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Effect of temperature on reproductive parameters and longevity of *Tyrophagus putrescentiae* (Acari: Acaridae)

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Abstract. The effect of temperature on reproductive parameters and longevity of the mold mite, *Tyrophagus putrescentiae* (Schrank) was examined at seven constant temperatures, ranging from 10 to 34 °C, and a relative humidity of 90 ± 5%. Preoviposition period and fecundity were adversely affected by extreme temperatures and the oviposition period increased as temperature was reduced. Different patterns were observed for longevity data for males and females, with greater longevities for males at intermediate temperatures and more similar values for both sexes at extreme temperatures. Polynomial and non-linear models provided a good fit of the relationship of reproductive and longevity parameters with temperature. The effect of temperature on the intrinsic rate of increase of *T. putrescentiae* populations was established by the non-linear Lactin model. The optimum temperature for development was obtained at 30 °C. At this temperature, the population doubling time is 1.75 days. The lower and upper thresholds for *T. putrescentiae* populations were established at 10.4 and 34.8 °C, respectively. Altogether, these data provide basic information to develop sound physical control strategies of the mold mite.

Introduction

The mold mite, *Tyrophagus putrescentiae* (Schrank), is a major stored product pest worldwide due to its wide host range of products (Hughes 1976) and its capacity to produce heavy infestations under favorable conditions. In Spain, this mite is a key pest of dry-cured ham stores (Arnau and Guerrero 1994), particularly in those specializing in traditional Spanish ham, as their mere presence often reduces the saleability of this high value product.

The level of damage caused by mites is related to the size of the population, which, in turn, is depending on how rapidly the population is able to increase in number (Cunnington 1976). The biological parameter commonly used to quantify this feature is the intrinsic rate of natural increase, which depends upon the survival of the individuals in the population, the rate of development of immature stages and the reproductive potential of the adults (Birch 1948). The correct assessment of this parameter is essential to establish the population dynamics of a pest and, therefore, to design a rational pest management

program. Moreover, the intrinsic rate of natural increase could also be used to determine the contribution of the different stages to the overall population.

The importance of predicting the relationship between reproductive parameters of insects and mites and environmental factors has led to the formulation of many mathematical models. Thus, different types of model have been developed, from simple polynomial functions (Lysyk 1998; Tsai and Wang 1999; Wang and Tsai 2000), to more complex models like the Lactin function (Lactin et al. 1995), the Maxima function (Richter and Söndgerath 1990) or the Weibull function (Pinder et al. 1978) to predict life history of pests and implications for their control.

One of the most important abiotic factors influencing the rate of increase of *T. putrescentiae* populations in the dry-cured ham stores is temperature. In a previous work, the effect of this factor on the survival and development of the immature stages of *T. putrescentiae* was already established by comparing the accuracy of different models to describe the relationship between the rate of development and temperature (Sánchez-Ramos and Castañera 2001). Nevertheless, there is little information on the effect of temperature on the reproduction of *T. putrescentiae* (Rivard 1959; Barker 1967) and no attempts have been made to establish thermal population thresholds.

The aim of the present work was to assess the effect of constant temperatures on the reproduction and life history parameters of *T. putrescentiae* as well as to develop simulation models to predict reproductive parameters and its population dynamics.

Material and methods

Mites

A stock culture of *T. putrescentiae* was established from infested samples of dry-cured ham obtained from drying store rooms in Almendralejo (Spain). The mites were maintained on brewers' yeast, and held in cylindrical plastic cages (9 cm diameter and 3 cm height). The cages were covered with round plastic plates having a 3 cm diameter hole in the center sealed with filter paper disks for ventilation. The rearing cages were kept in an environmental chamber (Sanyo MLR-350H, Sanyo, Japan) at 25 ± 0.5 °C and $90 \pm 5\%$ RH and dark conditions, within a watered plastic tray to prevent escaping and to maintain a high humidity. Adults were sexed by observing their secondary sexual characters (Hughes 1976).

Rearing cells described by Barker (1967) were used to carry out the assays. These cells consisted of concavity slides (15–18 mm concavity diameter and 0.5–0.8 mm depth of well) covered with a cover glass (22 × 22 mm) and sealed with a drop of water. Previously, one pair of adults (< 24 h old) was introduced inside each cell, together with a brewers' yeast flake, with the help of a thin camel hair brush.

Adult survival and reproduction

Assays were performed in environmental chambers (Sanyo MLR-350H, Sanyo, Japan) at constant temperatures of 10, 15, 20, 25, 30, 32.5 and 34 °C and 90 ± 5% relative humidity, and complete darkness. At each temperature, the stock cultures were reared for a month prior to the assays to acclimatize them (Fields 1992). To obtain males and females, quiescent tritonymphs were taken out of the acclimatized stock cultures and put inside rearing cells with fresh brewers' yeast flakes. The following day, the new adults were sexed and paired. Seventy pairs were established for each temperature. Eggs laid by each female were counted daily. Periodically, pairs were transferred to new rearing cells before eggs hatched. Daily checking was performed until females died. A stock culture of males was kept from the original quiescent tritonymphs to replace them when they died before the females. At each temperature, the percentage of fertile mating, the preoviposition and oviposition period, the eggs laid per female per day (daily fecundity), the total number of eggs per female (fecundity), and the male and female longevity were estimated. Curves of mean daily fecundity per female were determined. The starting number of fertile females was considered along the oviposition period of the cohort to obtain these curves. Survivorship curves were obtained by using the daily proportion of surviving males and females.

Life table parameters

Adult survival and reproduction data at each temperature were used to calculate the intrinsic rate of natural increase (r_m), the finite rate of natural increase (λ), the net reproductive rate (R_0), the population doubling time (PDT), the mean generation time (T) and the stable age distribution according to Birch (1948). The pre-reproductive period and survival were obtained from a previous work (Sánchez-Ramos and Castañera 2001). The program r_m 2.0 (Taberner et al. 1993) was used to calculate these parameters. This program allows obtaining an estimation of the intrinsic rate of natural increase (r_m) variance by means of a bootstrap resampling method. The number of replicates used was 500 as recommended by Meyer et al. (1986).

Analytical methods

The effect of temperature on the different reproductive and longevity parameters was analyzed by ANOVA. A χ^2 test was performed to assess the effect of temperature on the percentage of fertile mating. The level of significance was $p < 0.05$ in all cases. Analyses were made using Statgraphics Plus (Statgraphics 1997).

Different models were used to fit survival, reproductive parameters and population increase of *T. putrescentiae* with regard to temperature. Models

fitting and parameter estimation were made by using Statgraphics Plus (Statgraphics 1997) and TableCurve 2D (Jandel Scientific 1994).

The best fitted standard polynomial function of the observed data was used to estimate the oviposition period, number of eggs per female per day, total number of eggs per female, and male and female longevity. The general form of these polynomial functions is:

$$y = a_0 + a_1 T + a_2 T^2 + a_3 T^3 + \cdots + a_n T^n$$

where y represents the predicted reproductive or longevity parameter, T is temperature (°C), and a_i are parameters estimated using polynomial regression. The ANOVA of the regression and Student t-tests for each parameter were used as criteria to select the best polynomial function, using a level of significance of $p < 0.05$.

The relationship between the preoviposition period and temperature was best determined by using the following Y-transformed polynomial function selected from the library of TableCurve 2D (Jandel Scientific 1994):

$$1/y = a_0 + a_1 T + a_2 T^2 + a_3 T^3$$

where y is the preoviposition period, T is temperature (°C), and a_0, a_1, a_2 and a_3 are parameters determined using regression analysis.

A Maxima function (Richter and Söndgerath 1990) was used to fit the mean daily fecundity per female at each temperature. The equation is

$$f(t) = \alpha t e^{(-\tau)}$$

where $f(t)$ represents the mean daily fecundity per female, α and τ are parameters, and t is time.

Survival of males and females at each temperature were fitted by a Weibull function (Pinder et al. 1978), whose general form is

$$S(t) = e^{-(t/b)^{\beta}}$$

where $S(t)$ represents the probability of surviving to a given age, b is the parameter that describes the scale, β is the parameter that describes the shape of the curve and t is time.

The modification of the Eq. (6) of Logan et al. (1976) made by Lactin et al. (1995) was used to fit the intrinsic rate of natural increase (r_m) obtained for the different temperatures. The expression of this model is

$$r_m(T) = e^{\rho T} - e^{[\rho T_{\max}(T_{\max} - T)/\Delta]} + \lambda$$

where T is temperature; $r_m(T)$ is the intrinsic rate of natural increase at temperature T; $T_{\max}$ is the supraoptimal temperature at which $r_m(T) = \lambda$; Δ is the range of temperatures between $T_{\max}$ and the temperature at which $r_m(T)$ is maximum; ρ describes the acceleration of the function from the low-temperature threshold to the optimal temperature; parameter λ allows the curve to

intersect the abscissa at suboptimal temperatures and, thus, allows estimation of a lower developmental threshold. It is the asymptote to which the function trends at low temperatures.

The Maxima, Weibull and Lactin functions were fitted by iterative non-linear regression based on Marquardt algorithm (Marquardt 1963).

Results

Adult survival and reproduction

The effect of temperature was highly significant for the different reproductive parameters analyzed (percentage of fertile mating: $\chi^2 = 76.9$; preoviposition period: $F = 372.6$; oviposition period: $F = 74.1$; fecundity: $F = 85.7$; daily fecundity: $F = 182.3$; male longevity: $F = 89.8$; female longevity $F = 47.7$; d.f. = 6 and $p < 0.0001$, in all cases). The percentage of fertile mating was near 100% at temperatures ranging between 15 and 34 °C, while it was reduced to nearly 69% at 10 °C. As temperature increased, the preoviposition period rapidly decreased to reach the lowest value (1.2 days) at 30 °C. Above this temperature, the preoviposition period increased again, though this increase was much less pronounced than at low temperatures (35.7 days at 10 °C). In general, the oviposition period increased with decreasing temperatures, though the longest period was found at 15 °C with nearly 54 days. Fecundity was adversely affected by extreme temperatures, so that the lowest number of eggs was found at 10 and 34 °C. The highest fecundity (≈555 eggs per female) was obtained at 20 °C, but the maximum number of eggs per female per day (≈24 eggs) was recorded at 25 °C, whereas the minimum value (0.7 eggs per female per day) was obtained at 10 °C.

Male and female longevity followed different patterns (Figure 1). Thus, while female longevity increased as temperature decreased, the greatest longevity for males was at 20 °C, with decreasing longevities above and below this temperature, though no significant differences were found for males in the range of temperatures from 10 to 20 °C ($p > 0.05$, Newman–Keuls test). In addition, a two-way ANOVA revealed that males' longevity is significantly greater than that of females ($F = 291.9$; d.f. = 1; $p < 0.0001$), as well as a significant interaction between temperature and sex with regard to longevity ($F = 22.3$; d.f. = 6; $p < 0.0001$). Hence, the difference in longevity between males and females is much greater at intermediate temperatures than at extremes.

The preoviposition period was well fitted by the *Y*-transformed polynomial function selected. The total number of eggs per female, and male and female longevity were well fitted by quadratic regression, while the oviposition period and the number of eggs per female per day were best fitted by linear and cubic regression, respectively (Figure 1).

The Maxima function fitted well the population mean daily fecundity data for all temperatures, with R^2 values greater than 0.91, except for 10 °C, which

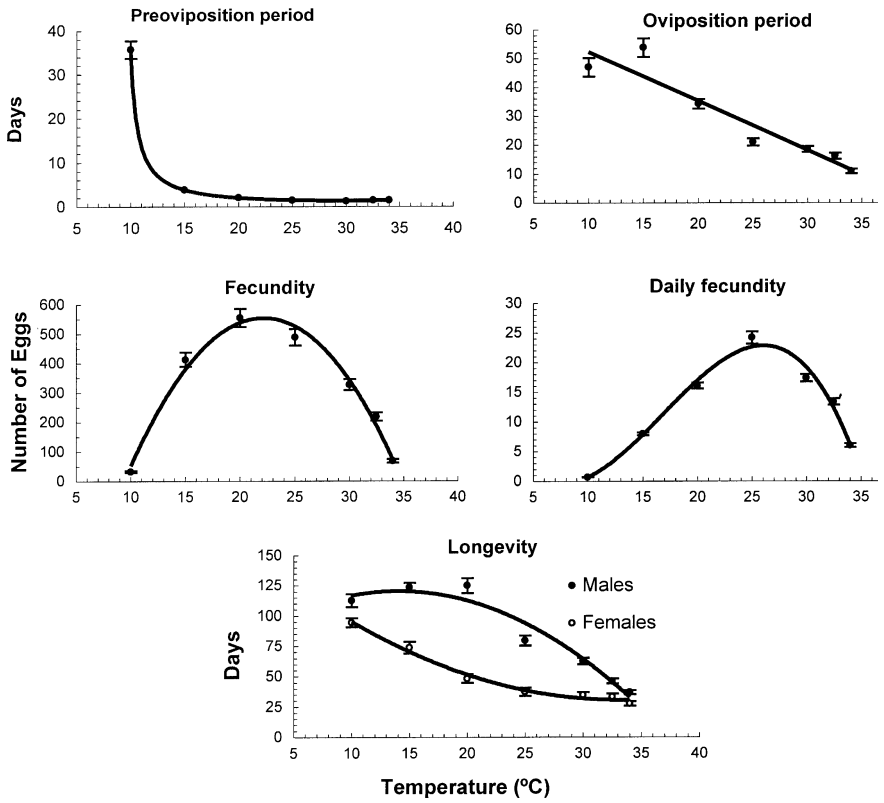

Figure 1. Effects of temperature on preoviposition period, oviposition period, mean number of eggs per female, mean number of eggs per female per day, and male and female longevity of *T. putrescentiae*. R^2 and parameters ± SE for regression lines are: Preoviposition period: $R^2 = 0.9999$; $a_0 = -0.242 \pm 0.140$; $a_1 = 0.0036 \pm 0.0268$; $a_2 = 0.00303 \pm 0.00154$; $a_3 = -0.0000687 \pm 0.0000263$; Oviposition period: $R^2 = 0.8969$; $a_0 = 69.402 \pm 6.532$; $a_1 = -1.706 \pm 0.259$; Fecundity: $R^2 = 0.9822$; $a_0 = -1116.110 \pm 105.530$; $a_1 = 150.939 \pm 10.430$; $a_2 = -3.410 \pm 0.230$; Daily fecundity: $R^2 = 0.9796$; $a_0 = 14.762 \pm 15.438$; $a_1 = -4.407 \pm 2.466$; $a_2 = 0.374 \pm 0.120$; $a_3 = -0.0074 \pm 0.0018$; Males' longevity: $R^2 = 0.9505$; $a_0 = 77.419 \pm 32.169$; $a_1 = 6.151 \pm 3.179$; $a_2 = -0.220 \pm 0.070$; Females' longevity: $R^2 = 0.9863$; $a_0 = 163.476 \pm 11.404$; $a_1 = -8.012 \pm 1.127$; $a_2 = 0.121 \pm 0.025$.

had the lowest R^2 (0.73) (Table 1, Figure 2). The oviposition peaks predicted by this function were at 27, 15, 10, 6, 4, 5 and 3 days for 10, 15, 20, 25, 30, 32.5 and 34 °C, respectively.

The R^2 values obtained by the Weibull distribution for survival were greater than 0.96 for both sexes at all temperatures (Table 2). A differential pattern for males and females was obtained in the range of temperatures studied (Figure 3), being the shape parameter (β) of this function significantly greater for males than for females except for 10 °C, at which this situation is reversed (Table 2).

Table 1. Parameter estimates for the Maxima function describing the mean daily fecundity per female in *T. putrescentiae*.

Temperature (°C)	Parameter estimates		R^2
	$\alpha \pm$ SE	$\tau \pm$ SE	
10	0.0535 ± 0.0035	0.0375 ± 0.0015	0.7305
15	1.7628 ± 0.0538	0.0656 ± 0.0012	0.9457
20	5.8719 ± 0.1889	0.1021 ± 0.0019	0.9631
25	15.1207 ± 0.5013	0.1716 ± 0.0033	0.9782
30	17.2071 ± 0.6174	0.2289 ± 0.0047	0.9785
32.5	10.3945 ± 0.4529	0.2116 ± 0.0053	0.9697
34	7.1154 ± 0.6738	0.3193 ± 0.0175	0.9106

Life table parameters

At 10 °C the r_m was negative, which is an indication that below this temperature *T. putrescentiae* populations tend to disappear (Table 3). At 30 °C the highest r_m (0.397) as well as the lowest mean generation time (12.639) and the lowest population doubling time (1.75 days) were obtained. The Lactin model provided a good fit (R^2 of 0.9982) of the r_m values obtained for the different temperatures, establishing the lower and upper developmental threshold at 10.4 and 34.8 °C, respectively (Figure 4).

Figure 5 shows the stable age distribution estimated for *T. putrescentiae* populations at the range of temperatures where r_m was positive (15 to 34 °C). The adults accounted for a small percentage (4–11%) of the population, whereas the immature stages were the most abundant (89–96%), of which 65–75% were eggs and the rest were mobile stages (15–22%, larvae; 5–8%, protonymphs; and 3–6%, tritonymphs). The overall contribution of immature stages to population density shows a tendency to decrease as the temperature approaches the upper thermal threshold (34.8 °C) predicted.

Discussion

Different predictive models have been used successfully to describe the effect of temperature on different reproductive parameters in insects and mites (Lysyk 1998; Tsai and Wang 1999; Wang and Tsai 2000). Similarly, our results corroborate the high predictability of the relationship between the reproductive parameters of *T. putrescentiae* and temperature. Moreover, our data substantiate that temperature is a key parameter to be considered when estimating the reproductive capacity of the mold mite.

We have found that *T. putrescentiae* performed well within a wide range of temperatures (20–32.5 °C), and the reproductive parameters obtained, as well as the ones predicted by the models, substantiate the results obtained with

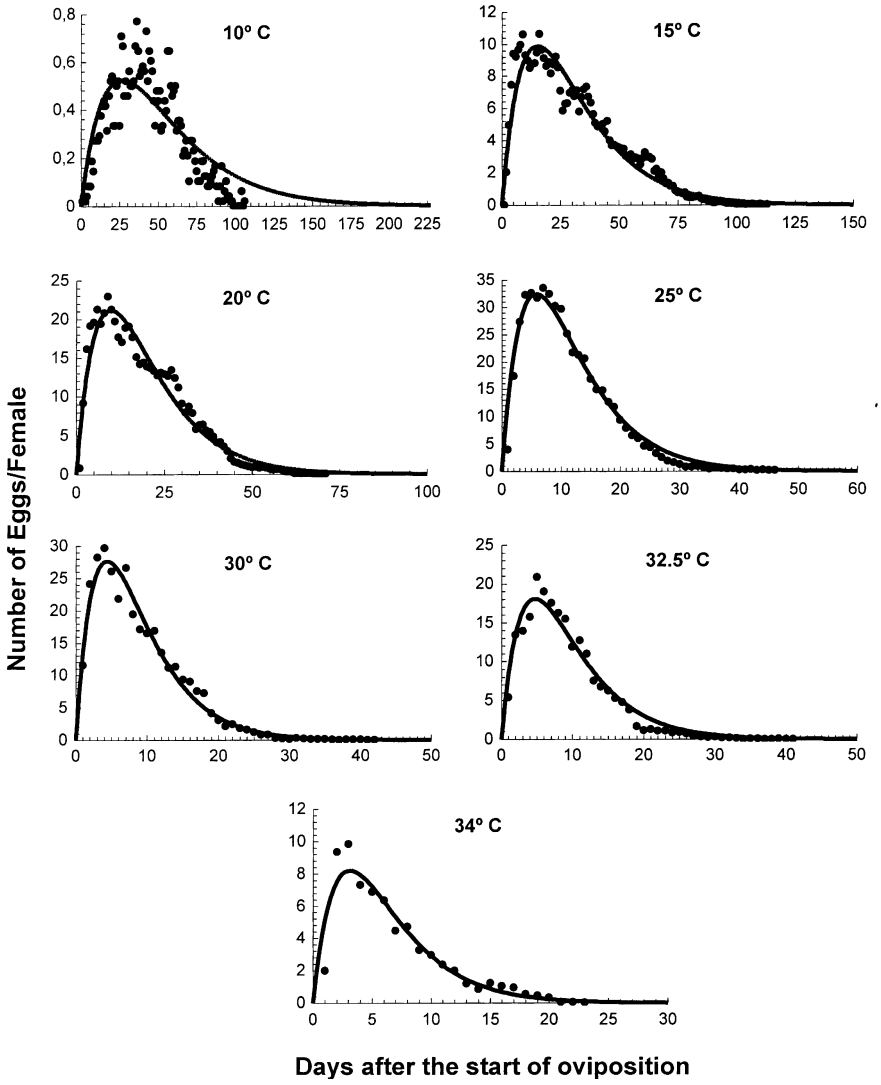

Figure 2. Mean daily fecundities (●) of *T. putrescentiae* and line of best fit by Maxima function (—) at seven constant temperatures.

other species of astigmatid mites (Barker 1967; Cunnington 1985; Arlian et al. 1990). Thus, the mean preoviposition period predicted by the polynomial model is about 30 h at 30 °C and smaller than 2 days above 22 °C and the oviposition period predicted by the linear model was inversely related to temperature. However, reproductive parameters were seriously impaired when temperatures were out of the range mentioned, particularly at 10 °C, which is below the lower developmental threshold of *T. putrescentiae* populations. At

Table 2. Parameter estimates for the Weibull function describing the evolution of survivorship of *T. putrescentiae* males and females at seven constant temperatures (T).

T (°C)	Males			Females		
	b ± SE	$\beta \pm$ SE	R^2	b ± SE	$\beta \pm$ SE	R^2
10	124.2855 ± 0.6354	2.9851 ± 0.0639	0.9821	97.5677 ± 0.3792	5.5716 ± 0.1551	0.9895
15	134.6415 ± 0.5555	6.9685 ± 0.2535	0.9758	88.2296 ± 0.5483	1.5574 ± 0.0251	0.9875
20	143.8753 ± 0.4163	2.6223 ± 0.0286	0.9936	50.8104 ± 0.4486	2.2304 ± 0.0619	0.9826
25	92.0319 ± 0.3905	2.8845 ± 0.0486	0.9914	39.3786 ± 0.6373	1.3400 ± 0.0434	0.9669
30	71.0112 ± 0.2665	3.5641 ± 0.0641	0.9937	39.3247 ± 0.2134	1.9192 ± 0.0289	0.9957
32.5	53.6315 ± 0.4002	3.1338 ± 0.1014	0.9825	39.3892 ± 0.5239	1.6476 ± 0.0571	0.9749
34	42.1220 ± 0.2500	3.1181 ± 0.0787	0.9924	33.0184 ± 0.5073	1.6756 ± 0.0695	0.9713

10 °C the proportion of fertile mating was severely reduced (69%), the pre-oviposition period was expanded about 30-fold in relation to the optimum, and mean daily fecundity was drastically reduced.

The maximum fecundity (555 eggs) was obtained at 20 °C, though the maximum daily fecundity (24 eggs) was recorded at 25 °C, and fit well those predicted by the quadratic regression model. These data suggest that, though the physiological processes involved in egg laying occur best at a specific temperature, the most favorable conditions for the increase of mite populations largely depend on the optimal conditions for daily egg production (Cunnington 1985). However, other factors, such as the duration of the developmental period or the pre-reproductive survival must also be considered in order to accurately establish the optimal temperature for population increase.

In general, the Maxima function well described the patterns of mean daily fecundity of *T. putrescentiae*, with the maximum value reached in an early stage of the population oviposition period. However, at 10 °C, this function failed to accurately describe the daily fecundity probably because this temperature is below the lower developmental threshold predicted. The high rate of fecundity is maintained at all temperatures only for a short period, decreasing rapidly until the oviposition stops. These results are in agreement with those reported for other astigmatid mites such as *Acarus siro* L. (Cunnington 1985), *Dermatophagoides pteronyssinus* (Trouessart) (Arlian et al. 1990), *Rhizoglyphus robini* Claparède (Fashing and Hefele 1991) or *Dermatophagoides farinae* Hughes (Arlian and Dippold 1996).

We have found that *T. putrescentiae* males lived longer than females, with bigger differences observed at the intermediate range of temperatures selected. Similar results have been reported for other species of astigmatid mites with high reproductive potential, such as *R. robini* (Fashing and Hefele 1991) or *A. siro* (Cunnington 1985; Parkinson et al. 1991). This finding could be partially explained by the higher physiological cost of females due to the continuous production of eggs. Additionally, the death of females would allow males to live longer due to a reduction in the metabolic cost associated with

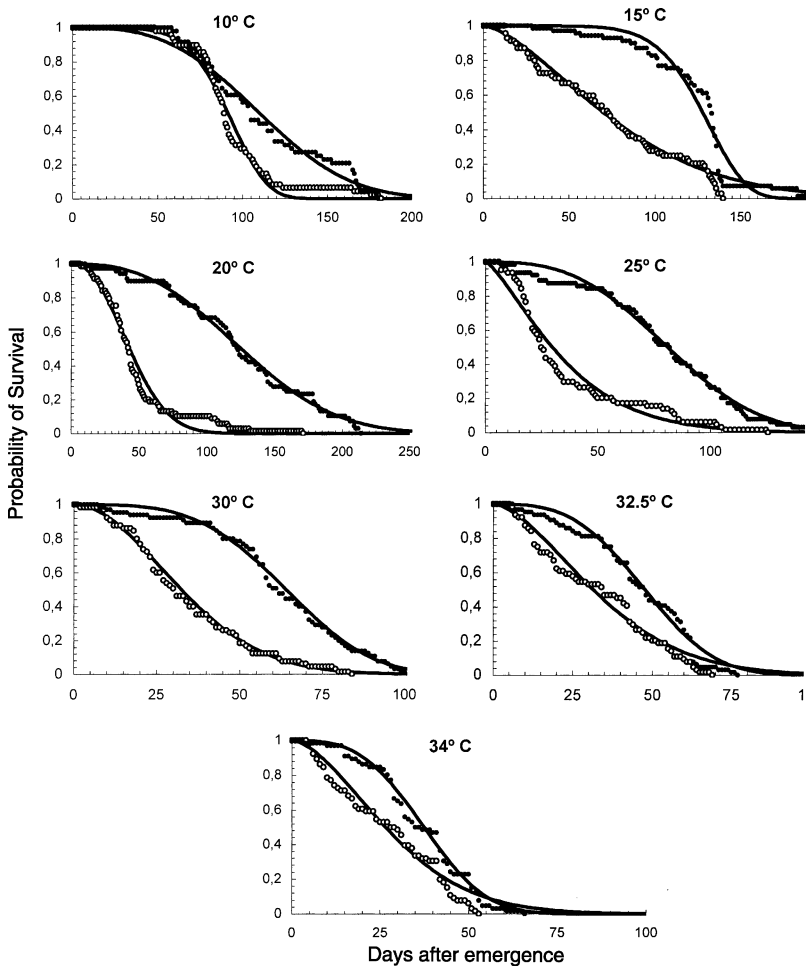

Figure 3. Survival probability of males (●) and females (○) of *T. putrescentiae*, and line of best fit by Weibull function (—) at seven constant temperatures.

Table 3. Life table parameters for *T. putrescentiae* at seven constant temperatures (T).

T (°C)	$r_m \pm$ SE	(95% Cl)[(1)]	λ	R_0	PDT	T
10	-0.0109 ± 0.0007	(-0.0123 to -0.0094)	0.9892	0.1703	–	162.8567
15	0.1008 ± 0.0007	(0.0994 to 0.1023)	1.1061	192.1057	6.88	52.1528
20	0.2052 ± 0.0017	(0.2019 to 0.2086)	1.2278	266.3165	3.38	27.2132
25	0.3189 ± 0.0038	(0.3113 to 0.3265)	1.3756	219.6839	2.17	16.9087
30	0.3970 ± 0.0044	(0.3882 to 0.4057)	1.4873	150.9649	1.75	12.6390
32.5	0.2989 ± 0.0042	(0.2906 to 0.3073)	1.3484	89.0591	2.32	15.0189
34	0.1456 ± 0.0048	(0.1361 to 0.1551)	1.1567	11.9193	4.76	17.0227

r_m: intrinsic rate of natural increase; [(1)] 95% confidence interval for r_m; λ: finite rate of natural increase; R_0: net reproductive rate; PDT: population doubling time (days); T: mean generation time (days).

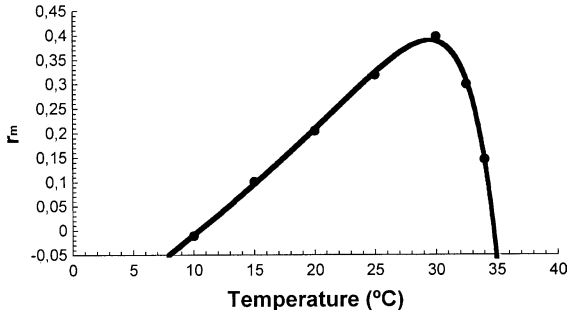

Figure 4. Lactin model for the intrinsic rate of natural increase (r_m) of *T. putrescentiae* as a function of temperature. (●) Observed r_m values; (—) line of best fit by non-linear least squares. $R^2 = 0.9982$. Parameters ± SE for non-linear regression curve: $\rho = 0.0167 \pm 0.0005$; $T_{max} = 37.4285 \pm 0.2754$; $\Delta = 2.3639 \pm 0.2032$; $\lambda = -1.1940 \pm 0.0123$.

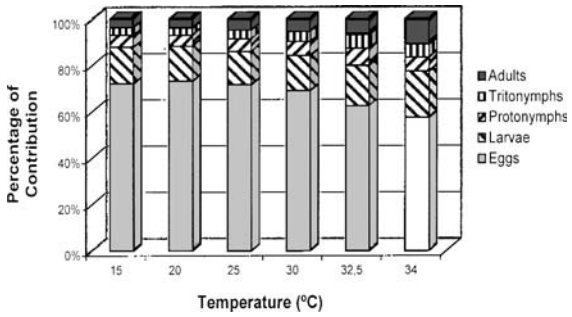

Figure 5. Stable age distribution for *T. putrescentiae* populations at six constant temperatures.

gametogenesis (Parkinson et al. 1991). There are well documented costs of mating in mites. Boczek (1974) found greater longevities for unmated females of *T. putrescentiae* as compared to mated females; Arlian et al. (1990) observed a similar result for *D. pteronyssinus*, in which the unmated females live about 50% longer than mated females; Cunnington (1985) showed that *A. siro* females isolated after the first copulation doubled their longevity as compared to females that remained with a male.

Considering the ideal patterns for the survival curves established by Slobodkin (1962) and their correspondence with the shape parameter (β) from the Weibull function, it was shown that the mortality rate in the case of males increased as they got elder, producing curves near the type I. In contrast, the shape of the curve in the case of females was more similar to type III, so that the rate of mortality was more or less constant along time. These differences in the mortality patterns could be related to the larger reproductive cost of females. The situation obtained at 10 °C was different to that found for the rest of temperatures, probably due to the longer preoviposition period (more than 35 days) registered at this temperature, and to the reduced number of eggs (0.7 per day) laid.

At the optimum temperature (30 °C), we have obtained a r_m value (0.397) higher than the one given by Barker (1967). This difference is due to the lower reproductive capacity observed by this author, but also by the greater mortality recorded for the immature stages. The acclimatization period used may account for the higher survival of the immature stages (Sánchez-Ramos and Castañera 2001) and the higher reproductive capacity reported here. This high r_m would allow *T. putrescentiae* to increase its population more than 9-fold per week at 25 °C, in agreement with the results reported by Cunnington (1976) at similar temperature.

The negative r_m value obtained at 10 °C seems to be related to the reduced fertility and fecundity registered at this temperature but also to the prolongation of the developmental period and to the high mortality of immature stages (Sánchez-Ramos and Castañera 2001). The excellent fitting obtained by the Lactin model (Lactin et al. 1995) allows us to establish accurately the thermal developmental thresholds for *T. putrescentiae* populations. These thermal thresholds were slightly different to those established previously for the development of immature stages of this mite (Sánchez-Ramos and Castañera 2001). Accordingly, the lower developmental threshold predicted is 2–6 °C higher whereas the upper threshold is 1–3 °C smaller. This is due to the fact that the intrinsic rate of increase also considers the mortality of immature and adult stages and the reproductive capacity of adults.

The stable age distribution estimated at the temperatures tested showed a greater number of eggs and a lower number of larvae, nymphs and adults in comparison to the data presented by Barker (1967). Interestingly, the populations of this mite have a high percentage of immature stages, particularly eggs, which suggests the need for developing sampling and control techniques that consider the prevalence of immobile stages in this species.

The population developmental thresholds obtained can be a useful tool for the development of sound physical control strategies of the mold mite as modification of temperature is a common control practice used for stored product pests. Nevertheless, field scale experiments would be needed to assess the feasibility of this control strategy.

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