

Effects of Constant Temperatures on Reproductive Parameters of the Psocid *Liposcelis rufa* (Psocoptera: Liposcelididae)

Gautam SG, Opit GP* and Giles KL

Department of Entomology and Plant Pathology, Oklahoma State University, 127 Noble Research Center, Stillwater, OK 74078-3033, USA

Abstract

The effects of eight temperatures on the reproductive parameters of the psocid *Liposcelis rufa* Broadhead (Psocoptera: Liposcelididae) were investigated at 75% RH. Peak oviposition rates (eggs/female/wk) at temperatures of 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C were 5.9, 7.7, 10.6, 13.7, 14.7, 15.4, 13.8, and 8.9, respectively. At these temperatures, *L. rufa* laid 49, 58, 64, 71, 86, 89, 94, and 94%, respectively, of the total number of eggs in the first 4 wks. The predicted overall oviposition rate or mean number of eggs laid by each female per wk over its lifetime increased with temperature and was highest at 38.3°C (3.82 eggs/female/wk). The longest preoviposition and postoviposition periods were observed at 22.5°C and were 4.4 d and 79.6 d, respectively. Oviposition period and longevity decreased with increasing temperature - at 22.5°C, these parameters were 145 and 229 d, respectively; and at 40°C, they were 26 and 36 d, respectively. The longest-lived individuals lived for 59, 47, 35, 22, 15, 17, 12, and 9 wk at 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C, respectively. Intrinsic rate of population increase increased with temperature until 32.5°C (0.18) and then declined. The temperature-dependent equations that we have developed for preoviposition period, postoviposition period, oviposition period, oviposition rate, fecundity, longevity, and percentage of life spent in oviposition can be used in simulation models to predict *L. rufa* population dynamics for the development of effective management strategies.

Keywords: Stored products; Longevity; Fecundity; Oviposition period; Stored grain

Stored-product psocids (Psocoptera) have developed a close association with man, his dwellings, and food storage facilities [1]. As a consequence, there have been consumer complaints related to psocids in some sectors of the food industry for the last 50 yrs [2]. In some countries such as Australia, they have now become the most frequently encountered storage pests in some areas [3]. Previously psocids were only considered as nuisance pests with very low economic importance, partly due to their small size and because of the limited information that was available on their ecology [4]. The relative importance of psocids as stored-product pests has arisen from their differential response to commonly used residual insecticides and the fumigant phosphine [5-7]. This has led to limited success in effectively controlling them where they occur. Psocids can cause significant weight losses of up to 10% in stored grains by feeding [8]. They also deteriorate the quality of stored-products due to the presence of extremely large numbers of live and dead insects and by the production of exuviae and feces [8]. Psocids actively spread fungal pathogens thereby making them a human health threat [9,10]. However, the fact that markets now view psocids as contaminants has significantly contributed to their recognition as stored-product pests worldwide [11].

In a study conducted in a feed mill (G.P.O., unpublished data) and an animal feed warehouse [12] in Stillwater, OK, USA, six and seven species of psocids, respectively, were found infesting these facilities. Species found in the feed mill were *Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae), *Liposcelis decolor* (Pearman), *Liposcelis entomophila* (Enderlein), *Liposcelis pearmani* Lienhard, *Liposcelis rufa* Broadhead, and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae); all the aforementioned species plus *Liposcelis paeta* Pearman were found infesting the animal feed warehouse. In order of decreasing abundance, *L. decolor*, *L. bostrychophila*, *L. reticulatus*, and *L. rufa* were the four most abundant species in the feed mill. Similarly, the order of abundance in the animal feed warehouse was *L. decolor*, *L. bostrychophila*, *L. entomophila*, and *L. rufa*. Large numbers of *L. rufa*, *L. decolor*, and *L. entomophila* have also been found infesting steel

bins containing wheat at the Stored Product Research and Education Center (SPREC), Stillwater, OK [13]. In these bins, *L. rufa* was second to *L. decolor* in abundance. Prior to the report by Gautam et al. [13], *L. rufa* had also been reported from Hawaii (USA) on litter and pitfall trap samples [14], and on imported wood in Australia [15], but not on stored grain. However, it has been reported on stored rice in Portugal [16] which suggests that *L. rufa* may actually be a much more serious pest of stored commodities than is currently recognized.

In order to effectively manage *L. rufa* in food storages where its population growth is prolific, sound knowledge of its ecology is required. Gautam et al. [13] investigated the effects of temperature and relative humidity on *L. rufa* population growth and development. That study showed populations of *L. rufa* increased under conditions of 22.5 to 30°C at 55% RH and 22.5 to 40°C at 75% RH; and population growth at 32.5 and 37.5°C at 75% RH were similar. At 35 and 37.5°C and 75% RH, *L. rufa* population increased by 73- and 60-fold, respectively, over a period of 30 d. In addition, female *L. rufa* were shown to have two to five instars and temperature-dependent developmental equations for male and female eggs, individual nymphal, combined nymphal, and combined immature stages were developed. However, there are currently no published studies on the effects of temperature on reproductive parameters of this pest. Information on how temperature affects reproductive parameters can be used in simulation models to

*Corresponding author: George P Opit, Department of Entomology and Plant Pathology, Oklahoma State University, 127 Noble Research Center, Stillwater, OK 74078, USA, Tel: 405-744-9408; Fax: 405-744-6039; E-mail: george.opit@okstate.edu

Received November 15, 2011; Accepted March 22, 2012; Published March 24, 2012

Citation: Gautam SG, Opit GP, Giles KL (2012) Effects of Constant Temperatures on Reproductive Parameters of the Psocid *Liposcelis rufa* (Psocoptera: Liposcelididae). Entomol Ornithol Herpetol S1:002. doi:10.4172/2161-0983.S1-002

Copyright: © 2012 Gautam SG, et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

predict population dynamics under different environmental conditions. Therefore, the objective of the present study was to determine the effects of temperatures on reproductive parameters of *L. rufa*.

Materials and Methods

Insects

Cultures used in this study were started with insects collected from steel bins containing wheat (*Triticum aestivum*) located at the Stored Product Research and Education Center, Stillwater, OK. Voucher specimens of 100 male and female *L. rufa* preserved in 95% ethyl alcohol that were used for this study were deposited at K. C. Emerson Entomology Museum at Oklahoma State University under lot numbers 100 (males) and 101 (females). Psocids were reared on a mixture of cracked hard red winter wheat, rice krispies (Kellogg Company, Battle Creek, MI), and wheat germ (93, 5, and 2% wt/wt: referred to as psocid diet hereafter) in 360-ml glass canning jars with mite-proof lids [17]. The inner top one-third portion of the glass jar was coated with Fluon® (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids from gathering on the lids. The cultures were maintained at $30 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH.

Obtaining 1- to 2-week-old adults

One to two-wk-old female *L. rufa* were obtained by placing 0.5 g of colored psocid diet [18], five particles of cracked wheat, 20 mg of wheat germ, and 30 adult females from our cultures in each of two hundred 35-mm-diameter Petri dishes (Greiner Bio-One, Kaysville, UT). Females are easily distinguishable from males because they are much larger. The inner walls of the Petri dishes were coated with Fluon® to prevent psocids from escaping. Colored diet was used as substrate for laying eggs because *L. rufa* prefers laying on and among diet particles, which makes it easier to determine if adequate numbers of eggs are being laid for the experiment. The Petri dishes were placed on false floors in four Rubbermaid plastic boxes (37 x 22 x 13 cm) which contained saturated NaCl beneath their false floors to maintain $75 \pm 5\%$ RH [19]. The plastic boxes used for the experiment were painted black to exclude light and mimic dark conditions in which *L. rufa* is usually found. The boxes were then kept in $30 \pm 1^\circ\text{C}$. After 7 d, all live females from each Petri dish were removed using a moist camel's-hair brush and the contents of 50 Petri dishes were poured in a 360-ml glass jar containing 80 g of psocid diet. The inner top one-third portion of each jar was coated with Fluon® and closed using a mite proof lid. The jars were returned to the incubator ($30 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH). After 30 d, adult psocids found in the jars were approximately 1-2 wk old [13].

Obtaining freshly emerged adults

Freshly emerged females for the experiment were obtained by placing 0.5 g of colored psocid diet, five particles of cracked wheat, 20 mg of wheat germ, and thirty 1- to 2-wk-old females in each of sixty 35-mm Petri dishes. The inner walls of the Petri dishes were coated with Fluon® to prevent psocids from escaping. The Petri dishes were then placed on perforated false floors in two plastic boxes (37 x 22 x 13 cm) which contained saturated NaCl solution beneath the false floors to maintain $75 \pm 5\%$ RH and were kept in an incubator maintained at $30 \pm 1^\circ\text{C}$. After 7 d, all live psocids were removed from each Petri dish using a moist camel's-hair brush. The colored diet containing eggs in each 35-mm Petri dish was transferred to a 9-cm Petri dish containing 20 pieces of cracked wheat. Transfer was done in such a way that the top part of the colored diet in each 35-mm Petri dish remained at the top in a 9-cm Petri dish to ensure psocids could move freely after hatching. Sixty 9-cm Petri dishes containing colored diet with psocid

eggs were then placed in a box (42 x 29 x 24 cm) containing saturated NaCl beneath the false floor to attain $75 \pm 5\%$ RH and held at $30 \pm 1^\circ\text{C}$. *L. rufa* females take approximately 25 d to develop from egg to adult at 30°C [13]. Therefore, after 10 d, each Petri dish was checked daily for freshly emerged adults. Freshly emerged adult females found were removed and used for determining reproductive parameters. The date each adult female was removed from a 9-cm Petri dish was noted. Adult females are easily distinguished from nymphs using body color - adults are brownish (darker colored) whereas nymphs are pale yellowish in color.

Diet equilibration

Five pieces of cracked wheat were placed in each of one hundred and sixty 35-mm Petri dishes whose inner walls were coated with Fluon®. The contents of all Petri dishes were then equilibrated at room temperature and $75 \pm 5\%$ RH over a 4-wk period before use. Fifty grams of colored diet were also equilibrated under the aforementioned conditions. On the day daily checking of 9-cm Petri dishes for freshly emerged adult females was initiated, 20 mg of colored diet were added to each of the 35-mm Petri dishes. Freshly emerged females were transferred from 9-cm Petri dishes to 35-mm Petri dishes with equilibrated diet; each 35-mm Petri dish received a single female. A single freshly emerged male was also placed in each 35-mm Petri dish with the freshly emerged female. The 20 mg of colored diet in each Petri dish provided a substrate for psocids to lay eggs. Petri dishes containing pairs of psocids were randomly assigned to each of eight plastic boxes (37 x 22 x 13 cm) containing saturated NaCl beneath the false floors.

Effects of temperature on reproductive parameters

The eight plastic boxes, containing 35-mm Petri dishes with pairs of newly emerged adult male and female *L. rufa* and equilibrated diet, were randomly assigned to one of eight incubators set at temperatures of 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C . Because adult emergence in the 9-cm Petri dishes could not provide all 160 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 adult females were allocated to each of the eight boxes (temperatures) each day until every box received 20 females. After each box received 20 females, all the adult males in the 9-cm Petri dishes were transferred to a single 9-cm Petri dish containing 15 g of red colored diet and 2.5 g of cracked wheat and were kept at $30 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH. This was done to ensure that the males used for replacement of dead or lost males (paired with females) during the course of the experiment were of similar age. However, loss or death of males seldom happened during the experiment.

Each Petri dish containing a pair of psocids was checked daily under a stereomicroscope (Stemi 2000-C, Carl Zeiss, Thornwood, NY) until the adult female in it died. During checking, any eggs found were counted and removed using a moist camel's-hair brush. When the amount of colored diet in a Petri dish was depleted to 30% of the original amount present (due to egg removal), 20 mg were added. However, addition of colored diet seldom happened. In order to keep the Petri dishes clean, psocid feces were removed using a moist camel's-hair brush during the checking of the Petri dishes for eggs.

Data analysis

The experiment had three temporal replications and the experimental design used was randomized complete block (RCBD) with sub sampling. All statistical procedures were accomplished using Statistical Analysis System software [20]. PROC GLM was used for analysis of variance (ANOVA) to determine the effects of temperature

on preoviposition period, postoviposition period, oviposition period, fecundity, longevity, and the percentage of total life span spent in oviposition. Data for the first five parameters and 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. Temperature-dependent equations for preoviposition period, postoviposition period, oviposition period, oviposition rate, fecundity, longevity, and percentage of the life span spent in oviposition were developed by regressing data for each of these parameters against temperature using Table Curve 2D [21]. Weekly survivorship data were subjected to survival analysis using PROC LIFEREG and the Wald chi-square to test the equality of the survival curves among different temperatures [20].

Life table parameters

The net reproductive rate (R_0) for each temperature was calculated using age-specific life tables [$R_0 = \sum l_x m_x$, where l_x and m_x are age-specific survival rate and fecundity, respectively] [22]. The generation time (T) for each temperature was calculated by adding the development time from egg to adult [13] to the preoviposition period. The intrinsic rate of increase (r) [22] was calculated as:

$$r = \ln(R_0)/T.$$

The population doubling time, t , was calculated as:

$$t = 0.693/r.$$

Results

Temperature had significant effect on all the parameters studied. Numbers of eggs laid during a female's lifetime varied from 63 at 30°C to 28 at 40°C (Table 1). At 22.5, 25, 27.5, 30, 35, and 37.5°C the highest

oviposition rates (eggs/female/wk) occurred in wk 2, and oviposition rates attained were 5.9, 7.7, 10.6, 13.7, 15.4, and 13.8 respectively (Figure 1). Oviposition rates (eggs/female/wk) were calculated by dividing the total number of eggs laid in a wk by the average number of females alive in that particular wk. At these temperatures, *L. rufa* laid 49, 58, 64, 71, 89, and 94%, respectively, of the total number of eggs in the first 4 wk. At 32.5°C, the highest oviposition rate occurred in wk 1 (14.7) and 86% of all eggs were laid in the first 4 wk. At 40°C, the highest oviposition rate occurred in wk 1 and was 8.9 eggs/female/wk (Figure 1); *L. rufa* laid 94% of all eggs in the first four wks at this temperature. The steepness of the decline in oviposition rates from the peak rate increased with temperature until 37.5°C then decreased (Figure 1). The highest individual oviposition rate recorded was at 35°C, and was 3.1 eggs/d (21.8 eggs/wk); the oviposition period for this female was 34 d during which it laid 106 eggs. However, the highest individual fecundity was recorded at 32.5°C and was 137 eggs over the lifetime of an individual that lived 76 d and had an oviposition rate of 1.8 eggs/d (12.6 eggs/wk). Based on the quadratic equation we developed, the overall oviposition rate or mean number of eggs laid by each female per wk over its lifetime increased with temperature up to 38.33°C (3.82 eggs/female/wk), and then decreased thereafter (Figure 2) (Table 2).

Survival analysis of the weekly survivorship data showed significant differences in survivorship among insects exposed to different temperatures (Wald $\chi^2 = 706.5$; $P < 0.0001$). Survivorship decreased more rapidly with increasing temperature. At 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C, it took 59, 47, 35, 22, 15, 17, 12, and 9 wks, respectively, for all females to die (Figure 1). For higher temperatures (32.5, 35, 37.5, and 40°C), the steepest decline in survivorship occurred immediately or nearly so after the peak oviposition rate had been reached (Figure 1).

Preoviposition and postoviposition periods generally decreased with temperature then increased (Figure 3A & Figure 3B) (Table 1

Temperature (°C)	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Longevity (d)	Fecundity (eggs/♀)	Percentage of lifespan spent in oviposition
22.5	4.43 ± 0.19	144.7 ± 4.9	79.6 ± 4.4	228.9 ± 6.1	34.5 ± 3.0	64.4 ± 2.4
25	2.52 ± 0.19	108.1 ± 4.9	59.2 ± 4.5	169.8 ± 6.1	44.5 ± 3.0	63.9 ± 2.4
27.5	1.49 ± 0.20	89.7 ± 5.1	29.9 ± 4.6	121.2 ± 6.3	54.6 ± 3.1	77.6 ± 2.5
30	0.99 ± 0.19	66.6 ± 4.8	19.8 ± 4.4	87.4 ± 6.1	62.5 ± 3.2	78.3 ± 2.4
32.5	1.14 ± 0.19	45.2 ± 4.8	9.4 ± 4.4	55.7 ± 6.0	58.7 ± 3.0	81.9 ± 2.4
35	0.85 ± 0.19	40.9 ± 4.8	10.2 ± 4.4	52.0 ± 5.9	54.1 ± 2.9	78.7 ± 2.4
37.5	2.15 ± 0.20	29.8 ± 5.0	6.2 ± 4.6	38.2 ± 6.3	44.4 ± 3.1	78.9 ± 2.5
40	1.99 ± 0.20	26.2 ± 4.9	8.2 ± 4.5	36.4 ± 6.2	27.9 ± 3.1	73.9 ± 2.5

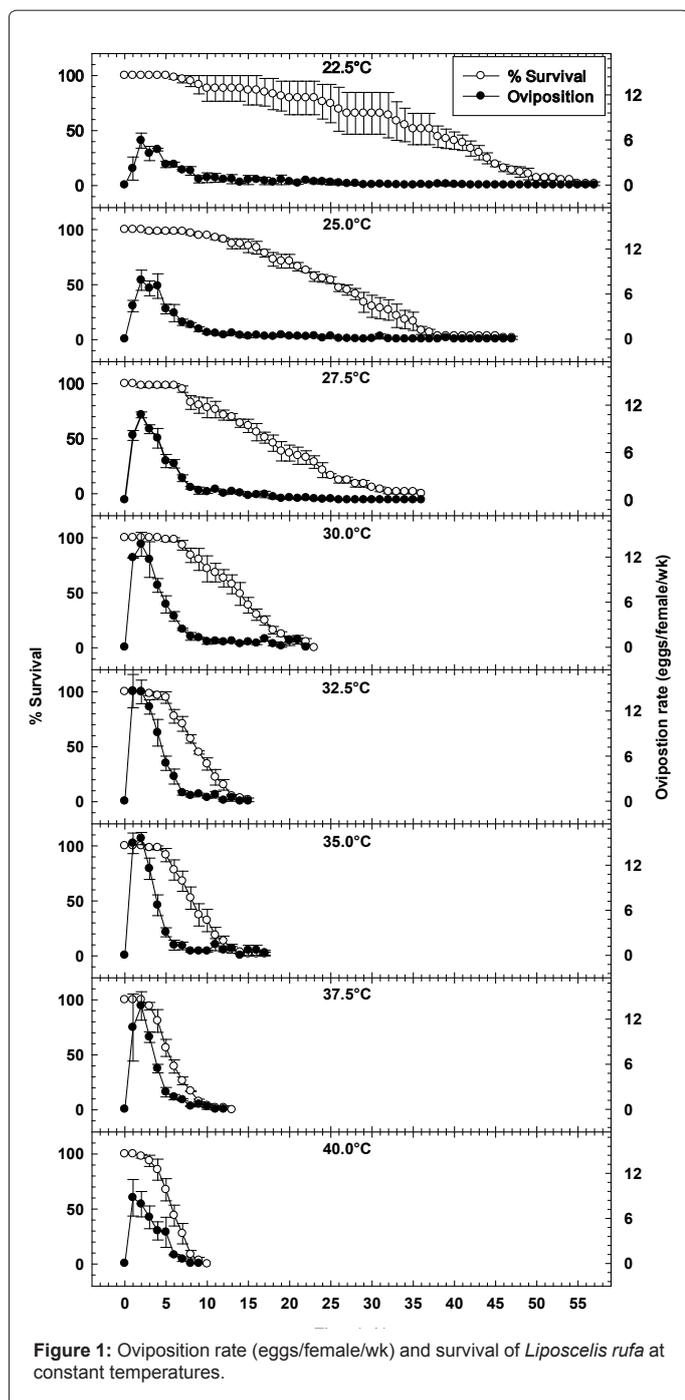
F values of ANOVA results for the preoviposition period, oviposition period, postoviposition period, longevity, fecundity, and percentage of lifespan spent in oviposition were 20.43, 24.73, 12.65, 43.41, 8.03, and 3.82. In all cases $df = 7, 14$ and $P < 0.0001$.

Table 1: Effects of constant temperatures on *L. rufa* preoviposition period (mean ± SE), oviposition period, postoviposition period, longevity, fecundity, and the percentage (%) of adult lifespan spent in oviposition.

Subject	Maximum R ²	Adj. R ²	F	a	b	c
Preoviposition period*	0.50	0.47	9.4	-53.22 ± 15.91	0.846 ± 0.260	867.13 ± 236.026
Oviposition period*	0.91	0.91	100.8	-404.26 ± 180.4	4.409 ± 2.954	10118.89 ± 2675.658
Postoviposition period*	0.91	0.90	93.5	-583.05 ± 121.14	7.944 ± 1.983	10940.93 ± 1796.770
Oviposition rate	0.81	0.73	27.6	-18.17 ± 5.47	1.201 ± 0.358	-0.01606 ± 0.00571
Longevity*	0.92	0.91	111.4	-1043.11 ± 285.31	13.23 ± 4.67	21968.929 ± 4231.622
Fecundity	0.58	0.56	13.8	-309.45 ± 71.11	23.91 ± 4.65	-0.3866 ± .074307
% life spent in Oviposition	0.62	0.53	11.9	-90.15 ± 40.66	10.16 ± 2.66	-0.1512 ± 0.04249

In cases with an asterisk (*), equation is of the type $y = a + bx + c/x$. In all other cases, equation is of the type $y = a + bx + cx^2$. P values and lack-of-fit P-values for preoviposition period, oviposition period, postoviposition period, oviposition rate, longevity, fecundity, and percentage of life span spent in oviposition were $P = 0.00119$, $P = 0$, $P = 0$, $P = 0$, $P = 0.00015$, and $P = 0.00036$, respectively; and 0.97, 0.97, 0.84, 0.24, 0.99, 0.99, and 0.57, respectively. In all cases $df = 2, 21$.

Table 2: Parameters describing the effects of constant temperatures on *L. rufa* preoviposition period, oviposition period, postoviposition period, oviposition rate (eggs/female/wk), longevity, fecundity, and percentage (%) of adult lifespan spent in oviposition.



and Table 2). The longest mean preoviposition period (4.4 d) was recorded at 22.5°C, but it then decreased with temperature before starting to increase. Based on the quadratic equation we developed, the predicted shortest preoviposition period was 0.94 d (32.03°C) (Figure 3A). Similarly, the longest mean postoviposition period (79.6 d) was recorded at 22.5°C, which decreased to 6.2 d at 37.5°C before increasing to 8.2 d at 40°C (Table 1). The predicted shortest postoviposition period was 6.6 d at 37.1°C (Figure 3B).

Oviposition period and longevity also decreased with temperature (Figure 3C & Figure 3D, respectively; Tables 1 and Table 2). At 22.5°C,

these parameters averaged 145 and 229 d, respectively, and at 40°C, they were 26 and 36 d, respectively. The longest individual lifespan recorded was 412 d at 22.5°C. Fecundity increased with temperature up to 30°C and then declined (Table 1), but the predicted optimal temperature for egg laying was 30.9°C and *L. rufa* laid 60.4 eggs at this temperature (Figure 3E). The percentage of the total lifespan spent in oviposition increased from 64% at 22.5°C to 82% at 32.5°C and then declined to 74% at 40°C (Table 1 & Table 2). However, the highest predicted value of percentage of total lifespan spent in oviposition was 80.5% at 33.5°C (Figure 3F).

Generation time and population doubling time declined with temperature until 32.5°C (22.8 and 3.9 d, respectively) and then increased (Table 3 and Table 4). Intrinsic rate of population increase increased with temperature until 32.5°C (0.178) and then declined (Table 3 and Table 4). The net reproductive rate increased with temperature until 30 and 32.5°C (61.6 and 60.7) and then declined at higher temperatures (Table 3 and Table 4).

Discussion

All reproductive parameters varied with temperature. Intrinsic rate of population increase for *L. rufa* increased with temperature until 32.5°C (0.178) 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. rufa* at 22.5, 25, 27.5, 30, 35, 37.5, and 40°C equals 0.39, 0.53, 0.73, 0.90, 0.88, 0.87, and 0.75, respectively. Highest intrinsic rates of increase for *L. reticulatus* [23], *Liposcelis badia* Wang, Wang, and Lienhard [24], *L. bostrychophila* [25], *L. decolor* [26], *L. paeta* [27], *Liposcelis tricolor* Badonnel [28], and *Liposcelis yunnaniensis* Li and Li [29] occurred at 32.5, 27.5, 30, 32.5, 30, and 35°C, respectively. Intrinsic rates of increase at these temperatures were 0.128, 0.0455, 0.0946, 0.0609, 0.0542, 0.0367, and 0.0554, respectively. At optimal temperatures for intrinsic rate of increase, *L. rufa* has the highest potential for population growth among these psocid species. Even at suboptimal temperatures for intrinsic rate of population increase, the potential for *L. rufa* population growth was higher than that of some of the aforementioned *Liposcelis* spp. Besides the fact that these psocids belong to different species, other possible reasons for lower intrinsic rates of increase in *L. badia*, *L. bostrychophila*, *L. decolor*, *L. paeta*, *L. tricolor*, and *L. yunnaniensis*

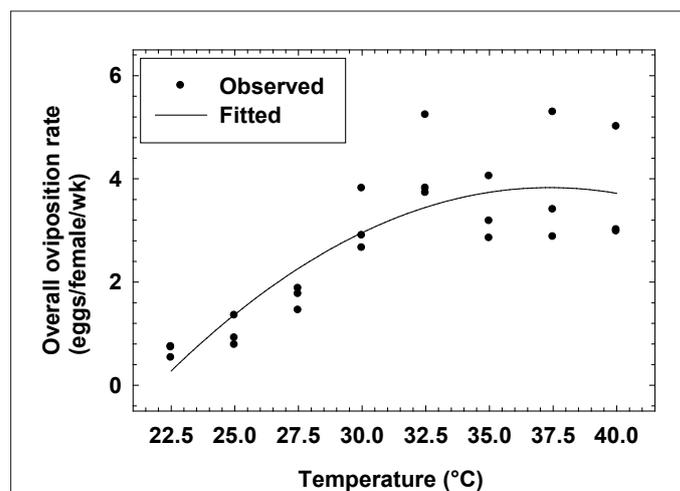


Figure 2: Overall oviposition rate (eggs/female/wk) of *Liposcelis rufa* at constant temperatures. This refers to the general oviposition rate or mean number of eggs laid by each female per wk over its lifetime. Parameters for the fitted line are in Table 2.

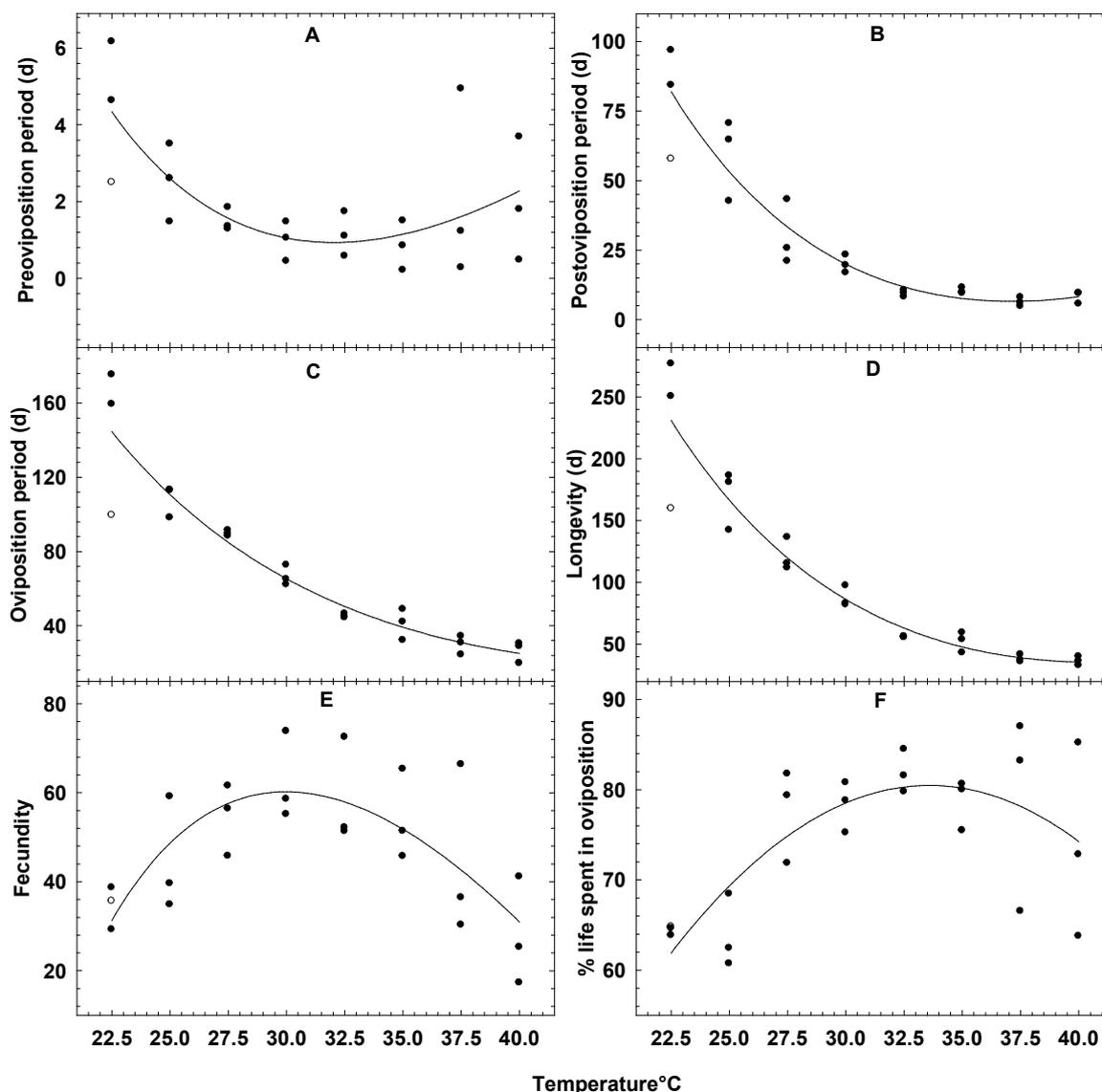


Figure 3: Preoviposition period, postoviposition period, oviposition period, longevity, fecundity, and percentage of life spent in oviposition for *Liposcelis rufa* at constant temperatures. Parameters for the fitted lines are in Table 2.

[24-29] may be that mothers of females in these studies were not of a standardized age, females used were reared from eggs at constant temperatures used for the experiments, and diets were different from those used in the present study and the *L. reticulatus* study [23].

Fecundity was highest at 30°C (63 eggs per female). The lowest fecundity was observed at 40°C (28 eggs per female), a temperature at which most *Liposcelis* species cannot reproduce and survive for long. We found that on average, *L. rufa* can live for up to 5 wks at 40°C. The optimum temperature for population growth of psocid species infesting stored-products ranges from 30 to 35°C [17,18,23,30]. However, in a study on the effects of temperature and relative humidity on *L. rufa* population growth and development, Gautam et al. [13] showed that this species can reproduce at temperatures as high as 40°C. We found that the predicted overall oviposition rate of *L. rufa* increased with temperature up to 38.3°C (3.82 eggs/female/wk). The present study and

that of Gautam et al. [13] indicate that *L. rufa* is adapted to warm and humid environments. This may explain why *L. rufa* has been found on wheat stored in steel bins in Oklahoma, with higher temperatures, but has to date not been found in Kansas.

L. decolor [26,31], *L. paeta* [27,31], and *L. yunnaniensis* [29] are the only other psocid species reported to be adapted to higher temperatures. In the present study, we found that the intrinsic rate of increase, fecundity, and longevity of *L. rufa* are greater than those of *L. decolor*, and *L. paeta* at higher temperatures [26,27]. For example, at 37.5°C, the intrinsic rate of population increase, fecundity, and longevity for *L. decolor* and *L. paeta* are 0.0112, 17.8, and 27; and 0.0504, 20.5, and 25, respectively; whereas the values of these parameters for *L. rufa* are 0.155, 44.4, and 38 d, respectively. In the case of *L. yunnaniensis* [29], these parameters are 0.0416, 12.5, and 39 d, respectively. These data show that *L. rufa* is more suited to warm conditions than even *L. paeta*,

L. decolor, and *L. yunnaniensis*. According to Guedes et al. [32], the presence of heat inducible proteins in the genus *Liposcelis* may explain the tolerance of these four species to higher temperatures.

As expected, oviposition period was longer and the percentage of eggs laid in the first 4 wks was smaller at lower temperatures than at higher temperatures. At 22.5, 25, 27.5, 30, 35, and 37.5°C, oviposition peaked in the second wk and peak oviposition rates (eggs/female/wk) were 5.9, 7.7, 10.6, 13.7, 15.4, and 13.8, respectively. The last egg oviposited at these temperatures was after 41, 39, 25, 21, 17, and 10 wk, respectively, and the percentages of eggs laid in the first 4-wk period were 49, 58, 64, 71, 89, and 94%, respectively. At 32.5°C, oviposition rate was highest in the first wk (14.7 eggs/female/wk) and the last egg oviposited was after 13 wk; *L. rufa* laid 86% of the total number of eggs in the first 4 wk at this temperature. At 40°C, oviposition peaked in the first wk and oviposition rate was 8.9 eggs/female/wk; and the last egg oviposited was after 7 wk. At 40°C, 94% of the eggs were laid in the first 4 wk. These observations may be explained by the fact that the physiological processes of converting resources to eggs and of egg maturation are temperature dependent [33]. According to that study, under suboptimal temperature conditions, realized fecundity declines because insects divert resources towards the maintenance of body functions instead of reproduction. Other studies have also shown that oviposition rate peaks occur earlier with increasing temperature. For example, *L. reticulatus* oviposition rate peaked in wk 3 and 2 at 22.5 and 30°C, respectively [23].

L. rufa produces fewer eggs compared to stored-product beetle pests. 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 [34,35]. According to Throne [36] a maize weevil female, *Sitophilus zeamais* Motschulsky, can lay as many as 6.7 eggs/d at optimal conditions. However, psocids appear to compensate for their low fecundity by having higher intrinsic rates of increase. For example, the intrinsic rate of increase of *L. rufa* at 25°C is 0.097 whereas that of *T.*

castaneum ranges between 0.005 and 0.025 [37]. This may explain why much larger psocid populations are found infesting stored products compared to beetles.

We observed that *L. rufa* 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 which could reduce the life span [38,39]. Therefore, at higher temperatures (not detrimental to *L. rufa*), they may also be allocating significantly more energy resources to egg production than maintenance of body functions thereby resulting in reduced performance and survival [38-41]. It is reasonable to assume that at 22.5 and 40°C, *L. rufa* has a proportionately shorter oviposition period than at optimal temperatures because of the diversion of resources from egg production and maturation to body maintenance that may occur at these temperatures. This may also explain why the percentage of the total lifespan spent in oviposition increased from 64% at 22.5°C to 82% at 32.5°C and then declined to 74% at 40°C. Decline in oviposition period with temperature has also been shown in *L. reticulatus* [23], where this parameter increased from 79% at 22.5°C to 85% at 32.5°C and declined to 75% at 35°C. Similar results have been demonstrated for *L. badia* [24], *L. decolor* [26], and *L. paeta* [27]. The longest-lived *L. rufa* individual lived for 412 d at 22.5°C, which is exceptionally high when compared to the longevity of other psocids.

Preoviposition period at 22.5, 25, 27.5, 37.5, and 40°C was longer than at 30, 32.5, and 35°C. It declined with temperature up to 32.03°C and then increased. This is most probably due to already stated reasons related to metabolic rates, resource allocation, egg production, and egg maturation. Postoviposition period declined with temperature up to 37.11°C and then increased for the already stated reasons used to explain trends for other parameters. Similar trends for postoviposition period were shown by Opit et al. [23] for *L. reticulatus*.

Our data have shown that *L. rufa* has a higher intrinsic rate of increase compared to other psocid pest species. It oviposits over a wide temperature range of 22.5 to 40°C, but the greatest numbers of eggs are laid at 30°C. *L. rufa* appears to be adapted to surviving at higher temperatures and relative humidities (40°C and 75% RH) and may therefore be a bigger pest problem in hot and humid climates than is currently recognized. We have also shown that *L. rufa* adults can live for 59 wk at 22.5°C. Finally, we have developed temperature-dependent equations for preoviposition period, postoviposition period, oviposition period, fecundity, longevity, oviposition rate, and percentage of lifespan spent in oviposition, which can be used in simulation models to aid in developing more effective management strategies for this stored-product pest species.

Acknowledgements

We extend our appreciation to Edmond Bonjour and Kandara Shakya for their

Temperature (°C)	N	r	R ₀	T	t
22.5	57	0.069 ± 0.003	35.67 ± 3.40	51.8 ± 1.06	10.09 ± 0.45
25	57	0.095 ± 0.005	46.27 ± 6.54	39.8 ± 0.59	7.34 ± 0.39
27.5	54	0.129 ± 0.003	54.66 ± 4.15	30.9 ± 0.17	5.37 ± 0.14
30	57	0.161 ± 0.006	61.61 ± 5.92	25.5 ± 0.29	4.30 ± 0.14
32.5	58	0.178 ± 0.007	60.68 ± 8.97	22.8 ± 0.33	3.89 ± 0.19
35	59	0.156 ± 0.006	52.75 ± 6.06	25.4 ± 0.34	4.47 ± 0.19
37.5	53	0.155 ± 0.016	39.57 ± 7.70	23.7 ± 1.42	4.56 ± 0.48
40	55	0.134 ± 0.017	26.42 ± 7.28	23.9 ± 0.93	5.31 ± 0.67

N, number of females in the analysis; r, intrinsic rate of population increase (off-spring/individual/day); R₀, net reproductive rate (females per female); T, generation time (d); and t, population doubling time (d).

Table 3: Life table parameters (mean ± SE) of *L. rufa*.

Subject	Maximum R ²	Adj. R ²	F	a	b	c
r	0.86	0.80	48.6	-0.78 ± 0.11	0.056 ± 0.007	-0.00084 ± 0.00012
Ro	0.62	0.55	16.6	-308.67 ± 67.40	24.102 ± 4.416	-0.39 ± 0.0704
T **	0.99	0.97	434.8	107.98 ± 10.66	-6026.46 ± 633.77	107397.49 ± 9150.69
t*	0.93	0.91	128.2	-75.50 ± 7.90	1.197 ± 0.129	1320.19 ± 117.16

In cases without an asterisk (*), equation is of the type $y = a + bx + cx^2$. In the case with an asterisk (*), it's of the type $a + bx + c/x$, and in the case with a double asterisk (**), it's of the type $a + b/x + c/x^2$. In all cases $df = 2,21$, and $P < 0.0001$. Lack-of-fit P-values for r, R₀, T, and t were 0.47, 0.99, 0.054, and 0.93, respectively.

Table 4: Parameters describing the effects of constant temperatures on *L. rufa* intrinsic rate of population increase (r), net reproductive rate (R₀), generation time (T), and population doubling time (t).

technical support; and Ali Zarrabi and Hassan Melouk for reviewing an earlier draft of this manuscript. In addition, we extend our appreciation to Edward Mockford who confirmed the identity of *L. rufa*. This work was funded by the Oklahoma Agricultural Experiment Station (Project No. OKL02695). Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by Oklahoma State University.

References

1. Turner BD (1994) *Liposcelis bostrychophila* (Psocoptera: Liposcelididae), a stored-product pest in the UK. *Int J Pest Manag* 40: 179-190.
2. Turner BD, Maude-Roxby H, Pike V (1991) Control of the domestic insect pest *Liposcelis bostrychophila* (Badonnel) (Psocoptera): an experimental evaluation of the efficiency of some insecticides. *Int Pest Contr* 33: 153-157.
3. Rees D (2003) Psocoptera (psocids) as pests of bulk grain storage in Australia: a cautionary tale to industry and researchers. *Advances in stored-product protection, Proceedings of the 8th International Working Conference on Stored-Product Protection*.
4. Athanassiou CG, Arthur FH, Opit GP, Throne JE (2009) Insecticidal effect of diatomaceous earth against three species of stored-product psocids on maize, rice, and wheat. *J Econ Entomol* 102: 1673-1680.
5. Opit GP, Throne JE, Flinn PW (2009) Temporospatial distribution of the psocids *Liposcelis entomophila* and *L. decolor* (Psocoptera: Liposcelididae) in steel bins containing wheat. *J Econ Entomol* 102: 1369-1376.
6. Nayak MK, Collins PJ, Reid SR (1998) Efficacy of grain protectants and phosphine against *Liposcelis bostrychophila*, *L. entomophila*, and *L. paeta* (Psocoptera: Liposcelidae). *J Econ Entomol* 91: 1208-1212.
7. Nayak MK, Collins PJ (2008) Influence of concentration, temperature and humidity on the toxicity of phosphine to the strongly phosphine-resistant psocid *Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae). *Pest Manag Sci* 64: 971-976.
8. Kucerová Z (2002) Weight losses of wheat grains caused by psocid infestation (*Liposcelis bostrychophila*: Liposcelididae: Psocoptera). *Plant Prot Sci* 38: 103-107.
9. Obr S (1978) Psocoptera of food-processing plants and storages, dwellings and collections of natural objects in Czechoslovakia. *Acta Entomol Bohemoslov* 75: 226-242.
10. Kalinovic I, Rozman V, Liska A (2006) Significance and feeding of psocids (Liposcelididae, Psocoptera) with microorganisms. *Proceedings of the 9th International Working Conference on Stored-Product Protection*.
11. Nayak MK (2006) Psocid and mite pests of stored commodities: small but formidable enemies. *Proceedings of the 9th International Working Conference on Stored-Product Protection*.
12. Opit GP, Bonjour EL, Beeby R (2011) Seasonal abundance and distribution of psocids in an animal feed warehouse. *Proceedings of the International Organization for Biological and Integrated Control West Palaearctic Region Section Working Group of Integrated Protection of Stored Products* 69: 111-122.
13. Gautam SG, Opit GP, Giles KL (2010) Population growth and development of the psocid *Liposcelis rufa* (Psocoptera: Liposcelididae) at constant temperatures and relative humidities. *J Econ Entomol* 103: 1920-1928.
14. Mockford EL, Krushelnycky PD (2008) New species and records of *Liposcelis* Motschulsky (Psocoptera: Liposcelididae) from Hawaii with first description of the male of *Liposcelis bostrychophila* Badonnel. *Zootaxa* 1766: 53-68.
15. Rees D (2008) Distribution and status of Psocoptera infesting stored products in Australia. *Proceedings of the 6th International Working Conference on Stored-Product Protection*.
16. Kucerová Z, Carvalho ZM, Stejskal V (2006) Faunistic records of new stored product psocids (Psocoptera: Liposcelididae) for Portugal. *Proceedings of the 9th International Working Conference on Stored-Product Protection*.
17. Opit GP, Throne JE (2009) Population growth and development of the psocid *Liposcelis brunnea* (Psocoptera: Liposcelididae) at constant temperatures and relative humidities. *J Econ Entomol* 102: 1360-1368.
18. Opit GP, Throne JE (2008) Population growth and development of psocid *Lepinotus reticulatus* at constant temperatures and relative humidities. *J Econ Entomol* 101: 605-615.
19. Greenspan L (1977) Humidity fixed points of binary saturated aqueous solutions. *J Res Natl Bur Stand A* 81: 89-96.
20. SAS Institute (2007) The SAS system for Windows, version 8. SAS Institute, Cary, NC.
21. Systat Software Inc (2002) TableCurve 2D, version 5.01. Systat Software Inc., San Jose, CA.
22. Birch LC (1948) The intrinsic rate of natural increase of an insect population. *J Anim Ecol* 17: 15-26.
23. Opit GP, Throne JE, Payton ME (2010) Reproductive parameters of the parthenogenetic psocid *Lepinotus reticulatus* (Psocoptera: Trogiidae) at constant temperatures. *Environ Entomol* 39: 1004-1011.
24. Jiang HB, Liu JC, Wang ZY, Wang JJ (2008) Temperature-dependent development and reproduction of a novel stored product psocid, *Liposcelis badia* (Psocoptera: Liposcelididae). *Environ Entomol* 37: 1105-1112.
25. Wang JJ, Tsai JH, Zhao ZM, Li LS (2000) Development and reproduction of the psocid *Liposcelis bostrychophila* (Psocoptera: Liposcelididae) as a function of temperature. *Ann Entomol Soc Am* 93: 261-270.
26. Tang PA, Wang JJ, He Y, Jiang HB, Wang ZY (2008) Development, survival and reproduction of the psocid *Liposcelis decolor* (Psocoptera: Liposcelididae) at constant temperatures. *Ann Entomol Soc Am* 101: 1017-1025.
27. Wang JJ, Ren Y, Wei XQ, Dou W (2009) Development, survival, and reproduction of the psocid *Liposcelis paeta* (Psocoptera: Liposcelididae) as a function of temperature. *J Econ Entomol* 102: 1705-1713.
28. Dong P, Wang JJ, Hu F, Jia FX (2007) Influence of wolbachia infection on the fitness of the stored-product pest *Liposcelis tricolor* (Psocoptera: Liposcelididae). *J Econ Entomol* 100: 1476-1481.
29. Hassan MW, Dou W, Chen L, Jiang HB, Wang JJ (2011) Development, survival, and reproduction of the psocid *Liposcelis yunnanensis* (Psocoptera: Liposcelididae) at constant temperatures. *J Econ Entomol* 104: 1436-1444.
30. Rees DP, Walker AJ (1990) The effect of temperature and relative humidity on population growth of three *Liposcelis* species (Psocoptera: Liposcelididae) infesting stored products in tropical countries. *Bull Entomol Res* 80: 353-358.
31. Beckett SJ and Morton R (2003) The mortality of three species of Psocoptera, *Liposcelis bostrychophila* Badonnel, *Liposcelis decolor* Pearman, and *Liposcelis paeta* Pearman, at moderately elevated temperatures. *J Stored Prod Res* 39: 103-115.
32. Guedes RN, Zhu KY, Opit GP, Throne JE (2008) Differential heat shock tolerance and expression of heat-inducible proteins in two stored-product psocids. *J Econ Entomol* 101: 1974-1982.
33. Berger D, Walters R, Gotthard K (2008) What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. *Funct Ecol* 22: 523-529.
34. Rees D (2004) *Insects of stored products*. CSIRO Publishing, Collingwood, Victoria.
35. Pedersen JR (1992) *Insects: identification, damage and detection. Storage of cereal grain and their products*. American Association of Cereal Chemists, Inc., St. Paul, MN.
36. Throne JE (1994) Life history of immature maize weevils (Coleoptera: Curculionidae) on corn stored at constant temperatures and relative humidities in the laboratory. *Environ Entomol* 23: 1459-1471.
37. Pimentel MA, Faroni LR, Tótoia MR, Guedes RN (2007) Phosphine resistance, respiration rate and fitness consequences in stored-product insects. *Pest Manag Sci* 63: 876-881.
38. Papaj DR (2000) Ovarian dynamics and host use. *Annu Rev Entomol* 45: 423-448.
39. Jervis MA, Boggs CL, Ferns PN (2005) Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. *Ecol Entomol* 30: 359-375.
40. Jervis MA, Ferns PN, Boggs CL (2007) A trade-off between female lifespan and larval diet breadth at the interspecific level in Lepidoptera. *Evol Ecol* 30: 359-375.
41. Carey JR (2001) Insect biodemography. *Annu Rev Entomol* 46: 79-110.