival independent of relative humidity (Table 3). This result should be probably attributed to the zero death rates observed at 25°C in the pollen only diet and at 15 and 25°C in the mixed diet. Contrarily, in the *T. urticae* eggs only diet, the effect of temperature and relative humidity did not follow any clear trend and, although 30% relative humidity provided the lowest survival rates at 15 and 25°C, it provided the highest at 30°C. Remarkably, the percentage of escapees was similar in the two diets supplemented with *T. urticae* eggs (up to 52%) and higher than when pollen only was available. The number of dead individuals was highest when only *T. urticae* eggs were offered as a food source (around 11%).

In the case of the tetranychid-specialist predator *N. californicus*, survival was higher when the mite had access to *T. urticae*...
eggs, either alone (86.5%) or combined with pollen (85.9%), and decreased when pollen was the only food source available (31.6%) (Figure 3). However, when we analysed the survival for each diet, we observed that the GLM model provided a good fit (p < .05) only in the case of pollen alone (Table 3). This failure was attributed to the fact that all individuals survived (no dead or stuck-in-the-glue specimens) at the combinations 25 and 30°C with 50% relative humidity for *T. urticae* eggs and mixed diets, respectively. For the pollen only food, survival was highest at 25°C, much lower at 15°C and became zero at 30°C. For the other two diets, survival never dropped below 60.0%.

For the *Tetranychus* sp.-specialist predator *P. persimilis*, survival (Figure 3) was significantly affected by diet (Table 3). The highest survival occurred when this phytoseiid had access to *T. urticae* eggs only (47.7%), closely followed by the mixed diet (44.4%). Lowest survival was observed when this phytoseiid had access to pollen only (21.5%). Interestingly, the mixed diet was the only one resulting in no dead specimens. However, same as the other two phytoseiids, moderate to high escapee rates were observed even in this case. 'T' was the single factor affecting survival for all diets. ‘RH’ was significant for the mixed diet only (Table 3). This mixed diet resulted in the absolute highest survival at 25°C tested, and 70% relative humidity (93.8% survival), with no dead individuals observed at any of the different combinations of temperature and relative humidity. When we offered pollen and *T. urticae* eggs separately, survival was highest at 15°C (31.2 and 63%, respectively).

The number of eggs preyed by *E. stipulatus* was affected by ‘T’ and ‘RH’ in both diets (Table 4). The highest predation rates were observed when *E. stipulatus* was offered a mixture of pollen and *T. urticae* eggs (average of 11.4 ± 1.4 eggs eaten versus 7.9 ± 1.6 for the *T. urticae* eggs only diet) (Figure 4). However, we observed similar predation rates at 15 and 25°C and 70% relative humidity when *T. urticae* eggs constituted the only food source available. The predation rate of *N. californicus* also was significantly affected by ‘T’ and ‘RH’ for the two diets considered (Table 4). In general, highest predation rates were observed at 30°C irrespective of relative humidity and, within each temperature, at 70% relative humidity (Figure 4). The number of eggs preyed by *P. persimilis* (Figure 4) was affected by ‘T’, ‘RH’ their interaction in both diets (Table 4). Pollen provision affected predation rates because the number of eggs preyed decreased when offered a mixed diet (20.6 ± 1.6) compared with *T. urticae* eggs only (28.5 ± 2.1). For both diets, predation significantly decreased at 15°C independently of relative humidity, and there were no differences between 25 and 30°C.

The number of eggs laid by *E. stipulatus* at the different temperature and relative humidity combinations was significantly different in diets with either *T. urticae* or pollen alone (Table 5). However, when we offered a mixture of *T. urticae* eggs and pollen, these differences disappeared (Table 5). These results should probably be attributed to this species’ extremely low fecundity in our assays, which was always below one egg per female and day (Figure 5).

For *N. californicus*, oviposition was affected by ‘T’ and ‘RH’ (Table 5), and it was lowest when the phytoseiid had access to pollen only (it was zero at 15 and 30°C irrespective of relative humidity) (Figure 5). Interestingly, this species was especially fecund at 30°C with much lower values at 15°C and intermediate at 25°C.

Same as *N. californicus*, in the case of *P. persimilis*, ‘T’ and ‘RH’ significantly affected oviposition (Table 5), which became almost zero when this mite had access to pollen only (Figure 5). From the other two food sources, the *T. urticae* eggs alone presented higher values (mean 2.8 ± 0.3 eggs) than the mixed diet (1.3 ± 0.2). For these food sources, oviposition was lowest at 15°C and increased along with temperature, with maximum values usually associated with intermediate relative humidity rather than to 70%.

### Table 2

| Parameters | Factors | *E. stipulatus* | *N. californicus* | *P. persimilis* |
|------------|---------|----------------|------------------|----------------|
| Survival   | Model   | 60.16; 20; <0.001 | 59.19; <0.001 | 66.88; <0.001 |
|            | T       | 20.89; 6; 0.002  | 10.79; 6; 0.095 | 9.82; 6; 0.132 |
|            | RH      | 5.34; 2; 0.069   | 3.31; 2; 0.191  | 6.37; 2; 0.041 |
|            | T*RH    | 33.80; 20; 0.001 | 42.60; 20; <0.001 | 50.92; 20; <0.001 |
| Predation  | Model   | 118.53; 17; <0.001 | 1.368.63; 17; <0.001 | 1.227.38; 17; <0.001 |
|            | T       | 57.74; 6; <0.001  | 1.125.27; 5; <0.001 | 1.283.33; 5; <0.001 |
|            | RH      | 57.74; 2; 0.526   | 6.85; 2; 0.033   | 16.74; 2; <0.001 |
|            | T*RH    | 20.82; 17; <0.013 | 1.378.35; 17; <0.001 | 1.620.61; 17; <0.001 |
| Oviposition| Model   | 28.29; 14; 0.042  | 376.62; 17; <0.001 | 233.28; 17; <0.001 |
|            | T       | 0.123; 4; 0.989   | 354.15; 5; <0.001 | 195.52; 5; <0.001 |
|            | RH      | 0.180; 2; 0.914   | 34.67; 2; <0.001  | 2.71; 2; 0.259  |
|            | T*RH    | 0.201; 14; 0.654  | 397.01; 15; <0.001 | 265.55; 17; <0.001 |
Fig. 3 Survival (stuck in the glue (grey bars), dead (black bars) and alive (white bars)) of (a) *Euseius stipulatus*, (b) *Neoseiulus californicus* and (c) *Phytoseiulus persimilis* when offered three different diets (pollen, *T. urticae* eggs and *T. urticae* eggs + pollen) considering three temperatures (15, 25 and 30°C) combined with three relative humidity values (30, 50 and 70% RH).

| Diet | Factors | *E. stipulatus* | *N. californicus* | *P. persimilis* |
|------|---------|-----------------|-------------------|----------------|
| *T. urticae* eggs + pollen | Model | 16.49; 8; 0.036 | 9.80; 8; 0.279 | 27.92; 8; <0.001 |
| | T | 5.25; 2; 0.038 | 3.08; 2; 0.214 | 14.06; 2; 0.001 |
| | RH | 1.58; 2; 0.455 | 1.59; 2; 0.451 | 6.27; 2; 0.043 |
| | T*RH | 9.82; 8; 0.056 | 5.83; 8; 0.212 | 4.20; 8; 0.379 |
| *T. urticae* eggs | Model | 11.59; 8; 0.170 | 4.77; 8; 0.782 | 15.77; 8; 0.046 |
| | T | 3.11; 2; 0.211 | 2.75; 2; 0.252 | 4.39; 2; 0.011 |
| | RH | 1.45; 2; 0.049 | 1.03; 2; 0.598 | 1.78; 2; 0.411 |
| | T*RH | 8.04; 8; 0.034 | 1.36; 8; 0.852 | 9.17; 8; 0.057 |
| Pollen | Model | 25.68; 8; 0.001 | 10.99; 6; 0.012 | 37.19; 8; <0.001 |
| | T | 14.61; 2; 0.001 | 0.14; 2; 0.011 | 17.87; 2; <0.001 |
| | RH | 2.49; 2; 0.287 | 5.05; 2; 0.800 | 2.48; 2; 0.289 |
| | T*RH | 6.37; 4; 0.173 | 5.92; 6; 0.041 | 8.64; 8; 0.071 |

Table 3 Statistics (F; df; p-value) of the different GLM models adjusted to survival for *E. stipulatus*, *N. californicus*, and *P. persimilis* for the different diets included in this assay and considering the factors temperature 'T', relative humidity 'RH' and their interactions as explanatory variables.
TABLE 4  Statistics (F; df; p-value) of the different GLM models adjusted to predation for E. stipulatus, N. californicus and P. persimilis for the different diets included in this assay and considering the factors temperature ‘T’, relative humidity ‘RH’ and their interactions as explanatory variables.

| Diet                  | Factors | E. stipulatus | N. californicus | P. persimilis |
|-----------------------|---------|---------------|-----------------|---------------|
| T. urticae eggs + pollen | Model   | 67.09; 8; <0.001 | 274.11; 8; <0.001 | 66.07; 8; <0.001 |
|                       | T       | 3.46; 2; 0.178  | 189.87; 2; <0.001 | 29.48; 2; <0.001 |
|                       | RH      | 14.51; 2; 0.001 | 37.21; 2; <0.001  | 2.11; 2; 0.349  |
|                       | T*RH    | 38.95; 8; <0.001 | 46.23; 8; <0.001  | 24.49; 8; <0.001  |
| T. urticae eggs       | Model   | 99.01; 8; <0.001 | 223.83; 8; <0.001 | 292.20; 8; 0.001 |
|                       | T       | 5.67; 2; 0.059  | 151.15; 2; <0.001 | 269.03; 2; <0.001 |
|                       | RH      | 20.59; 2; <0.001 | 16.95; 2; <0.001  | 1.78; 2; 0.682  |
|                       | T*RH    | 66.10; 8; <0.001 | 22.87; 8; <0.001  | 4.13; 8; 0.038  |

FIGURE 4  Predation of (a) Euseius stipulatus, (b) Neoseiulus californicus and (c) Phytoseiulus persimilis when offered two different diets, (1) T. urticae eggs and (2) T. urticae eggs + pollen, at 15°, 25° and 30°C combined with 30, 50 and 70% of RH. For each figure, bars with the same letter are not statistically different (Bonferroni p < .05).
We aimed to determine whether, in agreement with previous semi-field work (Urbaneja-Bernat et al., 2019), (a) *N. californicus* and *P. persimilis* were better adapted than *E. stipulatus* to hotter and drier conditions expected for Spanish citrus orchards under climate change, and (b) pollen could compensate this suspected poor adaptation of *E. stipulatus* to hot and dry conditions. Our results provide evidence of the extremely poor performance of *E. stipulatus*, especially in terms of reproduction compared to the other two phytoseiids, even when pollen was available under hot and dry conditions (Figures 3–5), these increases rarely exceeded or even matched the

### Table 5

Statistics (F; df; p-value) of the different GLM models adjusted to oviposition for *E. stipulatus*, *N. californicus* and *P. persimilis* for the different diets included in this assay and considering the factors temperature T*, relative humidity RH* and their interactions as explanatory variables.

| Diet                  | Factors   | *E. stipulatus* | *N. californicus* | *P. persimilis* |
|-----------------------|-----------|-----------------|-------------------|-----------------|
|                       | Model     | 9.99; 8; 0.266  | 99.26; 8; <0.001   | 89.31; 8; <0.001 |
|                       | T         | 2.82; 2; 0.244  | 50.42; 2; <0.001   | 210.71; 2; <0.001 |
|                       | RH        | 2.78; 2; 0.249  | 6.85; 2; 0.033     | 1.96; 2; 0.376  |
|                       | T*RH      | 4.23; 8; 0.375  | 103.54; 8; <0.001  | 199.20; 7; <0.001 |
|                       | Model     | 8.73; 8; 0.365  | 71.59; 8; <0.001   | 70.66; 8; <0.001 |
|                       | T         | 3.64; 2; 0.162  | 84.66; 2; <0.001   | 62.37; 2; <0.001 |
|                       | RH        | 0.27; 2; 0.873  | 1.52; 2; 0.772     | 2.91; 2; 0.232  |
|                       | T*RH      | 13.42; 4; 0.009 | 93.94; 8; <0.001   | 94.95; 8; <0.001 |
| Pollen                | Model     | 12.29; 8; 0.139 | 12.39; 5; 0.030    | 25.499; 8; 0.001 |
|                       | T         | 28.50; 2; <0.001| 7.00; 1; 0.008     | 17.67; 2; <0.001 |
|                       | RH        | 24.64; 2; <0.001| 3.50; 2; 0.061     | 15.69; 2; <0.001 |
|                       | T*RH      | 39.01; 7; <0.001| 16.01; 2; 0.003    | 11.08; 2; 0.011  |

### Figure 5

Oviposition of (a) *Euseius stipulatus*, (b) *Neoseiulus californicus* and (c) *Phytoseiulus persimilis* when offered three different diets: (1) *T. urticae* eggs, (2) *T. urticae* eggs + pollen and (3) pollen, at 15°, 25° and 30° combined with 30, 50 and 70% of RH. For each figure, bars with the same letter are not statistically different (Bonferroni p < .05).

### Discussion

We aimed to determine whether, in agreement with previous semi-field work (Urbaneja-Bernat et al., 2019), (a) *N. californicus* and *P. persimilis* were better adapted than *E. stipulatus* to hotter and drier conditions expected for Spanish citrus orchards under climate change, and (b) pollen could compensate this suspected poor adaptation of *E. stipulatus* to hot and dry conditions. Our results provide evidence of the extremely poor performance of *E. stipulatus*, especially in terms of reproduction compared to the other two phytoseiids, even when pollen was available under hot and dry conditions. Although pollen supply significantly increased survival, predation and oviposition of *E. stipulatus* under hot and dry conditions (Figures 3–5), these increases rarely exceeded or even matched the...
values observed for *N. californicus* and *P. persimilis*, especially for predation and oviposition. Because *T. urticae* could survive temperatures of 40°C and even achieve maximum oviposition rates at 35°C (Figure 1), a temperature that only *N. californicus* and *P. persimilis* could survive with limited reproduction (Figure 2), our results confirm that *T. urticae* outbreaks in citrus could become increasingly more frequent in the future.

We hypothesized that climate change could differentially impact second and third trophic levels of the mite community established around *T. urticae* in clementines. Our results demonstrate that the different parameters studied (survival, oviposition and predation) depend on both temperature and relative humidity and are affected by the available food source. Moreover, the magnitude of the impact was species-specific. Mean temperatures above 25°C, which can be taken as a proxy of summer climate change conditions in Spanish citrus-growing areas (Urbaneja-Bernat et al., 2019), were more detrimental to phytoseiids than to *T. urticae*, which presents maximum survival and oviposition at temperatures about 5°C higher than best-adapted phytoseiids, independently of relative humidity (Figure 1).

Probably because of the experimental setup used, where escapees could not seek shelter but instead died stuck in the glue, the highest impact of hot and dry conditions among phytoseiids was observed for the omnivore *E. stipulatus*. Theory would not predict, the highest impact of climate change on generalist instead of specialist predators, but this is what we were expecting based on previous semi-field assays (Urbaneja-Bernat et al., 2019). The survival of *T. urticae* in our experimental conditions was always above 60%, and it even reached 100% at 25°C and 30% relative humidity (Figure 1). This means that the strain we worked with, originally collected in a clementine orchard of La Plana Region, is quite tolerant to hot and dry conditions.

Although *N. californicus* and, particularly, *P. persimilis* could increase their predation rates on *T. urticae* eggs up to 30°C, and probably effectively regulate the herbivore below this temperature (i.e. predation rate > *T. urticae* oviposition rate) (Figures 1 and 2), at higher temperatures this regulation would probably disappear. The combined effect of lower predation and meagre oviposition rates for both phytoseiids plus the lower survival rate for *P. persimilis* would probably release *T. urticae* from effective natural regulation. However, this was not what we found when the same trophic chain were studied under semi-field conditions at spring and summer climate change conditions (Urbaneja-Bernat et al., 2019). Indeed, *E. stipulatus* lost effectiveness during hot and dry conditions, and this is in agreement with what we have found in the present study. However, both *N. californicus* and *P. persimilis* could keep *T. urticae* under control within the fluctuating temperature and relative humidity regimes registered in these semi-field assays (Urbaneja-Bernat et al., 2019). Some authors (Ferragut et al., 1987) do not consider *E. stipulatus* as a suitable biological control agent for *T. urticae*. However, both field (Pérez-Sayas et al., 2015) and semi-field (Grafton-Cardwell et al., 1997) assays in citrus point at the important role of this phytoseiid, which should be attributed to its higher abundance relative to other co-occurring phytoseiids rather than to its effectiveness, in the regulation of *T. urticae* populations in clementines. This predator is known to be poorly adapted to prey on *T. urticae* because it cannot invade the web produced by this spider mite (Abad-Moyano et al., 2010; Ferragut et al., 1992). However, we observed a non-negligible predation rate at low temperatures and high relative humidity regimes (15.6 eggs at 15–20°C and 70% relative humidity), which improved when *E. stipulatus* had access to pollen (Figure 4). As this is an omnivorous phytoseiid, considered a specialized pollen feeder (Ferragut et al., 1987; González-Fernández et al., 2009; Guzmán et al., 2016; Pina, Argolo, Urbaneja, & Jacas, 2012), the provision of pollen partly compensated the negative results observed in the laboratory when *T. urticae* was the only food source available (Figures 2-5). Whether this positive effect would translate into better control of the populations of *T. urticae*, though, remains doubtful. As already mentioned, Beltrà et al. (2017) demonstrated that the provisioning of pollen and sugars in Spanish citrus orchards had no impact on phytoseiids from June to September. Moreover, Montserrat, Guzman, et al. (2013) found that although pollen supply in avocados could boost the populations of omnivorous predatory mites (including *E. stipulatus*), this increase did not result in better control of the populations of another tetranychid pest mite, the persea mite, *Oligonychus perseae*.

*Neoseiulus californicus* has been traditionally associated with higher temperatures to heat and drought (Abad-Moyano et al., 2009; Ahn et al., 2010; Escudero & Ferragut, 2005; Walzer et al., 2007). However, this has not always been the case (Castagnoli & Simoni, 1999; Castagnoli et al., 2001; Croft et al., 1998; Ghazy et al., 2014; Nguyen et al., 2015), and this may be partly attributed to the use of different strains which may differ in their tolerance to harsh conditions. As this species was also the most tolerant to climate change conditions in our laboratory assays, its good performance in the field (Urbaneja-Bernat et al., 2019) was not a surprise, and it indeed performed better than what could be deduced based on these laboratory assays. This enhanced performance could be the result of two factors acting synergistically. On the one hand, in the laboratory, we worked at constant temperature regimes,
which can be taken as a worst-case scenario that does not allow the mite to recover, most likely at night, from maximum temperatures attained during the day at field conditions. It is known that fluctuating temperatures have usually a lower impact on arthropod physiology and behaviour than a constant temperature equivalent to their mean (Gotôh et al., 2014; Nguyen & Amano, 2010; Vangansbeke et al., 2013; Bayu et al., 2017). On the other, we observed that the number of phytoseiid escapees in our assays was more extensive than that of dead specimens (Figures 2 and 3), and this may be taken as indicative that in the real world, these individuals would have been able to survive in refuges (i.e. crevices or cracks in branches). This behaviour, which may impact predator fitness in terms of lost foraging time and reproduction opportunities when looking for shelter (Gillespie et al., 2012), may increase its survival under field conditions. These two factors could also apply to the third predator considered in this study, P. persimilis, as the number of escapees for this mite was even higher than observed for N. californicus (Figure 1b,c). Indeed, P. persimilis spends relatively more time searching and moving around the leaf than the other predatory mite species (Gontijo et al., 2012; Sabelis & Dicke, 1985). However, Skirvin and Fenlon (2003) showed that the mobility of P. persimilis is reduced at temperatures above 25°C. Nonetheless, we observed the highest number of escapees at 30 and 35°C. Therefore, the local P. persimilis strain used in our assays generally performed better than other strains of this phytoseiid at higher temperatures and lower relative humidity regimes (Abad-Moyano, Pina, Dembilio, et al., 2009; Escudero & Ferragut, 2005; Skirvin & Fenlon, 2003; Vangansbeke et al., 2015). Consequently, P. persimilis would most likely result in a good regulation of T. urticae populations, as it was actually observed in our semi-field assays (Urbanéja-Bernat et al., 2019).

To sum up, our results partly support the results observed under semi-field climate change conditions (Urbanéja-Bernat et al., 2019). On the one hand, they confirm the extremely fine-tuning of T. urticae response to hot and dry conditions. On the other hand, they confirm the extremely poor adaptation of E. stipulatus and the intermediate effect of hot and dry conditions on N. californicus and P. persimilis. This poor adaptation, combined with some behavioural adaptations that could not be considered in our laboratory assays, may explain semi-field results (Urbanéja-Bernat et al., 2019) where T. urticae was still naturally regulated at temperature and relative humidity conditions matching predicted hotter and drier conditions in the Mediterranean. Although the enormous impact observed on E. stipulatus at laboratory conditions when T. urticae eggs was the only food source available could be partly compensated by the provision of supplementary food (e.g. pollen), this effect does not seem enough to allow E. stipulatus to continue to play the essential role in natural regulation of T. urticae which it is playing nowadays at spring conditions. Importantly, our results also show that for the other two phytoseiids, access to pollen in combination with T. urticae eggs decreased the number of specimens found dead in the arenas and reduced predation and oviposition relative to the T. urticae-only diet. Further implications of this supplementary food on interspecific relationships between these predatory species, as E. stipulatus is considered a superior intraguild competitor (Abad-Moyano et al., 2010), could shed light on whether pollen supply in this particular system could be advisable or not.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION
JAJ and PUB conceived and designed research, and conducted the experiments. All authors analyzed results and wrote the manuscript.

DATA AVAILABILITY STATEMENT
Data supporting the information shown in the results have been uploaded to zenodo (https://doi.org/10.5281/zenodo.4267974). Pablo Urbanéja. (2020). Effect of pollen provision on life-history parameters of phytoseiid predators under hot and dry environmental conditions [Data set]. Zenodo. http://doi.org/10.5281/zenodo.4267974.

ORCID
Pablo Urbanéja-Bernat https://orcid.org/0000-0002-6995-5468
Josep A. Jaques https://orcid.org/0000-0003-1353-1727

REFERENCES
Abad-Moyano, R., Pina, T., Dembilio, Ó., Ferragut, F., & Urbanéja, A. (2009). Survey of natural enemies of spider mites (Acari: Tetranychidae) in citrus orchards in eastern Spain. Experimental and Applied Acarology, 47(1), 49–61. https://doi.org/10.1007/s10493-008-9193-3
Abad-Moyano, R., Pina, T., Ferragut, F., & Urbanéja, A. (2009). Comparative life-history traits of three phytoseiid mites associated with Tetranychus urticae (Acari: Tetranychidae) colonies in clementine orchards in eastern Spain: Implications for biological control. Experimental and Applied Acarology, 47(2), 121–132. https://doi.org/10.1007/s10493-008-9197-z
Abad-Moyano, R., Pina, T., Pérez-Panadés, J., Carbonell, E., & Urbanéja, A. (2010). Efficacy of Neoseiulus californicus and Phytoseiulus persimilis in suppression of Tetranychus urticae in young clementine plants. Experimental & Applied Acarology, 50(4), 317–328. https://doi.org/10.1007/s10493-009-9318-3
Aguilar-Fenollosa, E., Ibáñez-Gual, M. V., Pascual-Ruíz, S., Hurtado, M., & Jacas, J. A. (2011). Effect of ground-cover management on spider mites and their phytoseiid natural enemies in clementine mandarin orchards (I): Bottom-up regulation mechanisms. Biological Control, 59(2), 158–170. https://doi.org/10.1016/j.biocontrol.2011.06.013
Aguilar-Fenollosa, E., Ibáñez-Gual, M. V., Pascual-Ruíz, S., Hurtado, M., & Jacas, J. A. (2011). Effect of ground-cover management on spider mites and their phytoseiid natural enemies in clementine mandarin orchards (II): Top-down regulation mechanisms. Biological Control, 59(2), 171–179. https://doi.org/10.1016/j.biocontrol.2011.06.012
Aguilar-Fenollosa, E., & Jacas, J. A. (2014). Can we forecast the effects of climate change on entomophagous biological control agents? Pest Management Science, 70(6), 853–859. https://doi.org/10.1002/ps.3678
Aguilar-Fenollosa, E., Pascual-Ruíz, S., Hurtado, M. A., & Jacas, J. A. (2011). Efficacy and economics of ground cover management as a conservation biological control strategy against Tetranychus urticae in clementine mandarin orchards. Crop Protection, 30(10), 1328–1333. https://doi.org/10.1016/j.cropro.2011.05.011
Aguilar-Fenollosa, E., Pina, T., Gómez-Martínez, M. A., Hurtado, M. A., & Jacas, J. A. (2012). Does host adaptation of Tetranychus
Maoz, Y., Gal, S., Argov, Y., Coll, M., & Palevsky, E. (2011). Biocontrol of McMurtry, J. A., & Croft, B. A. (1997). Life-styles of Phytoseiid mites and Martínez-ferrer, M. T., Jacas, J. A., Ripollés-moles, J. L., & Aucejo-Janssen, A., & Sabelis, M. W. (1992). Phytoseiid life-histories, local IPCC (2014). Summary for Policymakers. Climate Change 2014: Synthesis McMurtry, J. A., Moraes, G. J. D. E., & Sourassou, N. F. (2013). Revision Nguyen, T. T. P., & Amano, H. (2010). Temperature at immature and adult stages affect mating duration and egg production of Neoseiulus californicus females mated once (Acari: Phytoseiidae). Journal of Asia-Pacific Entomology, 13(1), 65–68. https://doi.org/10.1016/j.aspen.2009.10.002 O’Neill, B. C., Oppenheimer, M., Warren, R., Hallegatte, S., Kopp, R. E., Pürtnner, H. O., Scholes, R., Birkmann, J., Foden, W., Licker, R., Mach, K. J., Marbaix, P., Mastrandrea, M. D., Price, J., Takahashi, K., van Ypersele, J.-P., & Yohe, G. (2017). IPCC reasons for concern regarding climate change risks. Nature Climate Change, 7(1), 28–37. https://doi.org/10.1038/nclimate3179 Pascual-Ruiz, S., Aguilar-Fenollcosa, E., Ibáñez-Gual, V., Hurtado-Ruiz, M. A., Martínez-Ferrer, M. T., & Jacas, J. A. (2014). Economic threshold for Tetranychus urticae (Acari: Tetranychidae) in cementine mandarins Citrus clementina. Experimental and Applied Acarology, 62(3), 337–362. https://doi.org/10.1007/s10493-013-9744-0 Pérez-Sayas, C., Pina, T., Gómez-Martínez, M. A., Camañes, G., Ibáñez-Gual, M. V., Jaques, J. A., & Hurtado Ruíz, M. A. (2015). Disentangling mite predator-prey relationships by multiplex PCR. Molecular Ecology Resources, 15(6), 1330–1345. https://doi.org/10.1111/1755-0998.12409 Pina, T., Argolo, P. S., Urbaneja, A., Jacas, J. A. (2012). Effect of pollen quality on the efficacy of two different life-style predatory mites against Tetranychus urticae in citrus. Biological Control, 61(2), 176–183. https://doi.org/10.1016/j.biocontrol.2012.02.003 Pozzebon, A., Loeb, G. M., & Duso, C. (2009). Grape powdery mildew as a food source for generalist predatory mites occurring in vineyards: Effects on life-history traits. Annals of Applied Biology, 155(1), 81–89. https://doi.org/10.1111/j.1744-7348.2009.00323.x Roy, M., Brodeur, J., & Cloutier, C. (2003). Effect of temperature on intrinsic rates of natural increase (rm) of a coccinellid and its spider mite prey. BioControl, 48, 57–72. https://doi.org/10.1023/A:1021289833664 Sabelis, M. W., & Dicke, M. (1985). Long-range dispersal and searching behaviour. In W. Helle, & M. W. Sabelis (Eds.), Spider Mites. Their Biology, Natural Enemies and Control. World Crop Pests 1b (pp. 141–160). Elsevier. Sentis, A., Hemptinne, J. L., & Brodeur, J. (2013). Effects of simulated heat waves on an experimental plant-herbivore-predator food chain. Global Change Biology, 19(3), 833–842. https://doi.org/10.1111/gcb.12094 Skirvin, D. J., & Fenlon, J. S. (2003). The effect of temperature on the functional response of Phytoseiulus persimilis (Acari: Phytoseiidae). Experimental & Applied Acarology, 31(1–2), 37–49. Smith, M. D. (2011). The ecological role of climate extremes: Current understanding and future prospects. Journal of Ecology, 99(3), 651–655. https://doi.org/10.1111/j.1365-2745.2011.01833.x Stavrinides, M. C., Daane, K. M., Lampinen, B. D., & Mills, N. J. (2010). Plant water stress, leaf temperature, and spider mite (Acari: Tetranychidae) outbreaks in California vineyards. Environmental Entomology, 39(4), 1232–1241. https://doi.org/10.1603/EN09288 Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. Philosophical Transactions of the Royal Society B: Biological Sciences, 372(1723), 20160135. https://doi.org/10.1098/rstb.2016.0135 Urbaneja-Bernat, P., Ibáñez-Gual, V., Montserrat, M., Aguilar-Fenollcosa, E., & Jaques, J. A. (2019). Can interactions among predators alter the natural regulation of an herbivore in a climate change scenario? The case of Tetranychus urticae and its predators in citrus. Journal of Pest Science, 92(3), 1149–1164. https://doi.org/10.1007/s10340-019-01114-8 Vangansbeke, D., Audenaert, J., Nguyen, D. T., Verhoeven, R., Gobin, B., Tirry, L., & De Clercq, P. (2015). Diurnal temperature variations affect development of a herbivorous arthropod pest and its predators. PLoS One, 10(4), e0124898. https://doi.org/10.1371/journal.pone.0124898 Vangansbeke, D., De Schrijver, L., Spranghers, T., Audenaert, J., Verhoeven, R., Nguyen, D. T., Gobin, B., Tirry, L., & De Clercq, P. (2013). Alternating temperatures affect life table parameters of Phytoseius persimilis, Neoseiulus californicus (Acari: Phytoseiidae).
and their prey *Tetranychus urticae* (Acari: Tetranychidae). *Experimental and Applied Acarology*, 61, 285–298. https://doi.org/10.1007/s10493-013-9704-8

Vela, J. M., Wong, E., Jaques, J. A., Ledesma, C., & Boyero, J. R. (2017). Mite diversity (Acari: Tetranychidae, Tydeidae, Iolinidae, Phytoseiidae) and within-tree distribution in citrus orchards in southern Spain, with special reference to *Eutetranychus orientalis*. *Experimental and Applied Acarology*, 73(2), 191–207. https://doi.org/10.1007/s10493-017-0180-4

Walzer, A., Castagnoli, M., Simoni, S., Liguori, M., Palevsky, E., & Schausberger, P. (2007). Intraspecific variation in humidity susceptibility of the predatory mite *Neoseiulus californicus*: Survival, development and reproduction. *Biological Control*, 41(1), 42–52. https://doi.org/10.1016/j.biocontrol.2006.11.012

Winston, P. W., & Bates, D. H. (1960). Saturated solutions for the control of humidity in biological research. *Ecology*, 41(1), 232–237. https://doi.org/10.2307/1931961

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Urbaneja-Bernat P, Jaques JA. Effect of pollen provision on life-history parameters of phytoseiid predators under hot and dry environmental conditions. *J Appl Entomol*. 2021;145:191–205. https://doi.org/10.1111/jen.12845