



Life table parameters of the red palm mite *Raoiella indica* (Acari: Tenuipalpidae) at various temperatures and for sexual and asexual reproduction

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Abstract

The red palm mite, *Raoiella indica* Hirst, is a threat to coconut, banana and native Arecaceae and Heliconiaceae in Brazil. This mite originated in the Eastern Hemisphere and was first reported in 2004 in the Americas, where the pest is spreading quickly and causing severe damage to its host plants. The objective of this work was to determine the life-history parameters of *R. indica* at constant temperatures, estimate its thermal requirements [threshold temperature (T_b) and thermal constant (K)] and also compare its life table parameters between sexual reproduction and parthenogenesis. The life tables were constructed on leaflets of *Adonidia merrillii* at 15, 20, 24, 27, 30 and 34 °C and 65% RH and a 12-h photoperiod. The longevity and the number of laid eggs of non-copulated adult females were evaluated at 27 °C. *Raoiella indica* had complete development, from egg to adult, only at 20, 24, 27 and 30 °C. At 15 °C, the eggs did not hatch, and at 34 °C, the mites survived only until the larval stage. For sexual reproduction, the optimal temperature was 27 °C, under which the reproductive parameters were higher. The reproductive parameters for sexual reproduction were higher than those for parthenogenesis. The T_b was 14.79 °C, and the thermal constant was 208.33 degree days. The life parameters estimated in this study can be used for modelling and predicting the population growth of *R. indica* in the field and consequently for improving their management strategies.

Keywords Life history · Invasive pest · Coconut · Modelling distribution · Thermal requirement

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Introduction

The red palm mite, *Raoiella indica* Hirst (Tenuipalpidae), was introduced in the Americas slightly more than 10 years ago (Flechtmann and Etienne 2004) and has spread quickly in the continent. Originating from the Eastern Hemisphere (Dowling et al. 2012), this mite was reported in the Americas in 2004, on the Caribbean island of Martinica (Flechtmann and Etienne 2004), and rapidly disseminated to other islands (Rodrigues et al. 2007). Approximately, 5 years later it reached the north, south and central mainland (Bowman and Hoy 2012; Carrillo et al. 2011; Kane et al. 2012; Navia et al. 2011; Vásquez et al. 2008).

Numerous colonies can be found on leaves of infested plants, which later become necrotic leading to heavy yield losses (even higher than 70%), such as reported for coconut production in Caribbean (Roda et al. 2012) and Mexico (Otero-Colina et al. 2016) and coconut and banana in Brazil (Gondim Jr et al. 2012). In the Americas, *R. indica* has not only built large populations and spread quickly but also extended its host range, attacking several exotic or wild palm species (Arecaceae) and plants of various monocotyledons families such as Cannaceae, Cycadaceae, Heliconiaceae, Musaceae, Pandanaceae, Strelitziaceae and Zingiberaceae (Carrillo et al. 2012a; Gondim Jr et al. 2012; Navia et al. 2015; Gómez-Moya et al. 2017).

Notwithstanding the importance of *R. indica* as an invasive pest in the Americas, some primary biological parameters have not been determined. Although some biological studies have been conducted in both the old and the new world, they were conducted under fixed temperatures ranging between 15 and 29 °C (González-Reyes and Ramos 2010; Flores-Galano et al. 2010; Vásquez et al. 2015; Gómez-Moya et al. 2017; Nusantara et al. 2017), thermal requirements have not been determined and a life table was not constructed.

Accurate information on the effects of climatic parameters, especially temperature, on the development and reproduction of *R. indica* is crucial for defining prevention and control measures. Models, including potential effects of climate change scenarios (Navia et al. 2016) based on occurrence reports and biological parameters and population dynamics available in the literature, have already been developed to predict the suitable areas for this mite in South America (Amaro and Morais 2013). These last authors used only presence data, and no physiological requirement was considered. However, the precision of these models could be greatly improved if data on the effect of temperature on *R. indica* life table parameters were available. Some species distribution models, such as Climex, have been built using estimates of the physiological requirements of species (Sutherst 2003).

Estimates of temperature effects on the development rate, survival and reproduction of pests are thus useful to predict the population dynamics in the field and consequently to improve their management strategies (Tanga et al. 2018). The selection of biological control agents is also improved when biological parameters of the target pest are known. In this study, the life-history parameters of *R. indica*, such as development, survival and reproduction, are presented at various constant temperatures and for both sexual and asexual (parthenogenesis) reproduction.

Materials and methods

Stock colony

The females used in this study were from the second generation of *R. indica* colonies collected on leaflets of the Manila palm, *Adonidia* (= *Veitchia*) *merrillii* (Becc.) Becc. (Arecaceae) in Boa Vista, Roraima, Brazil (2°45'27.8"N, 60°43'53.5"W), and maintained in the laboratory at 27 °C, 65% RH and a 12-h photoperiod. The colonies were reared on leaflets of *A. merrillii* (14 cm long), placed into plastic dishes (16 cm diameter) on a moistened polyethylene foam (1 cm thick) with distilled water and bordered with a moistened layer of hydrophilic cotton to keep the turgidity of the leaflet and to prevent the escape of the mites. The foam and cotton were kept continuously wet by the daily addition of distilled water. The leaflets of *A. merrillii* were replaced when they became yellow during the mobile phase of *R. indica*.

Biology of *Raoiella indica* at various constant temperatures

The effects of temperature on the life-history parameters of *R. indica* were studied in controlled incubation chambers at six constant temperatures (15, 20, 24, 27, 30 and 34 °C), in the Entomology Laboratory of Embrapa Roraima, Brazil. The relative humidity was maintained at 65%, and there was a 12-h photoperiod. The temperature and relative humidity inside the incubators were monitored using a digital thermohygrometer and fluctuated by 1 °C and 10%, respectively.

Each experimental unit consisted of a piece of one *A. merrillii* leaflet (5 cm long) maintained as in mass rearing. The leaflets were bordered with entomological glue to prevent the mites from being trapped in cotton and dying. Five adult females of *R. indica* were transferred to each experimental unit, and after 15 h, the adult female and the excess eggs were removed, leaving only one egg per unit. For each temperature, 60–70 units were established.

The units were observed at 24-h intervals, under a stereomicroscope with ×40 magnification, to determinate the mortality, duration of each stage and the daily fertility of mites until their death. When a female reached the teleiochrysalis stage, one male from the mass rearing was transferred to a new unit and replaced—if necessary—until the female died.

Longevity and reproduction by parthenogenesis reproduction

To compare the longevity and reproductive parameters of *R. indica* by sexual reproduction and parthenogenesis, 80 moulted adult females from the stock colony that had not copulated were observed at 27 °C under the same conditions as described above. The eggs laid by the females were also observed for sex determination.

Analysis of life tables

The analysis of life tables for *R. indica* at various temperatures was performed using standard methods by Southwood (1978) and Maia et al. (2000). Life table parameters,

such as net productive rate (R_0), intrinsic rate of natural increase (r_m) and mean generation time (T), were estimated.

The duration of each stage and oviposition and pre-oviposition periods at the various temperatures were compared using Kruskal–Wallis ($\alpha=0.05$). Dunn test was used as post hoc test to determine which temperatures were different from others. Survival and fertility parameters at different temperatures were analysed using one-way ANOVA ($\alpha=0.05$). If significant differences were detected, then a Tukey HSD test was used. One-way ANOVA was also used to compare the fertility parameters for sexual versus parthenogenesis reproduction at 27 °C.

Thermal requirements

The threshold temperature (T_b) and thermal constant (K) were calculated by the thermal summation model (Campbell et al. 1974), using the linear relationship between temperature and the rate of development of *R. indica*: $1/D=a+bT$, where D is the development time and T is the ambient temperature (°C). The thermal constant ($K=1/b$) is the number of degree days or heat units above the threshold needed for the species to complete its development.

Results

Raoiella indica had complete egg-to-adult development only at 20, 24, 27 and 30 °C. At 15 °C, the eggs survived a mean of 66.7 days, when they had a normal format and colouration; however, after this period, they became discoloured, and wilted and did not hatch. At 34 °C, the mites survived only until the larval stage (Table 1).

There were significant differences between the durations of all life stages and cumulative development (egg to adult) at the various temperatures, and the durations were inversely proportional to temperature. The mean duration of all stages, except that of the egg, was higher at 20 °C. The development times from egg to adult at 20, 24, 27 and 30 °C were 35.8, 24.7, 17.9 and 13.3 days, respectively (Table 1).

The shortest duration of the egg stage was a mean of 3.67 days at 30 °C. The durations of the larval and protonymphal stages were the shortest and similar at 24, 27 and 30 °C. The shortest duration of the deutonymph stage was at 30 °C at 1.67 days. Female longevity was longest at 20 °C (70.1 days), intermediate at 24 and 27 °C (29.6 and 24.1 days, respectively), and shortest at 30 °C (3.5 days; Table 1).

The mean preoviposition period ranged from 1.0 day at 30 °C to 3.5 days at 20 °C. The oviposition period was similar at 20, 24 and 27 °C (13.5, 22.8 and 19.0 days, respectively) and shortest at 30 °C (1 day) (Table 1).

The relation between the development rate and temperature ranging from 15 to 30 °C was linear ($R^2=0.99$, $P<0.0001$). The estimated minimum temperature of development (T_b) was 14.79 °C, and the thermal constant (K) 208.33 degree days.

The survival of eggs was similar at the various temperatures ($F=2.78$, $P=0.087$), except at 15 °C, when all eggs died. Survival rates of mobile stages (larva, protonymph and deutonymph) and of egg-to-adult was higher and similar at 20, 24 and 30 °C (Table 2).

The reproductive parameters number of eggs/female, net reproductive rate (R_0) and intrinsic rate of natural increase (r_m) were highest at 27 °C for sexual reproduction (47.02 eggs/female, $R_0=24.21$ and $r_m=0.13$), suggesting that this is the

Table 1 Mean (± SE) developmental time for each stage and preoviposition and oviposition periods (days) of *Raoiella indica* at multiple temperatures

Temperature (°C)	N ¹	Developmental time (days)						Preoviposition		Oviposition
		Egg	Larva	Protonymph	Deutonymph	Egg-Adult	Female			
15	69	66.71 ± 1.33a								
20	75	24.95 ± 3.50b	32.68 ± 4.81a	19.98 ± 4.29a	8.42 ± 0.54a	35.76 ± 1.36a	70.09 ± 1.50a	3.52 ± 0.42a	–	13.46 ± 1.49ab
24	66	11.08 ± 0.17c	4.82 ± 0.11b	3.39 ± 0.21b	5.18 ± 0.23b	24.69 ± 0.23b	29.60 ± 1.89b	2.69 ± 0.21ab		22.83 ± 1.69a
27	65	6.28 ± 0.32d	5.35 ± 0.17c	1.41 ± 0.16c	5.79 ± 0.34b	17.89 ± 0.26c	24.13 ± 2.62b	1.61 ± 0.27b		19.00 ± 2.27a
30	60	4.68 ± 0.22e	3.66 ± 0.30d	2.14 ± 0.34bc	1.67 ± 0.67c	13.33 ± 0.33c	3.50 ± 0.50c	1.00 ± 0.00b		1.00 ± 0.00b
34	70	3.67 ± 0.15e	4.42 ± 0.33db	–	–	–	–	–		–
Kruskal–Wallis χ^2		336.97	138.91	113.61	51.47	118.68	72.76	13.12		17.82
df		5	4	3	3	3	3	3		3
P		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0044		0.0005

¹Initial number of replicates. Means within a column followed by the same letter are not significantly different (Dunn test: $P > 0.05$)

Table 2 Mean (\pm SE) survivorship (%) for each stage of *Raoiella indica* at multiple temperatures

Temperature (°C)	Egg	Larva	Protonymph	Deutonymph	Egg-Adult
15	0	–	–	–	–
20	87.14 \pm 6.16a	66.85 \pm 8.26b	79.49 \pm 5.34a	100.00 \pm 0.00a	46.90 \pm 9.51a
24	93.62 \pm 1.90a	98.77 \pm 1.23a	91.66 \pm 1.82a	93.86 \pm 3.41a	81.35 \pm 3.25a
27	78.24 \pm 1.70a	80.95 \pm 3.06ab	94.66 \pm 2.68a	91.41 \pm 4.82a	54.72 \pm 3.49a
30	88.33 \pm 6.01a	11.96 \pm 9.18c	16.67 \pm 16.67b	66.67 \pm 0.00b	1.11 \pm 1.11b
34	75.00 \pm 5.00a	0.0	–	–	–
F	2.78	34.36	14.79	8.09	14.56
df	5,10	4,8	3,6	3,6	3,6
P	0.087	<0.0001	0.0035	0.016	0.0037

Means within a column followed by the same letter are not significantly different (Tukey HSD test: $P > 0.05$)

optimal temperature for *R. indica*. The shorter mean generation time (T) was 24.78 and 15.25 days at 27 and 30 °C, respectively. The proportion of females was higher than 0.8 at all the temperatures (Table 3).

The survival curve (L_x) of *R. indica* at 20 °C shows a steep decrease at the end of the life cycle. At this temperature, the longest living mite died on day 110. At 24 and 27 °C, the survival curves indicated relatively constant mortality rate throughout the life expectancies. At 30 °C, mortality was high at the beginning of the life cycle, the mites lived a maximum of 17 days (Fig. 1).

Peak oviposition rate of *R. indica* was observed at 27 °C on days 27–30, with 4.1 eggs/female/day; eggs were laid until day 64. At 24 °C, the maximum rate of oviposition was on day 32, $m_x = 3.4$ eggs/female/day, and eggs were laid until day 70. At 20 °C, the highest fecundity was 0.56 eggs/female/day on day 41, and eggs were laid until day 75. At 30 °C, peak fecundity was low at 0.67 eggs/female/day, and eggs were laid on only 3 days, from days 13 to 16 (Fig. 1).

Table 3 Mean (\pm SE) number of eggs/female, net reproductive rate (R_0), intrinsic rate of increase (r_m), generation time (T) and sex ratio (proportion daughters) of *Raoiella indica* at multiple temperatures

Temperature (°C)	Egg/female	R_0	r_m	T	Sex ratio
20	11.75 \pm 1.76bc	5.00 \pm 0.95b	0.03 \pm 0.00c	46.25 \pm 3.04a	0.92
24	21.85 \pm 3.41b	17.99 \pm 3.42ab	0.07 \pm 0.00b	39.98 \pm 1.81a	0.96
27	47.02 \pm 3.85a	24.21 \pm 4.36a	0.13 \pm 0.01a	24.78 \pm 0.22b	0.84
30	0.07 \pm 0.07c	0.07 \pm 0.07b	–0.04 \pm 0.04d	15.25 \pm 0.0b	1
F	29.54	8.38	173.85	30.62	
df	3,6	3,6	3,6	3,6	
P	0.0005	0.01	<0.0001	0.0005	

Means within a column followed by the same letter are not significantly different (Tukey HSD test: $P > 0.05$)

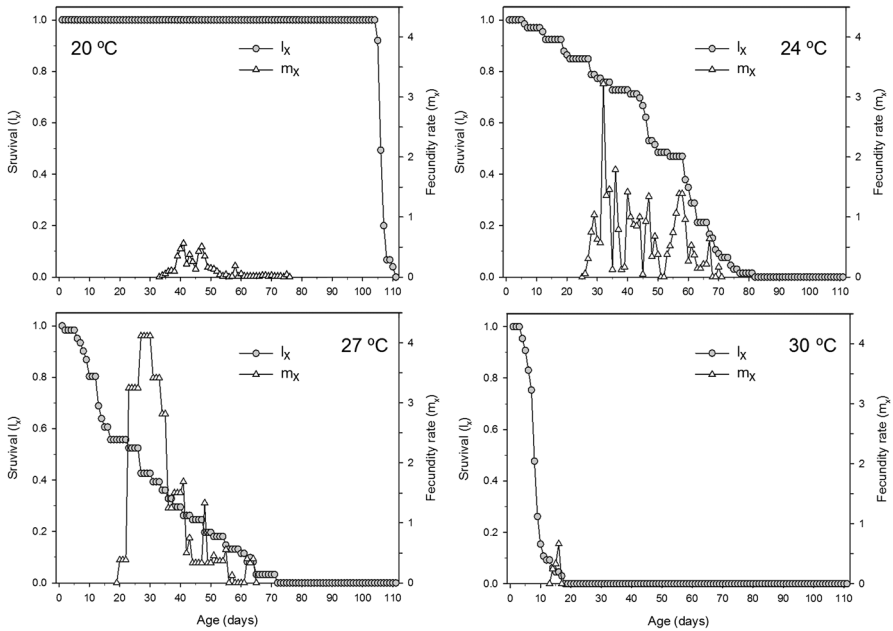


Fig. 1 Survival (l_x) and fecundity rate (m_x) of *Raoiella indica* at 20, 24, 27 and 30 °C

The reproductive parameters estimated for *R. indica* (no. eggs/female, R_0 and r_m) at 27 °C for sexually reproducing females were significantly higher than those for parthenogenetic females. The generation time (T), female longevity and preoviposition period were low for sexual reproduction. The oviposition periods did not differ (Table 4). The eggs laid by virgin females resulted in males, which confirms the arrhenotokous parthenogenesis of *R. indica*.

Discussion

The reproductive parameters of *R. indica* at 27 °C obtained in this study were generally higher than those reported by other authors who carried out experiments at similar temperatures. At 27 °C, for sexual reproduction, the mean number of eggs/female was 47, which was 3× higher than the 14 eggs/female at 26–28 °C observed by Nusantara et al. (2017) or 12.6 eggs/female at 26.3 ± 1.3 °C (Gonzalez-Reyes and Ramos 2010; Lima et al. 2011). These laboratory studies all had detached coconut leaflets.

Even when the biology of *R. indica* was studied on *A. merrillii*, the net reproductive rate (R_0) estimated at 27 °C (24.21) for sexual reproduction was 13.8× higher than that estimated at 29 ± 0.5 °C by Vásquez et al. (2015) ($R_0=1.76$) and 3× higher than that estimated at 30 ± 4.61 °C by Gómez-Moya et al. (2017) ($R_0=8.1$). These authors performed their studies on plants in screenhouses, and they suggested the development of *R. indica* is negatively affected when it is fed with detached leaves as they may close their stomata locally where this mite feeds (Beard et al. 2012). At least for *A. merrillii*, leaf detachment did not affect the performance of *R. indica* probably because the detached leaves do not

Table 4 Mean (\pm SE) number of eggs/female, net reproductive rate (R_0), intrinsic rate of increase (r_m), generation time (T), female duration (days) and preoviposition and oviposition periods (days) of *Raoiella indica* at 27 °C for sexual reproduction and parthenogenesis

Temperature (°C)	Egg/female	R_0	r_m	T	Female duration	Preoviposition	Oviposition
Sexual reproduction	47.02 \pm 3.85	24.21 \pm 4.36	0.13 \pm 0.01	24.78 \pm 0.22	24.13 \pm 2.62	1.61 \pm 0.27	19.00 \pm 2.27
Parthenogenesis	13.68 \pm 0.38	7.63 \pm 0.21	0.07 \pm 0.00	30.05 \pm 0.45	36.21 \pm 1.13	4.47 \pm 0.13	21.35 \pm 0.80
F	74.25	14.47	56.53	112.66	24.60	100.69	1.51
df	1,5	1,5	1,5	1,5	1,109	1,103	1,109
P	0.0010	0.019	0.0017	0.0004	<0.0001	<0.0001	0.22

close their stomata (E.G. Fidelis, personal observation), and they keep their physiological characteristics. In fact, during the experiment, the leaflets kept green and turgid until 68 days at 15 °C when we observed the eggs, 30 days at 20 °C and 7 days at 34 °C, showing that the rearing units with *A. merrillii* leaflets were adequate for *R. indica*. This result can explain the lower reproductive rates observed in studies with coconut leaflets at similar temperatures (Nusantara et al. 2017; Gonzalez-Reyes and Ramos 2010; Lima et al. 2011; Vásquez et al. 2015). In the field, coconut is considered the preferential host of *R. indica*, when this mite reaches high population levels (Gondim Jr. et al. 2012; Kane et al. 2012; Otero-Colina et al. 2016). However, we carried out previous experiments using detached leaflets of coconut and observed that the coconuts dried and became brown after 3–4 days; for this reason, the biology of *R. indica* was studied on *A. merrillii*.

The shorter reproductive rates of *R. indica* observed by Gómez-Moya et al. (2017), even on plants, can be related to the high mean temperature inside the screenhouse (30 ± 4.6 °C). At a constant 30 °C, we observed that *R. indica* had low survival and reproductive rates. The temperature inside the screenhouse was approximately 3 °C higher than the average temperature of 27 °C in of Boa Vista, Roraima, Brazil (INMET 2018), where this mite reaches a high population density in the field (Gondim Jr et al. 2012).

The development time of *R. indica* at 27 °C was similar to that in other studies. As in this work, at 24–29 °C the mite takes approximately 18–30 days to complete egg to adult development (Nusantara et al. 2017; Gonzalez-Reyes and Ramos 2010; Lima et al. 2011; Vásquez et al. 2015). The minimum temperature of development (T_b) of 14.8 °C estimated for *R. indica* in this study indicates that this species can establish in regions with mild temperatures, as southern Brazil. The mean minimum temperature for the northern region of Paraná State, for instance, where *R. indica* is present (Hata et al. 2017), is 17.5 °C, so this mite can develop well even during the coldest part of the year.

These thresholds can improve the models of potential distributions estimated by Amaro and Morais (2013) and Navia et al. (2016). According to these authors, the majority of the area in the south of Brazil has climatic conditions unfavourable for *R. indica*. The Maxent model calculated by Amaro and Morais (2013) showed that this entire region, except the coasts of Paraná and Santa Catarina, has very low suitability for *R. indica*. Navia et al. (2016) predicted the southern region is unfavourable during most of the year, except for the extreme north of Paraná from September to March and for western Rio Grande do Sul from November to February under the A2 gas emission scenarios from the Intergovernmental Panel on Climate Change. Recently this mite was reported in the west of São Paulo (southeastern Brazil) (Oliveira et al. 2016), northern Paraná (southern Brazil) (Hata et al. 2017), Minas Gerais, Goiás, Distrito Federal and the centre of Bahia (Melo et al. 2018), all regions that had been predicted to have very low suitability for the establishment of *R. indica* according to these models.

The temperature ranges and levels of favourability proposed by Navia et al. (2016) should be changed, according to these results. For example, the levels of favourability for the range of $35 < T \leq 40$ °C should be unfavourable for all relative humidity ranges. A new range between 15 and 20 °C should be proposed for low favourability and another from 10 to 15 °C for unfavourability. The life table parameters and thermal requirements estimated in this study for *R. indica* will be useful to improve the Maxent model. Including information about physiological requirements can improve the reliability of *R. indica* distribution models (Ebeling et al. 2008; Elith et al. 2010, Prasad et al. 2012), also for other countries in South America where their host plants have socioeconomic importance.

According to our results, *R. indica* can develop and has high reproductive rates at low temperatures ($T_b = 14.79$ °C) and relative humidity (ca. 65%). It can be a challenge for the

implementation of biological control programmes, mainly using the most important natural enemy of *R. indica*, *Amblyseius largoensis* (Muma) (Acari: Phytoseiidae) (Carrillo et al. 2012b; Gondim Jr et al. 2012; Moraes et al. 2012; Morais et al. 2016). Temperature would not be a limiting factor for this predator to become established as its minimum temperature for development (Tb) of 13.5 °C is similar to that of *R. indica* (Galvão et al. 2007). This predator does not develop at relative humidity below 72% (Gómez-Moya et al. 2018); therefore, biological control using this natural enemy can be limited during the dry season and in drier regions, such as some parts of northeastern Brazil.

Knowing life table parameters at multiple temperatures and the thermal requirements of *R. indica* can be useful for predicting population growth in the field and consequently for implementing control measures (Fand et al. 2014). However, the model of prediction could further be improved if the effects of rain, relative humidity and fluctuating temperatures were known. The life-history parameters presented here were obtained at constant temperatures, under laboratory conditions; however, in the field, the temperature variation is high and this mite may present fluctuating development and reproductive rates. Therefore, the models of potential distributions for *R. indica* should consider, besides the thermal requirements and presence data, the population dynamics of the mite in the field. Some species distribution models, such as Climex, consider the spatio-temporal dynamics of species in the field and seasonal patterns of favourable climatic conditions and, therefore, produce more accurate models (Silva et al. 2017).

This study is the first to estimate biological parameters for *R. indica* under parthenogenetic reproduction. This species can reproduce by arrhenotokous parthenogenesis, and unfertilized eggs develop into haploid males (Nagesha Chandra and Channa Basavanna 1984). This reproduction strategy enables this mite to easily colonize new areas, e.g. by human dispersion (via infested material), including over long distances or by wind.

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