

## Fertility life tables of *Raoiella indica* (Trombidiformes: Tenuipalpidae) at different temperature and humidity levels

Tablas de fertilidad y vida de *Raoiella indica* (Trombidiformes: Tenuipalpidae) en diferentes niveles de temperatura y humedad

DAVID MARTÍNEZ MEJÍA<sup>1</sup>, GABRIEL OTERO-COLINA<sup>2</sup>, REBECA GONZÁLEZ-GÓMEZ<sup>3</sup>,  
ALEJANDRO PÉREZ-PANDURO<sup>4</sup> and JAVIER VALLE-MORA<sup>5</sup>

<sup>1</sup> M. Sc. Colegio de Postgraduados, Postgrado en Entomología y Acarología, km 36.5 Carretera México-Tezcoco, CP 56230. Montecillo, Texcoco, Edo. de México, México, [dmartinez\\_guerrero@hotmail.com](mailto:dmartinez_guerrero@hotmail.com), <https://orcid.org/0000-0001-9709-7790>. <sup>2</sup> Ph. D. Colegio de Postgraduados, Postgrado en Entomología y Acarología, km 36.5 Carretera México-Tezcoco, CP 56230. Montecillo, Texcoco, Edo. de México, México, [gotero@colpos.mx](mailto:gotero@colpos.mx), <https://orcid.org/0000-0002-0529-1295>. <sup>3</sup> Ph. D. CONACYT - El Colegio de la Frontera Sur. Carretera Antigua Aeropuerto km 2.5, CP 30700, Tapachula, Chiapas, México, [rgonzalez@ecosur.mx](mailto:rgonzalez@ecosur.mx), <https://orcid.org/0000-0002-3896-6762>. <sup>4</sup> Ph. D. Colegio de Postgraduados, Postgrado en Entomología y Acarología, km 36.5 Carretera México-Tezcoco, CP 56230. Montecillo, Texcoco, Edo. de México, México, [aperez@colpos.mx](mailto:aperez@colpos.mx), <https://orcid.org/0000-0001-9759-3858>. <sup>5</sup> M. Sc. El Colegio de la Frontera Sur, Carretera Antigua Aeropuerto km 2.5, 30700, Tapachula, Chiapas, Mexico, [jvalle@ecosur.mx](mailto:jvalle@ecosur.mx), <https://orcid.org/0000-0003-0254-5701>.

Corresponding author: Gabriel Otero-Colina.  
Ph. D. Colegio de Postgraduados, Postgrado en Entomología y Acarología, km 36.5 Carretera México-Tezcoco, CP 56230. Montecillo, Texcoco, Edo. de México, México, [gotero@colpos.mx](mailto:gotero@colpos.mx), <https://orcid.org/0000-0002-0529-1295>.

Suggested citation:  
MARTÍNEZ MEJÍA, D.; OTERO-COLINA, G.; GONZÁLEZ-GÓMEZ, R.; PÉREZ-PANDURO, A.; VALLE-MORA, J. 2019. Fertility life tables of *Raoiella indica* (Trombidiformes: Tenuipalpidae) at different temperature and humidity levels. Revista Colombiana de Entomología 45 (1): e7810 <https://doi.org/10.25100/socolen.v45i1.7810>

Received: 09-Nov-2017

Accepted: 07-Oct-2018

Published: 30-Aug-2019

Revista Colombiana de Entomología  
ISSN (Print): 0120-0488  
ISSN (On line): 2665-4385  
<http://revistacolombianaentomologia.univalle.edu.co/>

Open access



BY-NC-SA 4.0  
(<https://creativecommons.org/licenses/by-nc-sa/4.0/deed.es>)

Publicadores / Publishers:  
Sociedad Colombiana de Entomología  
SOCOLEN (Bogotá, D. C., Colombia)  
<http://www.socolen.org.co>  
Universidad del Valle (Cali, Colombia)  
<http://www.univalle.edu.co/>

© 2019 Sociedad Colombiana de Entomología  
- SOCOLEN y Universidad del Valle - Univalle

**Abstract:** A study of fertility life tables of *Raoiella indica* was carried out on coconut (*Cocos nucifera*) leaflets at controlled temperature and relative humidity (RH) in Texcoco, Mexico, with the objective of estimating the parameters of population increase of this mite. Cohorts of 12-hour-old *Raoiella indica* eggs were incubated at 22.5, 25, 27.5 or 30 °C and 40-50 % RH, as well as 27.5 °C with 30-40, 60-70 or 80-90 % RH. They were observed daily until the last mite died. Females that attained adulthood were provided with two males to promote mating and their oviposition was recorded daily. Each one-day-old male was put in contact with a female quiescent deutonymph daily to determine how many times a male could copulate after the deutonymph became an adult. With all temperatures and RH's, mortality was evenly distributed throughout the observations. Developmental rate, reproduction, and, consequently, parameters of population increase were significantly associated with temperature. The highest rate of population increase took place at 27.5 °C and 40-40 RH. By itself, RH did not significantly affect those variables, although its extreme values showed slight negative effects. Approximately four females per male were observed. Males copulated with 4.56 females on average; this suggests that between 20 and 30 % of the males are enough to fertilize all females present.

**Keywords:** Acari, invasive pest, life cycle, red palm mite.

**Resumen:** Se realizó un estudio de tablas de vida y fecundidad de *Raoiella indica* en foliolos de palma de coco (*Cocos nucifera*) a temperatura y humedad relativa (HR) controladas, en Texcoco, México, con el objetivo de estimar los parámetros de incremento poblacional de este ácaro. Cohortes de 50 huevos de *Raoiella indica* de 12 horas de edad se incubaron a 22,5, 25, 27,5 o 30 °C y 40-50 % de HR, así como a 27,5 °C con 30-40, 60-70 u 80-90 % de HR. Se les observó diariamente hasta que murió el último. A las hembras que alcanzaron el estado adulto se les proporcionaron dos machos para promover su apareamiento y luego se registró diariamente su oviposición. Machos de un día de edad se pusieron diariamente en contacto cada uno con una deutoninfa quiescente hembra para observar cuántas veces un macho podía copular, cuando las deutoninfas alcanzaran el estado adulto. Con todas las temperaturas y HR's, la mortalidad se distribuyó uniformemente a lo largo de las observaciones. Tasa de desarrollo, reproducción y, consecuentemente, parámetros de incremento poblacional, estuvieron significativamente asociados con la temperatura. La mayor tasa intrínseca de incremento poblacional ocurrió a 27,5 °C y 40-50 % de HR. Por sí sola, la HR no afectó significativamente a dichas variables, aunque sus valores extremos tuvieron ligeros efectos negativos. Se observaron aproximadamente cuatro hembras por cada macho. Los machos copularon en promedio con 4,56 hembras; ello sugiere que entre 20 y 30 % de machos bastan para fecundar a todas las hembras presentes.

**Palabras clave:** Acari, plaga invasora, ciclo de vida, ácaro rojo de las palmas.

### Introduction

*Raoiella indica* (Hirst, 1924) (Trombidiformes: Tenuipalpidae), the red palm mite, was originally described from India attacking coconut, *Cocos nucifera* L., 1753 (Hirst 1924). Other host plants recorded in previous studies were *Phoenix dactylifera* L., 1753, *Dictyosperma album* (Bory, 1804) (Womersley 1943; Moutia 1958) and

*Areca catechu* L., 1753 (Daniel 1979). These hosts belong to Arecales: Areceaceae.

The mite was widespread throughout countries bordering the Indian Ocean, with its western limit in Egypt and Israel (Gerson *et al.* 1983). It was detected for the first time in the New World in Martinique in 2004 (Flechtmann and Etienne 2004). It then spread to other Caribbean islands and later to continental America. Currently, it is found in Barbados, Brazil, Colombia, Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Jamaica, Martinique, Mexico, Puerto Rico, Saint Lucia, Saint Vincent and the Grenadines, Trinidad and Tobago, United States of America (Florida and Virgin Islands) and Venezuela (CABI 2016).

After its arrival on the American continent it has broadened the host range, but the preferred hosts belong to Musaceae and Areceaceae (Flores *et al.* 2010). Carrillo *et al.* (2012a) listed 91 species of plant hosts; this list continues to grow as the mite settles in new territories (González and Ramos 2010; Gondim *et al.* 2012; Gómez-Moya *et al.* 2017).

*R. indica* and all other tenuipalpid mites are phytophagous. However, this species differs from other con-familial species by feeding on stomatal cells (Beard *et al.* 2012). It reproduces sexually and also by arrhenotokous parthenogenesis (Helle *et al.* 1980). Its life cycle includes egg, larval, protonymphal, deutonymphal and adult stages of both sexes. At the end of each stage, it passes through a quiescent period when specimens extend their legs and neither move nor feed. Female predominance varies seasonally, 92 % during spring and 70 % during autumn (Moutia 1958).

The injuries inflicted by this mite on its host plants are severe, and it is considered a major invasive pest (Mendonça *et al.* 2005). Infestation levels are strongly seasonal, increasing in the dry and hot season, and spontaneously decreasing at the onset of the rainy season. It is less important in temperate or cold regions, being mostly a problem in tropical countries (Peña *et al.* 2010).

This study was conducted to determine fecundity life table parameters of *R. indica* on coconut leaflets, under different temperature and humidity conditions (Birch 1948).

## Materials and methods

**Rearing *R. indica*.** Coconut plants purchased in a *R. indica*-free area (Puente Nacional, Veracruz, Mexico, 2015, located at 19°19'38"N, 96°28'53"W, 104 masl) were carefully examined to verify they were not infested by this mite; any insect or mite present was manually eliminated. Using a fine brush, live *R. indica* specimens were transferred to those plants and kept in a growing chamber at 26 °C, photoperiod 12:12 h (light: dark), to establish colonies; mites were taken from the colonies as needed. All observations were carried out in Colegio de Postgraduados, Texcoco, Mexico, located at 19°27'46"N, 98°54'15"W, 2,246 masl.

**Life tables at different temperatures.** Four cohorts of almost uniform age were formed with 50 *R. indica* eggs each. To this end, leaflets highly infested by this mite were selected, removing all eggs with a fine brush. The leaflets were examined 24 h later, and all eggs laid during this period were assumed to be 12 h old. Leaflet sections (8 x 5 cm) were cut from mite-free coconut plants, removing all mites or insects under a stereomicroscope, and leaving a single egg on the abaxial surface of each section. The base of each section

was covered with a cotton pad, and between the leaflet and the cotton pad an adhesive barrier line (Tanglefoot™) was drawn. Two hundred and twenty arenas were prepared and placed in four groups of 50 (cohorts) in plastic pans. The remaining 20 were used to replace mites that died in early stages, likely because of manipulation.

Each of these egg cohorts was kept in an incubator (Thermo Scientific mod. TFFU2065FWA) previously calibrated to 22.5, 25, 27.5 or 30 ± 1 °C, with a 12:12 h (light: dark) photoperiod. The cotton pads were kept moist to prevent leaflet sections from wilting, and additional pans with water were put in the incubators until relative humidity was 40-50 %. When *R. indica* eggs hatched, each larva was transferred with a fine brush to a new arena where the leaflet section was placed abaxial surface down, at a 45° angle from horizontal. Arenas were observed once a day to follow development and survival of individual mites. Mites were transferred to new arenas approximately every 15 days when leaflets began to wither. Given that the gender of *R. indica* is easily recognizable only when they attain adulthood, survival curves for each cohort were drawn combining specimens of both genera.

**Fecundity life tables at different temperatures.** To construct fecundity tables for each cohort of *R. indica*, females reaching adulthood were registered. Two male mites about 24 h old were placed close to each young female for mating and left on the arena until their death. The process of rearing and selecting males is subsequently explained. The number of eggs laid by each female was recorded once a day. Counted eggs were removed from the arena so they would not be counted again.

According to Vera *et al.* (2002), the following parameters of population increase were estimated: generational time ( $T_g$ ), net reproductive rate ( $R_0$ ), finite rate of increase ( $\lambda$ ) and intrinsic rate of increase ( $r_m$ ). Estimation of the above parameters for *R. indica* implied several problems: the gender of the mites was recognized only when they attained adulthood; the proportion of sexes is biased towards females, which constitute between 70 and 90 % of total specimens (Moutia 1958); many specimens died in a pre-adult stage, so their gender could not be determined. In order to estimate the proportion of females to males, the gender of the mites from each cohort was determined the first day all had attained adulthood. Based on this data and supported by data of Moutia (1958), for estimation of population increase parameters, it was assumed that 80 % of all specimens in a cohort were females; similarly, 80 % of total eggs laid by the females were assumed as daughters.

**Fertility life tables at different levels of relative humidity.** Fertility life tables were constructed for mites reared at 27.5 ± 1 °C (temperature at which the highest  $r_m$  occurred) and relative humidity ranges of 30-40, 60-70 or 80-90 %. Mite cohorts were founded and handled as previously explained. To regulate relative humidity inside the incubators, temperature was first set at 27.5 °C and then an increasing number of water-filled pans were placed until humidity ranged between the pre-established limits. Relative humidity was monitored daily and water was added as needed.

**Mating behavior.** Fifteen, approximately 24 h, old adult males of *R. indica* were obtained to fertilize females in the fertility life

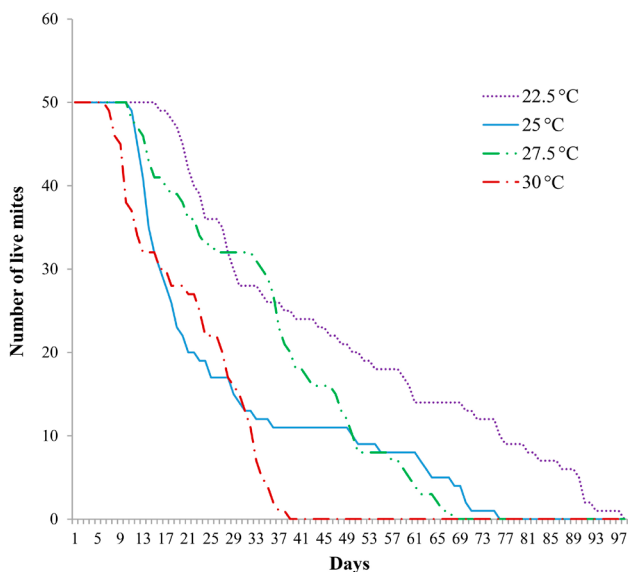
tables. For their capture, highly infested coconut leaflets were examined to obtain quiescent male deutonymphs, which were recognized by the pointed tip of their opisthosoma. They were transferred to coconut leaflets and, about 24 h after they molted (became adults), two of them were transferred with a fine brush to an arena where there was one female.

To determine how many times a male can mate, the males were placed individually on arenas, and a quiescent female deutonymph was transferred to each one arena, close to the male. The deutonymphs were recognized as females by their round opisthosoma. Each arena was observed at hourly intervals and, once a female started the molting process, it was observed continuously to record if the male mated her. After mating, the female was removed and, the following day, a new quiescent female deutonymph was introduced. This procedure was repeated until the male mite died.

**Data analysis.** Survival curves of mite cohorts reared under different combinations of temperature and relative humidity were compared using the Logrank test (Vera *et al.* 2002). Using the overlapping intervals test (Vera and Sotres 1991),  $r_m$  values and their confidence intervals were used to estimate projections of population increase and recognize differences among them. Development of individual mites was followed until they died. When the number of observed specimens was  $\geq 3$ , numerical values were subjected to an ANOVA and Fisher's least significant difference using SAS 9.0 (2002).

**Results**

**Survival curves at different temperature and relative humidity.** In all combinations of temperature and relative humidity, mortality of combined females and males occurred evenly along the entire life cycle (Figs. 1 and 2). The apparent zero mortality during the first days may have been due to difficulty in distinguishing a live egg from a dead one. In contrast, an increase in mortality occurred between days 6 and 20, when larvae and nymphs prevailed. Larvae and nymphs are soft and delicate, and could have died from manipulation.



**Figure 1.** Survival curve of *Raoiella indica* reared at four temperatures, relative humidity 40-50 %. The day when eggs were laid is defined as day zero.

The above facts might lead to underestimating egg mortality, and to overestimating larval and nymph mortality.

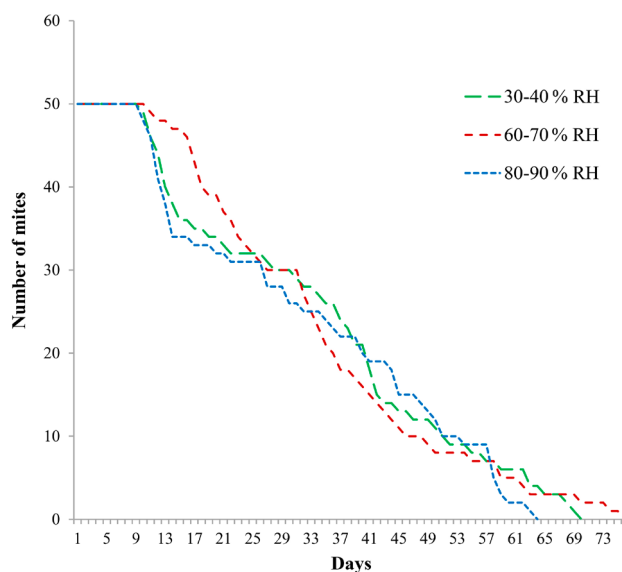
A clear inverse relation was found between temperature and mite lifespan. The survival curve of mites reared at 22.5 °C, 40-50 % RH, was significantly different from all the other curves (Logrank test,  $P = 0.05$ , Table 1). The longest life span of mites reared at that temperature was about 100 days. The survival curve of mites reared at 30 °C, 40-50 % RH, was significantly different from those of mites reared at 27.5 °C, with several combinations of relative humidity (Table 1). The longest life span of mites reared at 30 °C was 39 days (Fig. 1).

In contrast, when temperature was the same (27.5 °C) but relative humidity varied, all survival curves followed almost parallel courses and they were not significantly different (Logrank test,  $P = 0.05$ ). None of the relative humidity ranges particularly affected the *R. indica* survival pattern (Fig. 2; Table 1).

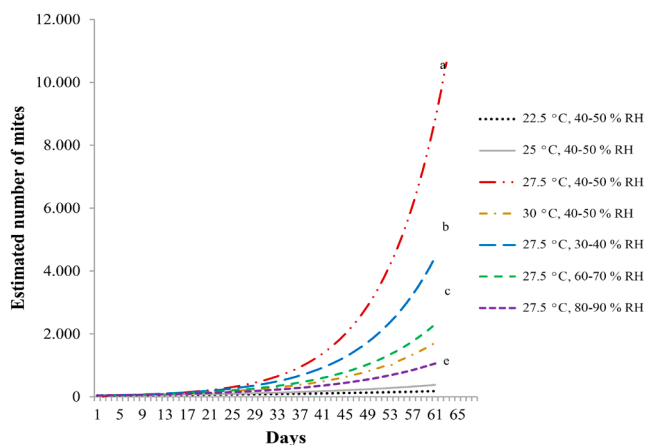
**Effect of temperature and relative humidity on rate of *R. indica* development.** The duration of each life stage, as well as of the complete immature phase, was inversely related to temperature for both sexes together. The shortest developmental time was observed at 30 °C (Tables 2 and 3). In contrast, there was no clear relation between levels of relative humidity (at 27.5 °C) and duration of life stages. Significant differences in duration of some life stages were observed, but there was no level of relative humidity that consistently resulted in longer or shorter life stages.

**Parameters of population increase.** The proportion of females to total adult specimens was  $0.793 \pm 0.147$  (standard deviation). Given that the cohorts were established with eggs of unknown gender, the differences in proportion of genders among cohorts cannot be attributed to rearing conditions.

Parameters of population increase for different combinations of temperature and relative humidity are shown in Table 4. In all cases,  $r_m$  was positive, showing that no combination of temperature and humidity limited *R. indica*



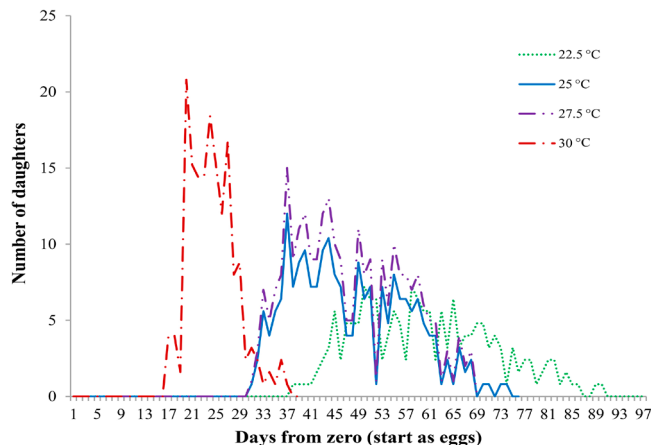
**Figure 2.** Survival curves of *Raoiella indica* reared in three ranges of relative humidity at  $27.5 \pm 1$  °C. The day when eggs were laid is defined as day zero.



**Figure 3.** Projection of *Raoiella indica* population increase at different combinations of temperature and relative humidity, based on parameters of population increase estimated by fertility life. Curves signaled by a different letter are significantly different according to Vera and Sotres (1991).

population increase. It was clear, however, that temperature was the main factor affecting the intrinsic rate of increase. The effect of temperature can also be appreciated in both generational time and indices of fecundity ( $\lambda$  and  $R_0$ ). The highest  $r_m$  value occurred when temperature was 27.5 °C and relative humidity 40-50 %. These conditions are thus the closest to optimal for development and population increase of *R. indica*.

With the test of overlapping intervals of Vera and Sotres (1991), projections of population increase were drawn



**Figure 4.** *Raoiella indica* fecundity curves at different temperatures and relative humidity 40-50 %

(Fig. 3). The results confirm temperature as the main factor affecting *R. indica* population increase, with 27.5 °C as closest to the optimal. At 22.5 °C, population increase is very slow, suggesting that injuries to host plants *R. indica* may cause under those conditions would be reduced. There was also an inverse relation between relative humidity and population increase, where curves of population increase were significantly different.

**Fecundity curves at different temperatures and levels of relative humidity.** Of all eggs laid by *R. indica* females during their entire oviposition periods at different combinations of

**Table 1.** Values of  $\chi^2$  for comparison of survival curves of *Raoiella indica* at different temperatures and ranges of relative humidity, Logrank test (Vera *et al.* 2002).

	25 °C, 40-50 % RH	27.5 °C, 40-50 % RH	30 °C, 40-50 % RH	27.5 °C, 30-40 % RH	27.5 °C, 60-70 % RH	27.5 °C, 80-90 % RH
22.5 °C, 40-50 % RH	17.23*	7.87*	27.49*	8.81*	24.96*	10.04*
25 °C, 40-50 % RH		0.55	2.75	51.36*	1.87	0.0003
27.5 °C, 40-50 % RH			26.16*	0.06	0.01	0.57
30 °C, 40-50 % RH				26.16*	0.0006	0.57
27.5 °C, 30-40 % RH					0.06	0.44
27.5 °C, 60-70 % RH						0.18

\* Significantly different, P = 0.05.

**Table 2.** Duration of life stages of *Raoiella indica* females reared at different temperatures and levels of relative humidity.

Temp. °C/ % RH	n	Eg	Lv A	Lv Q	Pn A	Pn Q	Dn A	Dn Q	Time Eg-Ad	Longev	Preov	Ov	Postov
22.5/40-50	13	9.6 a*	5.2 a	3.6 a	4.8 a	3.3 a	6.9 a	4.4 a	38.9 a	30.9 a	4.4 ab	23.8 ab	2.9 b
25/40-50	11	7.4 b	2.9 c	3.0 b	3.5 b	2.4 b	4.7 b	3.0 b	27.7 b	32.0 a	4.64 a	26.4 a	2.0 b
27.5/40-50	33	6.7 c	2.3 e	1.9 d	2.1 c	1.6 d	2.9 cd	2.1 c	20.7 de	22.4 b	3.1 dc	17.1 bc	2.2 b
30/40-50	23	4.6 e	2.0 e	1.6 d	2.1 c	1.2 e	2.2 cd	1.5 d	17.0 f	12.8 c	2.7 d	9.6 c	1.8 b
27.5/30-40	23	5.6 d	2.5 de	2.0 c	2.3 c	2.0 bc	2.6 cd	1.9 d	19.9 e	28.8 ab	3.3 bdc	22.8 ab	2.9 b
27.5/60-70	29	6.9 bc	2.9 cd	2.3 bc	2.5 c	1.9 cd	2.4 d	2.1 c	21.9 dc	22.7 b	3.0 dc	17.2 bc	2.6 b
27.5/80-90	17	4.7 e	3.7 b	2.2 bc	3.4 b	1.8 cd	3.0 c	2.7 b	22.4	28.2 ab	4.1 abc	19.7 ab	4.6 a

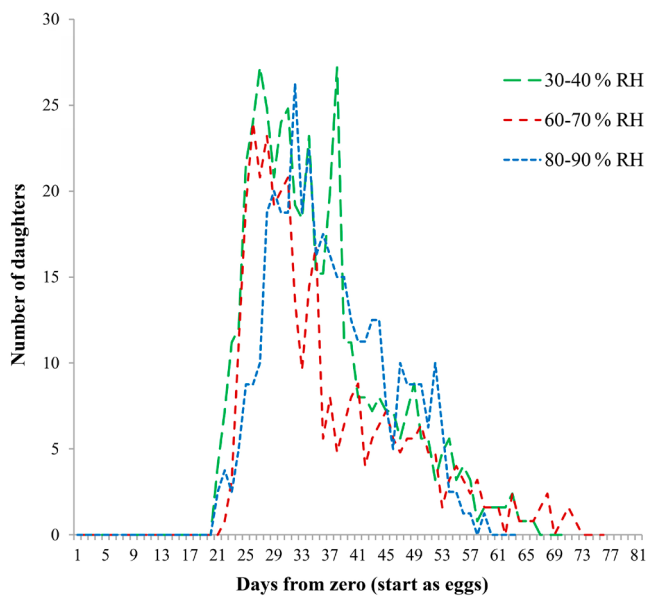
\* Values in the same column and with the same letter are not significantly different (least significant difference, P = 0.05). n: number of replicates, Eg: egg, Lv: larva, Pn: protonymph, Dn: deutonymph, Ad: adult, Longev: longevity, Preov: preoviposition, Ov: oviposition, Postov: postoviposition, A: active, Q: quiescent.

**Table 3.** Duration of life stages of *Raoiella indica* males reared at different temperatures and levels of relative humidity.

Temp. °C/ % RH	n	Eg	Lv A	Lv Q	Pn A	Pn Q	Dn A	Dn Q	Time Eg-Ad	Longev
22.5/40-50	10	9.5 a*	4.4 a	3.5 a	4.6 a	3.1	5.0 a	3.7 a	34.8 a	37.7 a
25/40-50	2	8.5 -	4.0 -	3.5 -	4.6 -	3.1 -	5.0 -	3.7 -	24.3 b	37.7 -
27.5/40-50	3	6.7 b	2.0 c	2.0 b	2.7 ab	1.7 b	2.0 bc	2.3 b	20.3 bc	26.0 ab
30/40-50	4	8.2 c	3.6 bc	3.0 b	4.0 b	2.6 b	4.0 bc	3.2 b	17.5 c	33.8 c
27.5/30-40	10	6.0 bc	2.3 c	1.4 b	3.0 ab	2.0 b	1.6 c	1.8 b	19.1 c	16.0 bc
27.5/60-70	2	7.0 -	3.0 -	2.5 -	2.0 -	1.5 -	2.0 -	2.5 -	21.5 bc	7.5 -
27.5/80-90	10	5.1 c	3.4 b	2.0 b	3.1 ab	1.9 b	2.8 b	2.1 b	21.4 bc	20.9 bc

\* Values in the same column with the same letter are not significantly different (least significant difference, P = 0.05). n: number of replicates, Eg: egg, Lv: larva, Pn: protonymph, Dn: deutonymph, Ad: adult, Longev: longevity, A: active, Q: quiescent.

temperature and relative humidity, 80 % were assumed to be females (daughters) (Figs. 4 and 5). A clear association with temperature was evident (Fig. 4). Females reared at 30 °C concentrated oviposition between days 15 and 37, with the highest rate from day 20 to day 29. In contrast, when reared at 22.5 °C, females laid eggs between days 37 and 92, peaking towards the center of that lapse. At 25 and 27.5 °C, fecundity curves followed similar patterns, egg-laying taking place between days 30 and 70, although total oviposition was higher at 27.5 °C.



**Figure 5.** Fecundity curves of *Raoiella indica* at 30-90 % relative humidity and temperature 27.5 °C.

Even though mites reared at 30 °C started egg laying long before those at other temperatures, the number of descendants (daughters) was lower, a fact that resulted in a lower net reproductive rate ( $R_0 = 4.2$ ). Mites reared at 22.5 °C started laying eggs later and continued longer; however, their  $R_0$  was also 4.2. Temperature resulting in the highest  $R_0$  (11.92) and  $r_m$  (0.0856) was 27.5 °C (Table 4).

In contrast, fecundity curves of mites reared at the same temperature but different levels of relative humidity started and ended at similar times and followed similar patterns, resulting in similar  $R_0$  values (Fig. 5). This shows that humidity alone at the tested levels did not have a significant effect on *R. indica* oviposition.

**Mating behavior.** When *R. indica* males were put in contact with female deutonymphs and once they reached adulthood, they were capable of mating with three to six of them (mean 4.56, n = 15) for their whole life. Mating took place almost immediately after the females molted (sometimes only partially). Whether a male mated more than once with the same female was not observed.

**Discussion**

The use of detached leaves, leaf discs or similar plant parts to prepare arenas, is a useful tool to follow development and reproduction of individual mites, mainly to construct life tables. However, some degree of artificiality is unavoidable, not only because there could be water stress that causes leaves or leaf discs to wilt after a variable number of days (Helle and Overmeer 1985), but because there is no competition (intra- or interspecific), there are no predators, temperature and humidity are kept almost constant, leaves are usually placed

**Table 4.** Parameters of population increase of *Raoiella indica* at temperatures from 22.5 to 30 °C and relative humidity from 30-40 to 80-90 %.

Rearing conditions	$R_0$	$T_g$	$r_m$	$\lambda$
22.5 °C, 40-50 % RH	4.22	59.341	0.0242	1.0245
25 °C, 40-50 % RH	5.38	46.617	0.0361	1.0367
27.5 °C, 40-50 % RH	19	34.377	0.0856	1.0894
30 °C, 40-50 % RH	4.2	23.362	0.0614	1.0633
27.5 °C, 30-40 % RH	11.92	34.347	0.0721	1.0748
27.5 °C, 60-70 % RH	8.84	35.323	0.0617	1.0636
27.5 °C, 80-90 % RH	6.48	35.935	0.0546	1.0561



with the abaxial surface up, food is theoretically unlimited, etc. (Vera *et al.* 2002).

This could be particularly relevant for *Raoiella* spp., that feed by inserting their cheliceral stylets through plant stomata (Ochoa *et al.* 2011). The use of leaf pieces is expected to result in closure of stomata, a fact affecting the capacity of mites to feed, and then the life cycle and reproduction would be affected (Beard *et al.* 2012). Cocco and Hoy (2009) failed to settle *R. indica* on leaf discs of banana and plantain, likely because discs wilted and consequently stomata closed. However, they also failed to settle this mite on potted banana and plantain plants, so other factors could be involved beside closure of stomata, such as the age of leaves, as studied by Otero-Colina *et al.* (2016).

In contrast, *R. indica* can be reared on coconut leaf pieces, as shown by Cocco and Hoy (2009), González and Ramos (2010) and Vásquez *et al.* (2015). There is no information about how long after coconut leaves are cut their stomata close (different from its normal function); similarly, it has not been determined if closed stomata impede *R. indica* mite feeding. To prolong the useful life of leaf sections, in the present study, 8 x 5 cm sections were used, instead of smaller portions (18 x 45 mm) as used by Cocco and Hoy (2009); their base was covered with water soaked cotton pads and those sections were replaced when they started to lose a turgid aspect.

As a result, in our research mites could reach adulthood and reproduced; life span and fecundity were similar to those estimated for *R. indica* in other studies under conditions closest to what we found as the optimal ones (Moutia 1958; Nageshachandra and Channabasavanna 1984). As population parameters can be compared between different environmental conditions, provided mites are handled the same way, it is postulated that the obtained values really represent the effect of temperature and relative humidity on development and reproduction of *R. indica*, the aim of this study.

All survival curves observed in this study, regardless of the combination of temperature and relative humidity, were type III according to the classification presented by Vera *et al.* (2002). In this type of survival curve, mortality is evenly distributed over time. This was consistent throughout our study. Survival curves drawn for other tenuipalpid species are different from those we observed. In two life tables of a species identified as *Brevipalpus phoenicis* (Geiskes, 1936) (Kennedy *et al.* 1996; Teodoro and Reis 2006), almost all specimens died at relatively advanced life stages, with type I survival curves (Vera *et al.* 2002). In another study, *Tenuipalpus heveae* (Baker, 1945) (also Tenuipalpidae) was shown to have high larval mortality, but most of the remaining specimens remained alive until adulthood (Feres *et al.* 2010). Thus, their survival curve was similar to type IV (Vera *et al.* 2002). The survival curves observed in the present study show that a lower proportion of *R. indica* survives to adulthood, and this was expected to have an effect on the parameters of population increase.

Consistently, the length of *R. indica* lifespan was inversely proportional to temperature. This was expected because it is well known that developmental rate of poikilothermic organisms is strongly affected by temperature, as has been observed many times and analyzed by Collinet *et al.* (2015). In contrast, it is noteworthy that relative humidity had an unimportant effect on the survival curves of *R. indica*, even though it ranged from 30 to 90 %. Moutia (1958), Hoy *et al.* (2006), Taylor *et al.* (2012), Prabheena and Ramani (2014),

among others, have noted that *R. indica* populations naturally diminish during the rainy season, when relative humidity is obviously higher. This leads us to postulate that not relative humidity, but rather the direct physical action of rainfall kills many mites. Another important mortality factor could be epidemics of pathogenic fungi infecting *R. indica*, which are prevalent during the rainy season as has been observed by Carrillo *et al.* (2012b) and Colmenarez *et al.* (2014). All the above data show that relative humidity, within the experimental range, had no significant impact on *R. indica* development and reproduction.

Several studies present values on the duration of *R. indica* developmental stages, as well as on egg-to-adult duration. Such data are not totally comparable with those of our work because temperature, humidity or host plants were different, or simply because the environmental conditions were not specified in those studies. However, they provide useful information. Examples are Moutia (1958), Hoy *et al.* (2006) and Vásquez *et al.* (2015). In all these studies, the time elapsed from egg to adult varied between 20 and 38 days, coinciding with our research (Tables 2 and 3). Using the above studies as a reference, it can be determined that *R. indica* has a developmental time typical for Tenuipalpidae, considerably longer than that of the closely related family Tetranychidae, where the lapse from egg to adult ranges from six to ten days (Crooker 1985). The family Tenuipalpidae has traditionally been considered less important than the family Tetranychidae because tenuipalps rarely attain high infestations, partially attributed to their slow development (Jeppson *et al.* 1975).

Because survival curves, duration of developmental stages and oviposition in *R. indica* were affected by temperature, the parameters of population increase were consequently related to temperature and to a lesser extent to relative humidity. The highest values of fecundity indices ( $R_0$  and  $\lambda$ ) were observed when mites were reared at 27.5 °C, whereas the lowest values corresponded to 22.5 and 30 °C, in all cases 40-50 % RH. Relative humidity above and below 40-50 % resulted in lower fecundity indices. The intrinsic rate of population increase ( $r_m$ ), whose value is affected by all the above indices, was equally the highest at 27.5 °C, 40-50 % relative humidity.

These values highlight *R. indica*'s affinity to warm climates and its tolerance to wide variations in relative humidity. Field observations of this mite have repeatedly shown that its infestation increases during the warmest part of the year and its world distribution is pantropical even after settling in America (Peña *et al.* 2010; CABI 2016).

Vásquez *et al.* (2015) estimated an  $r_m$  of 0.166 for *R. indica* feeding on coconut leaves. This value is notably higher than that estimated in our work (0.0856, Table 4). Because the authors of the cited study do not give details on how they calculated the parameters of population increase, it is difficult to interpret the difference. A possible explanation could be that in our study the parameters of population increase were estimated assuming that 80 % of all the specimens were females.

The  $r_m$  estimated for *R. indica* is low compared with those from the tetranychid species; for example, for *Tetranychus cinnabarinus* (Boisduval, 1867) it was 0.20 (Peralta and Tello 2011). It is also lower than values estimated for other tenuipalps; Kennedy *et al.* (1996) estimated  $r_m = 0.127$  for *B. phoenicis*, while Feres *et al.* (2010) found  $r_m = 0.06$  for *T.*

*heveae* reared on a susceptible clone of *Hevea brasiliensis* (Willd ex. A. Juss) (Malpighiales: Euphorbiaceae).

All the above data show that *R. indica* has a developmental rate and fecundity similar to those of other tenuipalpids, resulting in similar values of  $R_0$ ,  $\lambda$  and  $r_m$ . It is then surprising that this mite reaches very high field infestations on coconut palm (Kane *et al.* 2012), its main host and where it was reared during the current study, contrasting with other tenuipalpids which are commonly present in low populations on their respective hosts (Jeppson *et al.* 1975). A possible explanation for such high *R. indica* infestations could be that in its new distribution areas in America effective natural enemies have not had enough time to adapt to their new prey. In addition, *R. indica* seems to have a defense mechanism against predators; it secretes a liquid that accumulates as droplets on the tips of its dorsal setae; Carrillo *et al.* (2012b) suggest that it is a repellent.

Finally, the proportion of *R. indica* males to females may also impact its capacity of population increase. In other species of Tenuipalpidae, such as *Brevipalpus* spp., practically all specimens are potentially fertile females (Helle *et al.* 1980; Kennedy *et al.* 1996) that contribute to population increase. The proportion of *R. indica* males is higher (Moutia 1958; this study). Given that each male can mate with three to six females, a proportion of 20 to 30 % males is sufficient to fecundate all the females present.

#### Literature cited

- BEARD, J. J.; POOLEY, C.; OCHOA, R.; BAUCHAN, G. R.; DOWLING, A. P. G.; WELBOURN, W. C. 2012. External mouthpart morphology in the Tenuipalpidae (Tetranychoida): *Raoiella* a case study. *Experimental and Applied Acarology* 57: 227-255. <https://doi.org/10.1007/s10493-012-9540-2>
- BIRCH, L. C. 1948. The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* 17: 15-26. <https://doi.org/10.2307/1605>
- CABI. Centre for Agricultural Bioscience International. 2016. Invasive species compendium. Available in: <http://www.cabi.org/isc/datasheet/46792>. [Review date: 12 January 2016].
- CARRILLO, D.; AMALIN, D.; HOSEIN, F.; RODA, A.; DUNCAN, R. E.; PEÑA, J. E. 2012a. Host plant range of *Raoiella indica* (Acari: Tenuipalpidae) in areas of invasion of the New World. *Experimental and Applied Acarology* 57: 271-289. <https://doi.org/10.1007/s10493-011-9487-8>
- CARRILLO, D.; FRANK, J. H.; RODRIGUES, J. C. V.; PEÑA, J. E. 2012b. A review of the natural enemies of the red palm mite, *Raoiella indica* (Acari: Tenuipalpidae). *Experimental and Applied Acarology* 57: 347-360. <https://doi.org/10.1007/s10493-011-9499-4>
- COCCO, A.; HOY, M. A. 2009. Feeding, reproduction, and development of the red palm mite (Acari: Tenuipalpidae) on selected palms and banana cultivars in quarantine. *Florida Entomologist* 92: 276-291. <https://doi.org/10.1653/024.092.0212>
- COLLINET, H.; SINCLAIR, B. J.; VERNON, P.; RENAULT, D. 2015. Insects in fluctuating thermal environments. *Annual Review of Entomology* 60: 123-140. <https://doi.org/10.1146/annurev-ento-010814-021017>
- COLMENAREZ, Y.; MOORE, D.; POLAR, P.; VASQUEZ, C. 2014. Population trends of the red palm mite, *Raoiella indica* Hirst (Acari: Tenuipalpidae) and associated entomopathogenic fungi in Trinidad, Antigua, St Kitts and Nevis and Dominica. *Acarologia* 54: 433-442. <https://doi.org/10.1051/acarologia/20142141>
- CROOKER, A. 1985. Embryonic and juvenile development. p. 149-163. In: Helle, W.; Sabelis, M. W. (Eds.). *Spider mites their biology, natural enemies and control*, Vol. 1A. Elsevier, Leiden, The Netherlands. 405 p.
- DANIEL, M. 1979. Survey of the indigenous predators of arecanut phytophagous mites. pp. 227-235. In: Venkata, C. S. (Ed.). *Proceedings of the Second Annual Symposium on Plantation Crops. Plant protection (entomology, microbiology, nematology, plant pathology and rodentology)*. 555 p.
- FERES, R. J. F.; DEL'ARCO, M.; DAUD, R. D. 2010. Biological cycle of *Tenuipalpus heveae* Baker (Acari, Tenuipalpidae) on leaflets of three rubber tree clones. *Revista Brasileira de Entomologia* 54: 298-303. <https://doi.org/10.1590/S0085-56262010000200013>
- FLECHTMANN, C. H. W.; ETIENNE, J. 2004. The red palm mite, *Raoiella indica* Hirst, a threat to palms in the Americas (Acari: Prostigmata: Tenuipalpidae). *Systematic and Applied Acarology* 9: 109-110. <https://doi.org/10.11158/saa.9.1.16>
- FLORES, G. G.; MONTTOYA, A.; RODRÍGUEZ, H. 2010. Biología de *Raoiella indica* Hirst (Acari: Tenuipalpidae) sobre *Areca catechu* L. *Revista de Protección Vegetal* 25: 11-16.
- GERSON, U.; VENEZIAN, A.; BLUMBERG, D. 1983. Phytophagous mites on date palms in Israel. *Fruits* 38: 133-135.
- GÓMEZ-MOYA, C. A.; LIMA, T. P. S.; MORAIS, E. G. F.; GONDIM JR., M. G. C.; MORAES, G. J. 2017. Hosts of *Raoiella indica* Hirst (Acari: Tenuipalpidae) native to the Brazilian Amazon. *Journal of Agricultural Science* 9 (4): 86-94. <https://doi.org/10.5539/jas.v9n4p86>
- GONDIM JR., M. G. C.; CASTRO, T. M. M. G.; MARSARO JR., A. L.; NAVIA, D.; MELO, J. W. S.; DEMITE, P. R.; DE MORAES, G. J. 2012. Can the red palm mite threaten the Amazon vegetation? *Systematics and Biodiversity* 10: 527-535. <https://doi.org/10.1080/14772000.2012.752415>
- GONZÁLEZ, R. M.; RAMOS, M. 2010. Plantas hospedantes de *Raoiella indica* Hirst (Acari: Tenuipalpidae) en el municipio de Santiago de Cuba. *Revista de Protección Vegetal* 25: 5-6.
- HELLE, W.; OVERMEER, W. P. J. 1985. Rearing techniques. pp. 331-335. In: Helle, W.; Sabelis, M. W. (Eds.). *Spider mites their biology, natural enemies and control*, Vol. 1A. Elsevier, Leiden, The Netherlands. 405 p.
- HELLE, W.; BOLLAND, H. R.; HEITMANS, W. R. B. 1980. Chromosomes and types of parthenogenesis in the false spider mites (Acari: Tenuipalpidae). *Genetica* 54: 45-50. <https://doi.org/10.1007/BF00122407>
- HIRST, S. 1924. On some new species of red spider. *Annals and Magazine of Natural History Series* 9 (14): 522-527. <https://doi.org/10.1080/00222932408633151>
- HOY, M. A.; PEÑA, J. E.; NGUYEN, R. 2006. Red palm mite, *Raoiella indica* Hirst (Arachnida: Acari: Tenuipalpidae). University of Florida IFAS Extension EENY-397. Available at <http://entomology.ifas.ufl.edu/creatures>. [Review date: 03 January 2016].
- JEPPSON, L. R.; KEIFER, H. H.; BAKER, E. W. 1975. *Mites injurious to economic plants*. Univ. California Press. Berkeley and Los Angeles, California, USA. 710 p.
- KANE, E. C.; OCHOA, R.; MATHURIN, G.; ERBE, E. F.; BEARD, J. J. 2012. *Raoiella indica* (Acari: Tenuipalpidae): an exploding mite pest in the neotropics. *Experimental and Applied Acarology* 57: 215-225. <https://doi.org/10.1007/s10493-012-9541-1>
- KENNEDY, J. S.; IMPE, G.; HANCE, T.; LEBRUN, P. 1996. Demecology of the false spider mite, *Brevipalpus phoenicis* (Geijskes) (Acari, Tenuipalpidae). *Journal of Applied Entomology* 120: 493-499. <https://doi.org/10.1111/j.1439-0418.1996.tb01641.x>
- MENDONÇA, R. S.; NAVIA, D.; FLECHTMANN, C. H. W. 2005. *Raoiella indica* Hirst (Prostigmata: Tenuipalpidae), o ácaro vermelho das palmeiras-um ameaça para as Américas. *EMBRAPA Recursos Genéticos e Biotecnologia*. Brasília, Brazil. 37 p.
- MOUTIA, L. A. 1958. Contribution to the study of some phytophagous Acarina and their predators in Mauritius. *Bulletin*

- of Entomological Research 49: 59-75. <https://doi.org/10.1017/S0007485300053438>
- NAGESHACHANDRA, B. K.; CHANNABASAVANNA, G. P. 1984. Development and ecology of *Raoiella indica* Hirst (Acari: Tenuipalpidae) on coconut. pp. 785-790. In: Griffiths, D. A.; Bowman, C. E. (Eds.). *Acarology VI Vol. 2*. Ellis Horwood Limited, Chichester, England. 1296 p.
- OCHOA, R.; BEARD, J. J.; BAUCHAN G.R.; KANE, E. C.; DOWLING, A. P. G.; ERBE, E. F. 2011. Herbivore exploits chink in armor of host. *American Entomologist* 57: 26-29. <https://doi.org/10.1093/ae/57.1.26>
- OTERO-COLINA, G.; GONZÁLEZ-GÓMEZ, R. L.; MARTÍNEZ-BOLAÑOS L.; OTERO-PREVOST, G.; LÓPEZ-BUENFIL, J. A.; ESCOBEDO-GRACIAMEDRANO, R. M. 2016. Infestation of *Raoiella indica* Hirst (Trombidiformes: Tenuipalpidae) on host plants of high socio-economic importance for tropical America. *Neotropical Entomology* 45: 300-309. <https://doi.org/10.1007/s13744-016-0368-z>
- PEÑA, J. E.; CARRILLO, D.; RODRIGUES, J. C. V.; RODA, A. 2010. El ácaro rojo de las palmas, *Raoiella indica* (Acari: Tenuipalpidae), una plaga potencial para América Latina. In: Sánchez Gálvez, M. C.; Sandoval-Islas, J. S.; Estrada-Venegas, E. G. E. (Eds.). *Primer Simposio Internacional de Acarología en México – Memorias*. Universidad Autónoma Chapingo, Chapingo, México. 136 p.
- PERALTA, C.; TELLO, M. 2011. Tabla de vida de *Tetranychus cinnabarinus* (Acari: Tetranychidae) sobre tres variedades de melón, *Cucumis melo*. *Revista Colombiana de Entomología* 37: 21-26.
- PRABHEENA, P.; RAMANI, N. 2014. Seasonal incidence and injurious status of *Raoiella indica* (Hirst) (Acari: Tenuipalpidae) on arecanut palms of Kozhikode district of Kerala. *International Journal of Plant, Animal and Environmental Sciences* 4: 227-230.
- SAS. SAS Institute. 2002. *SAS Procedure's Guide*, version 9. SAS Institute, Cary, NY.
- TAYLOR, B.; RAHMAN, P. M.; MURPHY, S. T.; SUDHEENDRAKUMAR, V. V. 2012. Within-season dynamics of red palm mite (*Raoiella indica*) and phytoseiid predators on two host palm species in south-west India. *Experimental and Applied Acarology* 57: 331-345. <https://doi.org/10.1007/s10493-011-9482-0>
- TEODORO, A. V.; REIS, P. R. 2006. Reproductive performance of the mite *Brevipalpus phoenicis* (Geijskes, 1939) on citrus and coffee, using life table parameters. *Brazilian Journal of Biology* 66: 899-905. <https://doi.org/10.1590/S1519-69842006000500016>
- VÁSQUEZ, C.; COLMENAREZ, Y.; DE MORAES, J. G. 2015. Life cycle of *Raoiella indica* (Acari: Tenuipalpidae) on ornamental plants, mostly Arecaceae. *Experimental and Applied Acarology* 65: 227-235. <https://doi.org/10.1007/s10493-014-9858-z>
- VERA GRAZIANO, J.; PINTO, V. M.; LÓPEZ COLLADO, J.; REYNA ROBLES, R. 2002. *Ecología de poblaciones de insectos*. Segunda Edición. Colegio de Postgraduados. Texcoco, México. 138 p.
- VERA GRAZIANO, J.; SOTRES, D. R. 1991. Prueba de traslapo de intervalos para comparar tasas instantáneas de desarrollo poblacional. *Agrociencia serie Protección Vegetal* 2: 7-13.
- WOMERSLEY, H. 1943. Australian Acarina of the family Tricadenidae Oudemans 1938. *Records South Australia Museum, Queensland* 7: 245-248.

#### Origin and funding

*This work was carried out by the first author as a required activity to obtain a Master of Science degree. It was financed by Colegio de Postgraduados and Consejo Nacional de Ciencia y Tecnología, Mexico.*

#### Author contribution

*David Martínez Mejía. He was directly responsible of carrying out the experimental procedure, manipulation of the mites and analysis of results.*

*Gabriel Otero-Colina. He was the leader of the study, he was charged of coordinating the teamwork and conciliating the diverse contributions.*

*Rebeca González-Gómez. She was the advisor in the procedures to handle the mites, experimental design and critical review of the manuscript.*

*Alejandro Pérez-Panduro. He was the advisor in the ecological analysis of the results, experimental design and critical review of the manuscript.*

*Javier Valle-Mora. He was responsible of statistical analysis of the results and experimental design.*