Reproductive Parameters of the Parthenogenetic Psocid *Lepinotus reticulatus* (Psocoptera: Trogiidae) at Constant Temperatures

G. P. OPIT,[1,2] J. E. THRONE,[1] AND M. E. PAYTON[3]

Environ. Entomol. 39(3): 1004–1011 (2010); DOI: 10.1603/EN10011

ABSTRACT We investigated effects of temperature, at 70% RH, on the reproductive parameters of the parthenogenetic psocid *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae). The lowest fecundity (21) was at 35°C and the highest (41) at 27.5°C. At 22.5, 25, and 27.5°C, peak oviposition rates (eggs/female/week) occurred in week 3 and were 4.7, 6.6, and 7.8, respectively; also 51, 57, and 62%, respectively, of all eggs were laid in the first 4 wk. At 30, 32.5, and 35°C, peak oviposition rates occurred in week 2 and were 8.2, 9.0, and 7.4, respectively; 80, 85, and 98%, respectively, of all eggs were laid in the first 4 wk. The longest preoviposition period (4.4 d) was at 22.5 and 25°C, and the longest postoviposition period (13.1 d) was at 22.5°C. Oviposition period and longevity decreased with increasing temperature; at 22.5°C, these parameters were 66 and 83 d, respectively, and at 35°C, they were 18 and 24 d, respectively. Mean weekly oviposition rate increased with temperature and was highest at 32.5°C (5.8 eggs/female/week). At 22.5, 25, 27.5, 30, 32.5, and 35°C, it took 29, 20, 12, 11, 8, and 6 wk, respectively, for all females to die. Intrinsic rate of population increase increased with temperature until 32.5°C (0.128) and then declined. We have developed temperature-dependent equations for preoviposition period, postoviposition period, oviposition period, oviposition rate, and longevity. Reproductive parameters affect population dynamics, and information on these parameters can be used in simulation models to predict *L. reticulatus* population dynamics to aid in developing effective management strategies.

KEY WORDS stored products, longevity, fecundity, oviposition period, grain

The hot and humid conditions in tropical areas of the world are believed to be responsible for the heavy psocid (Psocoptera) infestations associated with stored cereal grains in these regions (Wang et al. 1998). However, heavy infestation of stored grain by psocids occurs in more temperate regions, such as the United States Midwest, as well (Throne et al. 2006, Opit et al. 2009). These infestations are mostly caused by psocids in the genera *Liposcelis* and *Lepinotus.* Psocid species known to infest stored grain in North America (Mockford 1993, Lienhard and Smithers 2002) are *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae), *Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae), *Liposcelis brunnea* Motschulsky, *Liposcelis corrodens* (Heymons), *Liposcelis decolor* (Pearman), *Liposcelis entomophila* (Enderlein), and *Liposcelis paeta* Pearman. In addition, *Liposcelis rufa* Broadhead has been found infesting wheat stored in steel bins in Stillwater, Oklahoma (G.P.O., unpublished data).

Psocids appear to be an increasing problem in stored grain in all parts of the world (Nayak 2006). In some countries such as Australia, they have now become the most frequently encountered storage pests in some areas (Rees 2003). Resistance of psocids to residual insecticides and the fumigant phosphine (Nayak et al. 1998, Nayak and Collins 2008) and the fact that markets increasingly view psocids as contaminants (Nayak 2006) have contributed to the worldwide rise of psocids to prominence.

In a sampling study conducted in 2004, Throne et al. (2006) found large numbers of only *L. entomophila* and *L. reticulatus* infesting wheat stored in steel bins in Manhattan, Kansas. There have been only a few studies on the biology of *L. entomophila* (Rees and Walker 1990; Leong and Ho 1995; Wang et al. 1998; Mashaya 1999, 2001) and of members of the genus *Lepinotus.* Finlayson (1949) followed the development of eight *Lepinotus patruelis* Pearman eggs to adult eclosion at 25°C and 70% RH; Opit and Throne (2008a) studied the effects of diet on population growth of *L. reticulatus;* and Opit and Throne (2008b) studied the effects of constant temperatures and relative humidities on population growth and development of *L. reticulatus.*

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[1] United States Department of Agriculture–Agricultural Research Service Center for Grain and Animal Health Research, 1515 College Avenue, Manhattan, KS 66502-2736.

[2] Corresponding author: Department of Entomology and Plant Pathology, Oklahoma State University, 127 Noble Research Center, Stillwater, OK 74078-3033 (e-mail: george.opit@okstate.edu).

[3] Department of Statistics, Oklahoma State University, 301 Math Sciences Building, Stillwater, OK 74078-1056.

There are currently no published studies on the effects of temperature on the reproductive parameters of *L. reticulatus,* which is a parthenogenetic species. Reproductive parameters affect population dynamics, and information on these parameters can be used in simulation models to predict *L. reticulatus* population dynamics. Therefore, the objective of the current study is to determine the reproductive parameters of this species over a range of temperatures.

Materials and Methods

Insects. Cultures used in the study were started with insects collected during the summer of 2004 in wheat (*Triticum aestivum* L.) stored in steel bins at the Center for Grain and Animal Health Research (Manhattan, KS). Voucher specimens were deposited in the Kansas State University Museum of Entomological and Prairie Arthropod Research under Lot 181. Psocids were reared on a mixture of 97% cracked hard red winter wheat, 2% Rice Krispies (Kellogg, Battle Creek, MI), and 1% brewer's yeast (wt:wt; referred to as psocid diet below) in 0.473-liter glass canning jars covered with mite-proof lids (Opit and Throne 2008a), and cultures were maintained at 30°C and 70 ± 5% RH.

Obtaining 1- to 2-Wk-Old Adults. A total of 1,200 fourth-instar *L. reticulatus* was transferred from a culture jar to an 800-ml glass jar containing 50 g of cracked wheat. The neck of the jar had a coat of Fluon (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids from escaping. We transferred psocids by first placing 20 g of psocid diet from the culture jars into a 9-cm-diameter petri dish with the wall coated with Fluon. A moist camel hair brush was then used to transfer thirty fourth instars into a 35-mm-diameter petri dish (Greiner Bio-One, Kaysville, UT) before transferring them into the glass jar. This process was repeated until 1,200 nymphs were transferred into the jar. The jar was then placed in an incubator maintained at 30 ± 1°C and 70 ± 5% RH. After 14 d, adult psocids found in the jar were ≈1–2 wk old because fourth instars take 8 d to complete development at 30°C (Opit and Throne 2008b).

Obtaining Freshly Emerged Adults. One gram of colored diet (Opit and Throne 2008b) and 20 particles of cracked wheat were placed in each of thirty 35-mm petri dishes. Thirty 1–2-wk-old adult female psocids were then placed in each petri dish, which had the walls coated with Fluon. The petri dishes were then placed on perforated false floors in two plastic boxes (28 × 19 × 9 cm high), which had saturated NaCl solution below the false floors to maintain 70 ± 5% RH (Greenspan 1977). The boxes were painted black to exclude light and were placed in an incubator maintained at 30 ± 1°C. After 4 d, all the psocids were removed from each petri dish. The colored diet containing eggs in each 35-mm petri dish was transferred to a 9-cm petri dish containing 2.5 g of cracked wheat. During transfer we ensured that the top part of the colored diet in each 35-mm petri dish remained at the top in the 9-cm petri dish to ensure psocids could move freely after hatching. The thirty 9-cm petri dishes were then placed in boxes containing saturated NaCl and held at 30 ± 1°C and 70 ± 5% RH. *L. reticulatus* takes ≈26 d to develop from egg to adult at 30°C (Opit and Throne 2008b), so, after 2 wk, each petri dish was checked daily for adult female psocids. Freshly emerged adult females found were removed and used for determining reproductive parameters of *L. reticulatus.* The date each adult female was removed from a 9-cm petri dish was noted. Adult females are easily distinguished from nymphs because they are darker than nymphs and have a pair of winglets absent in nymphs.

Equilibrating Diet. Five pieces of cracked wheat were placed in each of one hundred and twenty 35-mm petri dishes, which had the walls coated with Fluon. The contents of all petri dishes were then equilibrated at room temperature and 70 ± 5% RH over a 4-wk period before use. Twenty-five grams of colored diet were also equilibrated under the aforementioned conditions. On the day we initiated the daily checking of 9-cm petri dishes for adult females, 20 mg of colored diet was added to each of the 35-mm petri dishes. Colored diet was used to provide a substrate for psocids to lay their eggs. Colored diet was used because it facilitates finding *L. reticulatus* eggs. Twenty petri dishes containing equilibrated diet were placed in each of six plastic boxes (28 × 19 × 9 cm high) containing saturated NaCl below their false floors to maintain 70 ± 5% RH.

Effects of Temperature on Reproductive Parameters. One newly emerged adult female was placed in each 35-mm petri dish containing equilibrated diet; the six plastic boxes, containing newly emerged adults and equilibrated diet, were randomly assigned to one of six incubators set at temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, and 35.0°C. Because adult emergence in the 9-cm petri dishes could not provide all the 120 adult females required to set up all the petri dishes on a single day, care was taken to ensure that a similar number of freshly emerged adults was allocated to each of the six boxes (temperatures) each day until each box received 20 females.

Each petri dish was checked daily until the adult female in it died, and any eggs found were counted and removed each day. When the amount of colored diet in petri dishes was depleted to 30% of the original amount present (as a result of egg removal), 20 mg was added. Replenishment occurred only once. During the checking of petri dishes for eggs, psocid excrement was also removed using a moist brush to keep the petri dishes clean. This experiment had four replications over time.

Data Analysis. The experimental design was a randomized complete block with subsampling. All statistical procedures were accomplished using Statistical Analysis System software (SAS Institute 2001). PROC GLM was used for analysis of variance to determine the effects of temperature on preoviposition period, oviposition period, postoviposition period, longevity, fecundity, and the percentage of total life span spent in oviposition. Data for the first five parameters and

Table 1. Effects of constant temperatures on *Lepinotus reticulatus* preoviposition period (mean ± SE), oviposition period, postoviposition period, longevity, fecundity, and the percentage of adult life span spent in oviposition

Temperature (°C)	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Longevity (d)	Fecundity (eggs/♀)	% life span spent in oviposition
22.5	4.4 ± 0.25	65.5 ± 2.3	13.1 ± 1.24	82.9 ± 2.3	31.7 ± 2.1b	78.5 ± 1.79bc
25	4.4 ± 0.25	48.8 ± 2.3	8.4 ± 1.24	61.6 ± 2.4	38.9 ± 2.1ab	79.4 ± 1.80bc
27.5	3.6 ± 0.23	40.6 ± 2.1	4.4 ± 1.16	48.7 ± 2.2	40.7 ± 2.0a	82.7 ± 1.68ab
30	3.3 ± 0.23	33.2 ± 2.2	3.0 ± 1.17	39.4 ± 2.2	36.4 ± 2.0ab	83.0 ± 1.70ab
32.5	2.8 ± 0.24	30.9 ± 2.2	2.0 ± 1.20	35.6 ± 2.3	39.2 ± 2.0ab	85.0 ± 1.74a
35	2.7 ± 0.23	18.4 ± 2.1	2.8 ± 0.02	23.8 ± 2.2	21.3 ± 2.0c	75.2 ± 1.70c

Analysis of variance results were $F = 5.7$; df = 5, 15; $P = 0.004$ for the preoviposition period; $F = 47.5$; df = 5, 15; $P < 0.001$ for oviposition period; $F = 12.6$; df = 5, 15; $P < 0.001$ for the postoviposition period; $F = 34.5$; df = 5, 15; $P < 0.001$ for longevity; $F = 8.9$; df = 5, 15; $P = <0.001$ for fecundity; and $F = 4.4$; df = 5, 15; $P = 0.012$ for percentage of life span spent in oviposition. We were unable to quantify the relationships between fecundity and percentages of life span spent in oviposition at different temperatures using a biologically meaningful equation, so means within these two columns followed by different letters are significantly different using a least significant difference test.

the percentage of the life span spent in oviposition were transformed using the square-root and arcsine square-root transformations, respectively, to stabilize variances before analysis. Untransformed means and standard errors are reported to simplify interpretation. For the parameters fecundity and percentage of the life span spent in oviposition, we used a least significant difference test to determine differences among numbers of eggs laid and percentages of life span spent in oviposition at different temperatures, despite the quantitative independent variable, because we were not able to quantify the relationships using a biologically meaningful equation. Temperature-dependent equations for preoviposition period, oviposition period, postoviposition period, and longevity were developed by regressing data for each of these parameters against temperature using TableCurve 2D (Systat Software 2002). Weekly survivorship data were subjected to survival analysis using PROC LIFEREG and the Wald χ^2 to test the equality of the survival curves among different temperatures (SAS Institute 2002).

Life Table Parameters. The net reproductive rate (R_o) for each temperature was calculated using age-specific life tables ($R_o = \sum l_x m_x$, where l_x and m_x are age-specific survival rate and fecundity, respectively) (Birch 1948). The generation time (T) for each temperature was calculated by adding development time from egg to adult (Opit and Throne 2008b) to the preoviposition period. The intrinsic rate of increase (r) (Birch 1948) was calculated as follows: $r = \ln(R_o)/T$. The population doubling time, t (Rockwood 2006), was calculated as follows: $t = 0.693/r$.

Results

Numbers of eggs laid during a female's lifetime varied from 21 at 35°C to 41 at 27.5°C; there was no significant difference between fecundity at 27.5°C and at 25, 30, and 32.5°C (Table 1). At 22.5, 25, and 27.5°C, the highest oviposition rates (eggs/female/week) occurred in week 3, and oviposition rates attained were 4.7, 6.5, and 7.9, respectively (Fig. 1). At these temperatures, *L. reticulatus* laid 51, 57, and 62%, respectively, of all eggs in the first 4 wk. At 30, 32.5, and 35°C, the highest oviposition rates occurred in week 2, and oviposition rates attained were 8.2, 9.0, and 7.4, respectively (Fig. 1). At these temperatures, *L. reticulatus* laid 80, 85, and 98%, respectively, of all eggs in the first 4 wk. The steepness of the decline in oviposition rate from the peak rate increased with temperature (Fig. 1). The greatest number of eggs laid was 109 at 30°C; the oviposition period of the psocid that laid these eggs was 44 d. This means eggs were laid at a rate of 2.5 eggs per day (17.5 eggs per week); this was the highest oviposition rate recorded. Mean weekly oviposition rate increased with temperature (Fig. 2; Table 2).

Survival analysis of the weekly survivorship data indicated significant differences among insects exposed to different temperatures (Wald $\chi^2 = 649.9$, df = 1, $P < 0.001$). Survivorship decreased more rapidly with increasing temperature. At 22.5, 25, 27.5, 30, 32.5, and 35°C, it took 29, 20, 12, 11, 8, and 6 wk for all females to die (Fig. 1). For all temperatures except 35°C, the steepest decline in survivorship occurred immediately after the peak oviposition rate had been reached (Fig. 1).

Preoviposition and postoviposition periods generally decreased with increasing temperature (Fig. 3, A and B; Tables 1 and 2). The longest mean preoviposition period (4.4 d) was recorded at 22.5 and 25°C and decreased to 2.7 d at 35°C. The longest mean postoviposition period (13.1 d) was recorded at 22.5°C, and decreased to 2.0 at 32.5°C before increasing to 2.8 d at 35°C.

Oviposition period and longevity also decreased with increasing temperature (Fig. 3, C and D, respectively; Tables 1 and 2). At 22.5°C, these parameters averaged 66 and 83 d, respectively, and at 35°C, they were 18 and 24 d, respectively. The longest life span was 198 d and was recorded at 22.5°C. The percentage of the total life span spent in oviposition increased from 78.5% at 22.5°C to 85.0% at 32.5°C, and then declined to 75.2% at 35°C (Table 1).

Generation time and population doubling time declined with temperature until 32.5°C and then increased (Table 3). Intrinsic rate of population increase increased with temperature until 32.5°C (0.128 offspring per individual per day) and then declined (Table 3). The net reproductive rate increased with temperature until 27.5°C (35.67 offspring per individual in

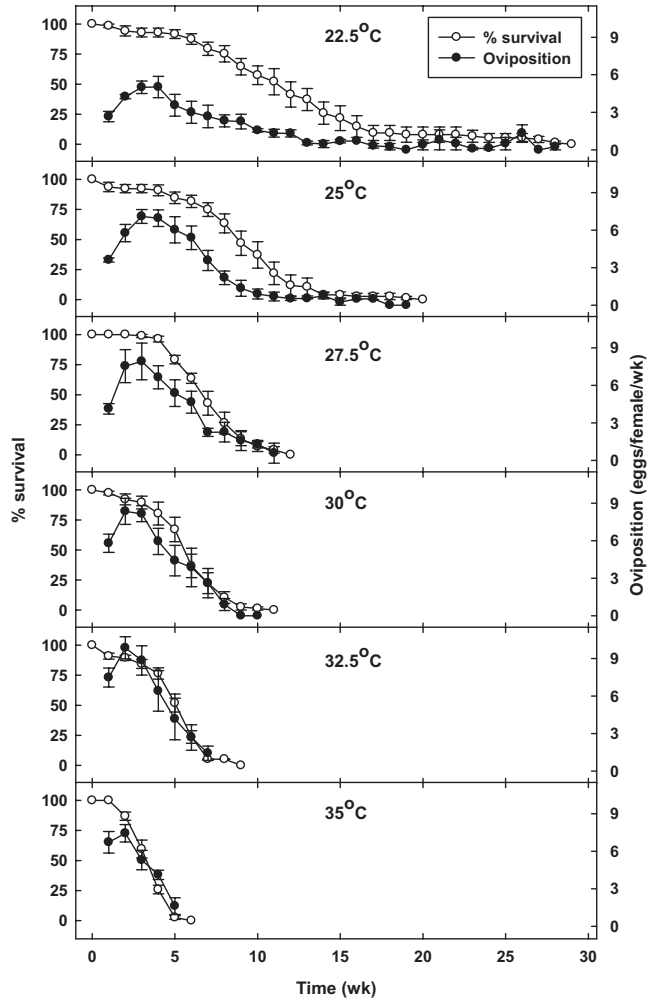

Fig. 1. Oviposition and survival of *L. reticulatus* at constant temperatures.

a lifetime) and then declined (Table 3). Quadratic equations described the relationship between temperature and intrinsic rate of population increase, net reproductive rate, generation time, and population doubling time well (Table 4).

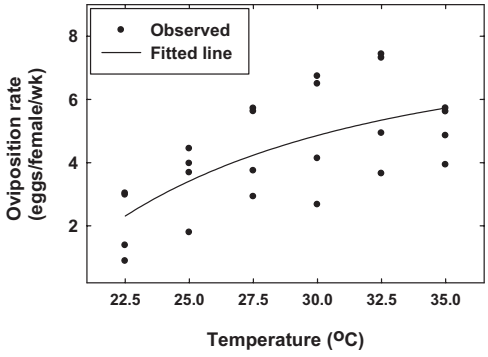

Fig. 2. Oviposition rate of *L. reticulatus* at constant temperatures. Parameters for the fitted line are in Table 2.

Discussion

All reproductive parameters varied with temperature. Intrinsic rate of population increase for *L. reticulatus* increased with temperature until 32.5°C (0.128) and then declined. If the intrinsic rate of increase at 32.5°C is considered the optimal fitness of 1, then the fitness of *L. reticulatus* at 22.5, 25, 27.5, 30, and 35°C equals 0.52, 0.70, 0.84, 0.87, and 0.84, respectively. Highest intrinsic rates of increase for *Liposcelis badia* Wang, Wang, and Lienhard (Jiang et al. 2008), *L. bostrychophila* (Wang et al. 2000), *L. decolor* (Tang et al. 2008), *L. paeta* (Wang et al. 2009), and *Liposcelis tricolor* Badonnel (Dong et al. 2007) occurred at 27.5, 30, 32.5, 32.5, and 30°C, respectively. Intrinsic rates of increase at these temperatures were 0.0455, 0.0946, 0.0609, 0.0542, and 0.0367, respectively. At optimal

Table 2. Parameters describing the effects of constant temperatures on *Lepinotus reticulatus* preoviposition period, oviposition period, postoviposition period, oviposition rate, and longevity

Subject	Maximum R^2	R^2	F	a	b	c
Preoviposition period	0.43	0.38	13.7	1.39 ± 0.60	1,646.19 ± 444.30	-
Oviposition period	0.90	0.87	152.7	−8.33 ± 4.05	36,971.45 ± 2,992.18	-
Postoviposition period*	0.56	0.49	13.1	120.36 ± 40.19	−7.30 ± 2.84	0.11 ± 0.05
Oviposition rate	0.49	0.45	17.7	8.14 ± 0.95	−2,951.27 ± 701.70	-
Longevity	0.87	0.86	134.1	−13.76 ± 5.64	48,203.12 ± 4,162.70	-

In the case with an asterisk (*), df = 2, 21; equation is of the type $y = a + bx + cx^2$ with an adjusted R^2 value. In all other cases, df = 1, 22; equation is of the type $y = a + b/x^2$. In all cases, $P < 0.01$. Lack-of-fit P values for preoviposition period, oviposition period, postoviposition period, oviposition rate, and longevity were 0.42, 0.79, 0.99, 0.86, and 0.86, respectively.

temperatures for intrinsic rate of increase, *L. reticulatus* has the highest potential for population growth among these psocid species.

Fecundity was highest at 27.5°C, but fecundity at this temperature did not differ from that at 25, 30, and 32.5°C. Fecundity at 25, 30, and 32.5°C did not differ from that at 22.5°C. This is quite surprising and suggests that *L. reticulatus* is adapted to surviving in cool climates. The lowest fecundity was at 35°C, which may indicate the adverse effects of high temperatures on *L. reticulatus* and why it is not more prevalent in warmer regions of the world. Our data also show that the intrinsic rate of increase declines from 0.128 at 32.5°C to 0.107 at 35°C. The negative effects of high temperatures on *L. reticulatus* were also shown by Opit and Throne (2008a). They found that populations of *L. reticulatus* increased from 22.5 to 32.5°C at 75% RH. However, a temperature of 35°C resulted in retarded population growth and suggests this temperature has a detrimental effect on the survival and reproduction of *L. reticulatus.* Retarded population growth may partly be explained by the fact that only 9% of eggs that hatch develop into adults at 35°C (Opit and Throne 2008a). It is possible that the lack of heat-inducible proteins in *L. reticulatus* may be responsible for the adverse effects of high temperatures on this species (Guedes et al. 2008).

As expected, oviposition period was longer, and the percentage of eggs laid in the first 4 wk was less at lower temperatures than at higher temperatures. This observation may be explained by the fact that the physiological processes of converting resources to eggs and of egg maturation are quite temperature dependent (Berger et al. 2008). Reproduction peaks for *L. bostrychophila* (Wang et al. 2000), *L. tricolor* (Dong et al. 2007), *L. badia* (Jiang et al. 2008), *L. decolor* (Tang et al. 2008), and *L. paeta* (Wang et al. 2009) also occurred earlier with increasing temperature. Wang et al. (2000) also found that oviposition peaks for *L. bostrychophila*, which is also usually a parthenogenetic species (the first males were just

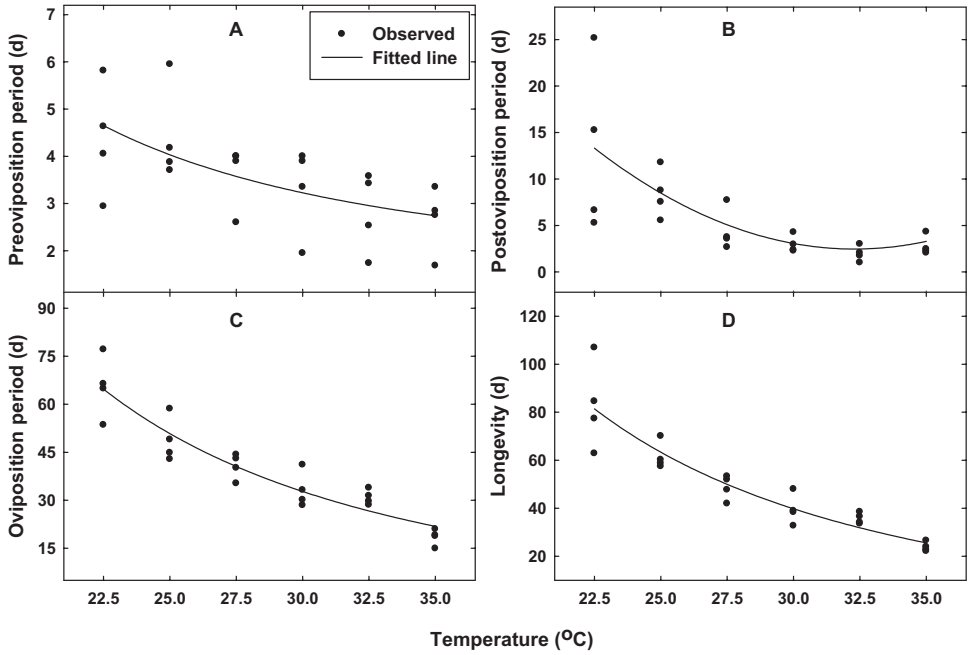

Fig. 3. Preoviposition, postoviposition, and oviposition periods and longevity of *L. reticulatus* at constant temperatures. Parameters for the fitted lines are in Table 2.

Table 3. Life table parameters (mean ± SE) of *Lepinotus reticulatus*

Temperature (°C)	*N*	*r*	R_o	*T*	*t*
22.5	73	0.066 ± 0.002	26.07 ± 2.50	49.0	10.5 ± 0.35
25.0	73	0.090 ± 0.005	33.68 ± 5.76	38.7	7.7 ± 0.41
27.5	77	0.108 ± 0.005	35.67 ± 5.37	32.7	6.4 ± 0.32
30.0	76	0.111 ± 0.004	27.09 ± 3.18	29.6	6.3 ± 0.21
32.5	77	0.128 ± 0.007	28.39 ± 4.75	25.7	5.4 ± 0.29
35.0	77	0.107 ± 0.004	16.26 ± 1.47	26.1	6.5 ± 0.23

N, no. females in the analysis; *r*, intrinsic rate of population increase; R_o, net reproductive rate; *T*, generation time (d); and *t*, population doubling time (d).

recently found]Mockford and Krushelnycky 2008]), appeared 2–3 wk after the initiation of oviposition.

L. reticulatus, *L. tricolor* (Dong et al. 2007), and *L. paeta* (Wang et al. 2009) produce the largest numbers of eggs at 27.5°C, whereas *L. bostrychophila* (Wang et al. 2000) produces the largest number of eggs at 27.5 and 30°C and *L. decolor* (Tang et al. 2008) at 32.5°C. At these optimal temperatures, *L. reticulatus*, *L. tricolor*, *L. bostrychophila*, *L. paeta*, and *L. decolor* produce 41, 54, 75, 108, and 130 eggs, respectively. It is noteworthy that at 35 and 37.5°C, *L. decolor* produces on average 74 and 25 eggs, respectively, and *L. paeta* produces 102 and 20 eggs, respectively. For these small (1 mm long), soft-bodied insects to produce such a large number of eggs at these high temperatures is quite remarkable and indicates an adaptation to warm climates. *L. badia* only produces an average of 19, 30, 18, and 15 eggs at 27.5, 30, 32.5, and 35°C, respectively, but produces the largest number of eggs (52) at 20°C (Jiang et al. 2008). Therefore, based on fecundity alone, the order of increasing adaptation to warm climates for these psocids is *L. badia*, *L. reticulatus*, *L. tricolor*, *L. bostrychophila*, *L. decolor*, and *L. paeta.* At the optimal egg-laying temperatures, the average lifetime fecundities of *L. bostrychophila*, *L. paeta*, and *L. decolor* are higher than those of *L. badia*, *L. reticulatus*, and *L. tricolor;* coupled with this, the first group can lay on average 52, 50, and 65 eggs, respectively, at the low temperature of 20°C. These two facts may explain why *L. bostrychophila*, *L. decolor*, and *L. paeta* are much more serious pests of stored products worldwide compared with *L. badia*, *L. reticulatus*, and *L. tricolor.* The fecundity of *L. reticulatus* is also probably lower than that of *L. entomophila* based on a study by Opit and Throne (2008a), which showed that the maximum number of progeny produced by five *L. reticulatus* females in 32 d at 30°C on a diet of cracked wheat was 115, whereas *L. entomophila* produced 502.

L. reticulatus and *L. bostrychophila* are parthenogenetic (other than a few male *L. bostrychophila* recently found, as noted above), whereas *L. decolor*, *L. paeta*, *L. tricolor*, and *L. badia* are known from both sexes. As noted above, fecundity at optimal temperatures for the two parthenogenetic species is 41 and 75, respectively, and for the nonparthenogenetic species is 130, 108, 54, and 52, respectively. Thus, whether there is a cost to parthenogenesis in these species is unclear. Costs of parthenogenesis in other invertebrates are also sometimes unclear. For example, there was no difference in fecundity of sexuals and parthenogens of the freshwater snail, *Campeloma limum* (Anthony), at one location, whereas the parthenogens were more fecund at another location (Crummett and Wayne 2009). However, parthenogenetic dragonflies of the species *Ischnura hastata* (Say) (Odonata: *Coenagrionidae*) are more fertile than sexual females (Lorenzo Carballa and Cordero Rivera 2007). Parthenogenesis and other reproductive abnormalities in psocids and other organisms may be associated with presence of *Wolbachia* (Werren et al. 2008), and removing the *Wolbachia* can lower fecundity (Dong et al. 2006).

Compared with stored-product beetle pests, *L. reticulatus* and other aforementioned psocid species produce fewer eggs. For example, *Rhyzopertha dominica* (Fabricius) (Coleoptera: Bostrichidae) and *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) produce 400 eggs in a lifetime of 3 mo; *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) produces up to 1,000 eggs in a lifetime of a few months (Pedersen 1992, Rees 2004). Throne (1994) showed that a maize weevil female, *Sitophilus zeamais* Motschulsky, can lay as many as 6.7 eggs per day at optimal conditions. However, psocids appear to compensate for their low egg production by having higher intrinsic rates of increase. For example, the intrinsic rate of increase of *L. reticulatus* at 25°C is 0.09, whereas that of *T. castaneum* ranges between 0.005 and 0.025 (Pimentel et al. 2006). This may explain why much larger psocid populations are found infesting stored products compared with beetles.

We found that *L. reticulatus* oviposition period and longevity declined with increasing temperature. A possible explanation for this may be that the higher egg maturation rates that occur at higher temperatures are associated with an overall higher metabolism that could reduce the life span (Papaj 2000, Jervis et al.

Table 4. Parameters (mean ± SE) for quadratic equations describing the effects of constant temperatures on *Lepinotus reticulatus* intrinsic rate of population increase (*r*), net reproductive rate (R_o), generation time (*T*), and population doubling time (*t*)

Subject	Maximum R^2	Adjusted R^2	*F*	A	b	c
Intrinsic rate of increase	0.86	0.76	40.1	−0.53 ± 0.11	0.04 ± 0.008	−0.0007 ± 0.0001
Net reproductive rate	0.43	0.27	6.1	−182.31 ± 86.27	15.83 ± 6.1	−0.29 ± 0.11
Generation time*	1.00	0.99	221.4	228.05 ± 20.19	−11.96 ± 1.43	0.18 ± 0.02
Population doubling time	0.90	0.86	74.3	64.23 ± 6.91	−3.74 ± 0.49	0.06 ± 0.008

In the case with an asterisk (*), df = 2, 3; in all other cases, df = 2, 21. In all cases, $P < 0.01$. Lack-of-fit *P* values for intrinsic rate of population increase, net reproductive rate, and population doubling time were 0.07, 0.59, and 0.21, respectively.

2005). At higher temperatures, they may also be allocating significantly more energy resources to egg production than maintenance of body functions, thereby resulting in reduced performance and survival (Papaj 2000; Carey 2001; Jervis et al. 2005, 2007). It is plausible that at 22.5 and 35°C, *L. reticulatus* has a proportionately shorter egg-laying period than at optimal temperatures because of the diversion of resources from egg production and maturation that may occur at these suboptimal temperatures. In fact, this may explain why the percentage of the total life span spent in oviposition increased from 78.5% at 22.5°C to 85.0% at 32.5°C and then declined to 75.2% at 35°C. Decline in oviposition period with temperature has also been shown in *L. badia* (Jiang et al. 2008), *L. decolor* (Tang et al. 2008), and *L. paeta* (Wang et al. 2009). Similarly, longevity has been shown to decline with temperature in *L. badia*, *L. tricolor* (Dong et al. 2007), *L. decolor*, and *L. paeta.* Contrary to what is observed for other species, longevity of *L. bostrychophila* increased with temperature from 20°C until 30°C and then declined (Wang et al. 2000). At 20°C, *L. decolor*, *L. paeta*, and *L. tricolor* lived for exceptionally long periods of 102, 102, and 262 d, respectively, compared with other psocids.

We found postoviposition periods for temperatures of 22.5, 25, and 27.5°C to be longer than preoviposition periods; at temperatures of 30, 32.5, and 35°C, they were either similar or shorter. Preoviposition period declined with temperature most probably because of already stated reasons related to resource allocation, egg production, and egg maturation. Postoviposition also showed the same trend, except there was an increase in the postoviposition period at 35°C for the same reasons. Unlike Wang et al. (2000), who found that all *L. bostrychophila* adults died within 1 wk after cessation of oviposition, we found this period to be 13 and 8 d at 22.5 and 25°C, respectively, in *L. reticulatus.* Unlike what we observed for *L. reticulatus*, preoviposition period declined with temperature before increasing in *L. badia*, *L. bostrychophila*, *L. decolor*, and *L. tricolor*; the trend for *L. paeta* was similar to that of *L. reticulatus.* At 20°C, *L. tricolor* has an exceptionally long preoviposition period of 70 d (Dong et al. 2007).

Our work has shown that *L. reticulatus* has a higher intrinsic rate of increase compared with other psocid species. It also oviposits over a wide temperature range of 22.5–32.5°C, but the greatest numbers of eggs are laid at 27.5°C. *L. reticulatus* appears to be adversely affected by temperatures ≥35°C and may, therefore, be a problem only in cooler climates. We have also shown that *L. reticulatus* adults can live for 2–3 mo at temperatures of 22.5 and 25°C. Finally, we have developed temperature-dependent equations for preoviposition period, postoviposition period, oviposition period, and longevity, which can be used in simulation models to aid in developing more effective management strategies.

Acknowledgments

We thank Ann Redmon and Jordan Duff for their technical support, and Richard Grantham, Justin Talley, Raul Guedes, and Jin Jun Wang for reviewing an earlier draft of this manuscript. In addition, we extend our appreciation to Edward Mockford, who confirmed the identity of *L. reticulatus*, and the Oklahoma Agricultural Experiment Station for partial support.

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Received 9 January 2010; accepted 5 March 2010.