

# Population Growth and Development of the Psocid *Liposcelis brunnea* (Psocoptera: Liposcelididae) at Constant Temperatures and Relative Humidities

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**ABSTRACT** We studied the effects of temperature and relative humidity on population growth and development of the psocid *Liposcelis brunnea* Motschulsky. *L. brunnea* did not survive at 43% RH, but populations increased from 22.5 to 32.5°C and 55–75% RH. Interestingly, we found population growth was higher at 63% RH than at 75% RH, and the greatest population growth was recorded at 32.5°C and 63% RH. At 35°C, *L. brunnea* nymphal survivorship was 33%, and populations declined or barely grew. *L. brunnea* males have two to four nymphal instars, and the percentages of males with two, three, and four instars were 13, 82, and 5%, respectively. Female *L. brunnea* have three to five instars, and the percentages of females with three, four, and five instars were 18, 78, and 4%, respectively. The life cycle was shorter for males than females. We developed temperature-dependent development equations for male and female eggs, individual nymphal, combined nymphal, and combined immature stages and nymphal survivorship. The ability of *L. brunnea* to multiply rather rapidly at 55% RH may allow it to thrive under conditions of low relative humidity where other *Liposcelis* species may not. These data give us a better understanding of *L. brunnea* population dynamics and can be used to help develop effective management strategies for this psocid.

**KEY WORDS** stored products, development rates, life history, grain

Psocids of the genus *Liposcelis* increasingly pose a threat to stored products (Rees 1998). Until recently, psocids were regarded only as nuisance pests feeding on molds (Kučerová 2002). However, weight losses caused by germ and endosperm consumption by psocids (McFarlane 1982, Kučerová 2002), frequent failure of standard practices of protection and disinfestation to control psocids (Wang et al. 1999a, Beckett and Morton 2003, Nayak et al. 2003, Nayak and Daghli 2007), and the fact that commodities infested by psocids can be rejected for export (Kučerová 2002, Nayak 2006) have led to the recognition of psocids as serious pests. Psocid species known to infest grain in North America (Sinha 1988, 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. Sinha (1988) had indicated that he had found *Liposcelis*

*rugosa* Badonnel in Canada, but Lienhard (1990) reported that these were actually *L. bostrychophila* that had been misidentified as *L. rugosa*.

We conducted studies in 2006 to determine which species of psocids were present in wheat stored in steel bins, a feed mill, and an elevator in Manhattan, KS (unpublished data). We found all seven species listed above that had previously been reported in the United States. There have been studies on the biology of *L. bostrychophila* (Rees and Walker 1990; Turner 1994; Wang et al. 1999b, 2000), *L. decolor* (Tang et al. 2008), *L. entomophila* (Rees and Walker 1990; Leong and Ho 1995; Wang et al. 1998; Mashaya 1999, 2001), *L. paeta* (Rees and Walker 1990), and *L. reticulatus* (Opit and Throne 2008). However, there are no published studies on the biology of *L. corrodens* or *L. brunnea*. Development of an effective management program for any pest is dependent on having sound knowledge of its ecology. Given the lack of information on ecology of *L. brunnea*, we initiated studies on population growth and development of *L. brunnea* to provide an experimental basis for developing pest management strategies for this pest. Our objectives were to determine the effects of constant temperature and relative humidity on population growth of *L. brunnea* and to quantify the effects of temperature on development of *L. brunnea*.

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### Materials and Methods

**Insects.** Cultures used in the study were started with insects collected during the summer of 2006 in a grain elevator at the Grain Marketing and Production Research Center in Manhattan, KS. Voucher specimens of 50 female *L. brunnea* preserved in alcohol that were used in this study were deposited in the Kansas State University Museum of Entomological and Prairie Arthropod Research under lot 203. Psocids were reared on a mixture of 93% cracked hard red winter wheat, 5% wheat germ, and 2% rice krispies (Kellogg Company, Battle Creek, MI) (wt:wt; referred to as psocid diet below) in 0.473-liter glass canning jars covered with mite-proof lids (Opit and Throne 2008), and cultures were maintained at 30°C and 75% RH.

**Effects of Temperature and Relative Humidity on Population Growth.** We determined the effects of temperature and relative humidity on the increase in number of psocids over a 30-d period at six temperatures (22.5, 25.0, 27.5, 30.0, 32.5, and 35.0°C) and four relative humidities (43, 55, 63, and 75%)—i.e., 24 temperature/relative humidity combinations. The top third of the inner surface of 120 vials was coated with Fluon (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids from escaping, and 5 g of cracked hard red winter wheat (*Triticum aestivum* L.) were placed in each vial. A screen (U.S. #40 mesh) was placed in the snap-cap lid to allow air movement. Vials were randomly placed in each of four plastic boxes (40 by 27.5 by 16 cm high) containing saturated solutions of  $K_2CO_3$ , NaBr,  $NaNO_2$ , and NaCl below perforated false floors to maintain relative humidities of 43, 55, 63, and 75% (Greenspan 1977), respectively, and the cracked wheat in the vials was equilibrated for moisture content at room temperature for 4 wk.

One- to 2-wk-old female *L. brunnea* for the experiment were obtained by placing 1 g of colored psocid diet (Opit and Throne 2008), 10 particles of cracked wheat, and 30 adult female psocids of unknown age from our culture in each of eighty 35-mm-diameter petri dishes (Greiner Bio-One, Kaysville, UT), which had a coat of Fluon on the walls to prevent psocids from escaping. Colored diet was used because we found that *L. brunnea* prefer laying eggs on and among diet particles, and colored diet makes it easier to see eggs and, therefore, make an assessment of whether sufficient numbers of eggs are being laid for the experiment. The petri dishes were placed on false floors in three Rubbermaid plastic boxes (30 by 23 by 9 cm high) that contained saturated NaCl solution. The boxes had been painted black to exclude light and mimic dark conditions in which *L. brunnea* is usually found. Boxes were placed in an incubator maintained at  $30 \pm 1^\circ C$  and  $70 \pm 5\%$  RH. Psocids were removed from each petri dish after 7 d, and the contents of all the petri dishes were poured into an 800-ml glass jar containing 250 g of psocid diet. The top part (neck) of the jar had a coat of Fluon and was closed using a mite-proof lid. The jar was placed back in the incubator. After 35 d, adult psocids found in the jar were

$\approx$ 1–2 wk old (based on preliminary work we had done that indicated that development of females from egg to adult took  $\approx$ 31 d at 30°C).

Five 1- to 2-wk-old adult females were added to each of the 120 vials containing equilibrated diet, which were incubated at each of the 24 temperature-relative humidity combinations. Six incubators were set at temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, and 35.0°C, and into each incubator were placed four plastic boxes (20 by 12.5 by 10 cm high) containing saturated solutions of  $K_2CO_3$ , NaBr,  $NaNO_2$ , and NaCl. Five vials containing diet equilibrated at room temperature and each relative humidity were randomly assigned to the corresponding relative humidity box in each incubator. Four positions were established in each incubator for the boxes to occupy. Every 7 d, the boxes in each incubator were shuffled so that each box spent a total of at least 7 d in each position during the course of the experiment to counteract any temperature variability that may have existed in the incubators. During shuffling, the boxes were also checked to ensure that the salt solutions were still saturated. Environmental conditions in each incubator were monitored using a temperature and relative humidity sensor (HOBO U12; Onset Computer, Bourne, MA). Live insects in each vial were counted after 30 d by spreading a portion of the contents of a vial on a 9-cm petri dish, which had a coat of Fluon on the walls, and removing motile *L. brunnea* using a moist brush under a stereomicroscope (Wild M5A; Wild Heerbrugg, Heerbrugg, Switzerland).

The experiment had three replications over time, and the experimental design was a randomized complete block (RCBD) with subsampling. Five vials were placed in each plastic box (20 by 12.5 by 10 cm high) during replications 1 and 3, and four were placed in each box in replication 2. All statistical procedures were accomplished using Statistical Analysis System software (SAS Institute 2001). PROC MIXED was used for analysis of variance (ANOVA) to determine the effects of temperature and relative humidity on the numbers of psocids in the vials, which were transformed using the square-root transformation to stabilize variances before analysis. Untransformed means and SEs are reported to simplify interpretation. We used a least significant difference (LSD) test to determine differences among mean numbers of psocids produced at different temperatures and relative humidities, despite the quantitative independent variables, because we were not able to quantify the relationship using a biologically meaningful equation (TableCurve 3D) (Systat Software 2002b).

**Effects of Temperature on Development.** The procedures for obtaining and setting up eggs for the experiment were similar to those used by Opit and Throne (2008). Generally, an egg was transferred into a flat cap of a 1.5-ml centrifuge tube (LabSource, Willowbrook, IL) by using a moist camel's-hair brush. The centrifuge cap was placed inside a 29- by 94-mm vial (Kimble Glass, Vineland, NJ) cap (25 mm diameter). The walls of both the centrifuge and vial caps were coated with Fluon. The vial cap (with a centri-

Table 1. Number (mean  $\pm$  SE) of motile *L. brunnea* present in vials after 30 d

Temperature ( $^{\circ}$ C)	% relative humidity			
	43	55	63	75
22.5	0.0 $\pm$ 0.0h	44.1 $\pm$ 4.9de	50.6 $\pm$ 2.8bcd	48.0 $\pm$ 3.4bcd
25	0.0 $\pm$ 0.0h	43.8 $\pm$ 5.9cde	61.2 $\pm$ 5.6abcd	50.4 $\pm$ 4.5bcd
27.5	0.0 $\pm$ 0.0h	57.4 $\pm$ 9.2bcd	69.4 $\pm$ 7.0abc	49.9 $\pm$ 4.1bcd
30	0.0 $\pm$ 0.0h	58.0 $\pm$ 8.9bcd	75.8 $\pm$ 6.9ab	55.0 $\pm$ 4.3bcd
32.5	0.0 $\pm$ 0.0h	27.2 $\pm$ 6.1e	86.6 $\pm$ 8.2a	51.7 $\pm$ 3.5bcd
35	0.0 $\pm$ 0.0h	2.3 $\pm$ 0.9gh	14.6 $\pm$ 3.2ef	7.7 $\pm$ 2.2fg

ANOVA results for temperature and relative humidity interaction were  $F = 3.7$ ;  $df = 15,46$ ; and  $P < 0.01$ . Means within a column or row followed by the same letter are not significantly different.

fuge cap inside it) was placed inside a 35-mm petri dish, and a cracked wheat kernel was placed in each centrifuge cap and vial cap. A single egg transferred from the colored diet was placed on the floor of each of 180 centrifuge caps, and the 35-mm petri dish lids replaced. Thirty centrifuge caps (with associated vial caps and petri dishes) containing eggs were randomly placed in each of six Rubbermaid plastic boxes (30 by 23 by 9 cm high; 180 centrifuge caps total) that were painted black and contained saturated NaCl solution to maintain 75% RH. One box was placed in each of six incubators set to maintain treatment temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, and 35.0 $^{\circ}$ C. The temperature recordings were checked weekly and the condition of the salt solutions daily, when psocids were being checked. Eggs were examined daily for egg hatch using a stereomicroscope at  $\times 25$  magnification. Two days after egg hatch, when psocids were strong enough to withstand handling, each first-instar nymph (N1) was dusted with rocket red fluorescent powder (Day Glo, Cleveland, OH). Each N1 was transferred from the centrifuge cap into the larger vial cap, and the centrifuge cap plus the cracked wheat particle in it were removed. Nymphs in vial caps were examined daily, using a stereomicroscope at  $\times 25$  magnification, to monitor development. Absence of red marking on the abdomen (and/or thorax) in treated nymphs indicated a molt had occurred. After each molt, insects were immediately marked again. In addition, vial caps in all treatments were examined daily for exuviae.

A fine camel hair brush, which was modified by reducing the number of hairs on it to one and then shortening the length of that hair to 7 mm, was used to apply the fluorescent powder. The single hair of the modified camel hair brush was gently dipped in a 35-mm petri dish half-full of fluorescent powder in such a way as to obtain as little of the powder as possible, and the powder on the brush was gently rubbed against the abdomen of the psocid to be marked. The psocid was not removed from the vial cap during the marking process. Any fluorescent powder that dropped on the vial cap floor was completely removed using a moist camel hair brush.

The experiment consisted of three replications over time. We did not test temperatures  $>35^{\circ}$ C because preliminary experiments had shown that *L. brunnea* eggs do not hatch at temperatures above 35 $^{\circ}$ C.

In the determination of the effects of temperature on the duration of development, data for male and

female psocids were analyzed separately. For both data sets, the design used for analysis was a RCBD with subsampling. PROC MIXED was used for ANOVA to determine the effects of temperature. In the analysis of the proportions of viable eggs and nymphs that developed to the adult stage (male plus female), the design for analysis was a RCBD. To analyze these proportions, PROC GLM was used for ANOVA after arcsine square-root transformation to stabilize variances. We used regression (TableCurve 2D; Systat Software 2002a) to describe the relationship between temperature and nymphal survivorship. The selection of an equation to describe the data were based on the magnitude and pattern of residuals, lack-of-fit tests, and whether the curve had a shape that was reasonable for describing the data. For egg viability, we used an LSD test to determine differences among proportions of eggs hatching at different temperatures, despite the quantitative independent variable, because we were not able to quantify the relationship using a biologically meaningful equation. Temperature-dependent development equations for male and female *L. brunnea* egg, individual nymphal, combined nymphal, and combined immature stages were developed by regressing development times against temperature using TableCurve 2D (Systat Software 2002a).

## Results

**Effects of Temperature and Relative Humidity on Population Growth.** No live *L. brunnea* were found in treatments maintained at 43% RH (Table 1). Numbers of *L. brunnea* increased most rapidly at 32.5 $^{\circ}$ C and 63% RH where there was a 17-fold increase in population (Table 1). At 35 $^{\circ}$ C, *L. brunnea* populations declined or barely grew. High population growth occurred at 22.5 $^{\circ}$ C and 55, 63, and 75% RH. Population growth at temperatures of 22.5–32.5 $^{\circ}$ C and 75% RH was similar. *L. brunnea* seems capable of surviving under a wide range of conditions ranging from 22.5 to 32.5 $^{\circ}$ C and 55 to 75% RH. Population growth was greater at 63% RH than at 75% RH (Table 1).

**Effects of Temperature on Male Development.** *Eggs.* Incubation time generally decreased with increasing temperature (Table 2), and a quadratic equation fit the data well (Fig. 1A; Table 3). Incubation time averaged 14.1 d at 22.5 $^{\circ}$ C and declined to 6.7 d at 35 $^{\circ}$ C.

**Table 2.** Duration (mean ± SE) of immature stages of male *L. brunnea* at six constant temperatures and 75% RH for individuals with three nymphal instars

Temperature (°C)	n	Duration (d)					
		Egg	N1	N2	N3	Nymphs	Eggs + nymphs
22.5	19	14.1 ± 0.4	10.9 ± 0.5	8.1 ± 0.3a	10.6 ± 0.6	29.5 ± 1.0	43.7 ± 1.0
25	8	11.5 ± 0.5	9.0 ± 0.6	5.7 ± 0.4b	8.1 ± 0.7	22.9 ± 1.1	34.4 ± 1.1
27.5	16	9.4 ± 0.5	8.3 ± 0.6	6.0 ± 0.4b	6.9 ± 0.7	21.2 ± 1.1	30.6 ± 1.1
30	14	7.1 ± 0.6	6.2 ± 0.8	6.1 ± 0.5b	6.3 ± 0.9	18.7 ± 1.5	25.7 ± 1.5
32.5	8	7.3 ± 0.5	6.8 ± 0.7	4.8 ± 0.4b	6.0 ± 0.8	17.5 ± 1.4	24.6 ± 1.4
35	9	6.7 ± 0.6	5.1 ± 0.8	5.5 ± 0.5b	7.8 ± 0.9	18.4 ± 1.5	25.2 ± 1.5

Means for N2 followed by different letters are significantly different.

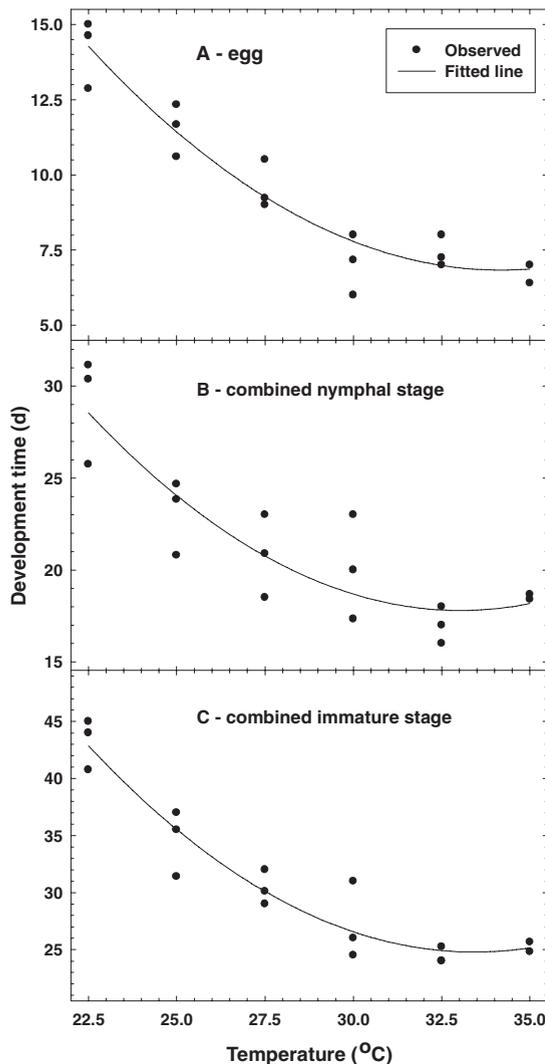
ANOVA results for egg, N1, N2, N3, combined nymphal, and combined immature stages were  $F = 37.1, 11.4, 14.5, 6.9, 18.1,$  and  $44.0,$  respectively; in all cases  $df = 5,10$  and  $P < 0.01.$

*Nymphal, Combined Nymphal, and Combined Immature Stages.* Duration of the nymphal, combined nymphal, and combined immature stages varied with

temperature (Table 2). A linear equation described the relationship between temperature and development time well for the first-instar stage (Fig. 2A; Table 3), and quadratic equations described the relationship well for the third instar (Fig. 2B), combined nymphal (Fig. 1B), and combined immature stages (Fig. 1C; Table 3). Development time decreased with increasing temperature in the first-instar stage (Fig. 2A). For the combined nymphal (Fig. 1B), combined immature (Fig. 1C), and third-instar (Fig. 2B) stages, development time decreased with temperature until it reached a minimum and then started to increase. For the second-instar stage, ANOVA results indicated that temperature did not affect development time, but we were concerned that duration at 22.5°C was considerably longer than at other temperatures (Table 2). Therefore, we used the LSD test for planned comparisons despite the nonsignificant  $F$ -value (Steel and Torrie 1960). Development time was longest at 22.5°C but was not different at other temperatures (Table 2).

**Effects of Temperature on Female Development.**  
*Eggs.* Incubation time generally decreased with increasing temperature (Table 4), and a quadratic equation fit the data well (Fig. 3A; Table 5). Incubation time averaged 12.9 d at 22.5°C and declined to 6.0 d at 32.5°C (Table 4).

*Nymphal, Combined Nymphal, and Combined Immature Stages.* Duration of the nymphal, combined nymphal, and combined immature stages varied with temperature (Table 4). Quadratic equations described the relationship between temperature and development time well for the first-, third-, and fourth-instar and combined immature stages; a linear equation described the relationship well for the combined nymphal stage (Table 5). Development time decreased with increasing temperature for the combined nymphal (Fig. 3B), combined immature (Fig. 3C), first-instar (Fig. 4A), and third-instar (Fig. 4B) stages. In the fourth-instar stage (Fig. 4C), development time decreased with increasing temperature until it reached a minimum and then started to increase. For the second-instar stage, ANOVA results indicated that temperature did not affect development time, but we were concerned that duration at 35°C was considerably shorter than at other temperatures (Table 4). Therefore, we used the LSD test for planned comparisons despite the nonsignificant  $F$ -value (Steel and



**Fig. 1.** Development of male *L. brunnea* at constant temperatures and 75% RH: (A) egg, (B) combined nymphal stage, and (C) combined immature stage.

**Table 3.** Parameters  $\pm$  SE for linear or quadratic equations describing the duration of the egg, individual nymphal, combined nymphal, and combined immature stages of male *L. brunnea* at constant temperatures

Subject	Maximum $R^2$	Adjusted $R^2$	$F$	a	b	c
Egg duration	0.94	0.90	79.1	70.5 $\pm$ 11.3	-3.73 $\pm$ 0.807	0.0545 $\pm$ 0.0141
N1 duration <sup>a</sup>	0.78	0.76 <sup>b</sup>	48.0	19.9 $\pm$ 1.75	-0.422 $\pm$ 0.0610	—
N3 duration	0.58	0.48	9.5	61.2 $\pm$ 16.9	-3.57 $\pm$ 1.20	0.0580 $\pm$ 0.0210
Nymphal duration	0.83	0.75	27.2	124 $\pm$ 27.9	-6.41 $\pm$ 1.99	0.0971 $\pm$ 0.0348
Egg + nymphal duration	0.93	0.90	83.6	194 $\pm$ 26.9	-10.1 $\pm$ 1.92	0.152 $\pm$ 0.0336

N1 and N3 represent the first and third nymphal instars, respectively.

Lack-of-fit  $P$  values for the duration of the egg, N1, N3, combined nymphal, and combined immature stages were 0.37, 0.91, 0.45, 0.51, and 0.81, respectively.

<sup>a</sup>  $df = 1,15$  and  $P < 0.001$ . In all other cases,  $df = 2,14$  and  $P < 0.01$ .

<sup>b</sup> Coefficient of determination ( $R^2$ ).

Torrie 1960). Development time at 35°C was considerably shorter than at other temperatures except 25°C (Table 4).

The mean developmental period of females was longer than that of males. This corresponded to females generally having one more instar than the males (Tables 2 and 4). We found that male *L. brunnea* have two to four nymphal instars, and the percentages of males with two, three, and four instars were 13, 82, and 5%, respectively. Female *L. brunnea* were found to have three to five nymphal instars, and the percentages of females with three, four, and five instars were 18, 78, and 4%, respectively.

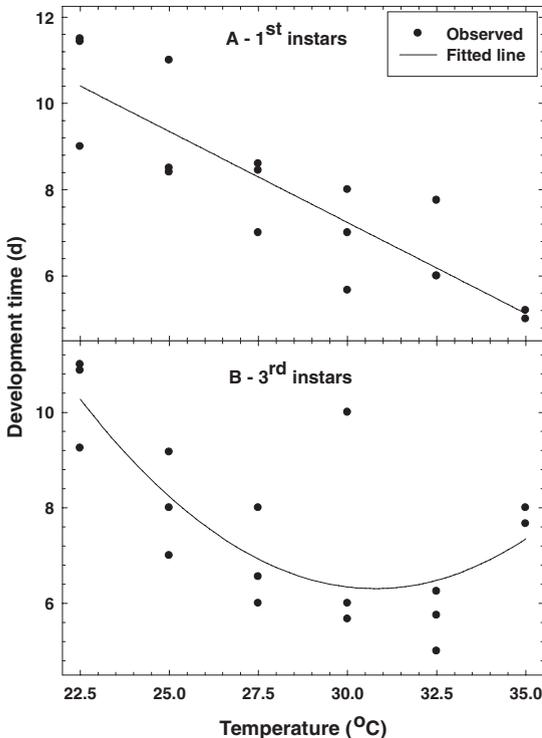
**Effects of Temperature on Egg Viability and Nymphal Survivorship.** Temperature had no effect on egg viability ( $F = 1.39$ ;  $df = 5,10$ ;  $P = 0.3$ ). The pro-

portion of viable eggs for all temperatures ranged from 0.7 to 1.0 and averaged 0.8 over all temperatures. Nymphal survivorship declined with increasing temperature (Fig. 5). The proportion of nymphs surviving to adults ranged from 0.33 at 35°C to 0.77 at 22.5°C, and a nonlinear equation fit the data well (Fig. 5).

## Discussion

*Liposcelis brunnea* populations generally increased at temperatures of 22.5–32.5°C and 55–75% RH; however, *L. brunnea* will not survive at 43% RH. Rees and Walker (1990) found that none of the three psocid species they studied (*L. bostrychophila*, *L. entomophila*, and *L. paeta*) was able to survive at relative humidities below 60%. Our results show that at least one species of *Liposcelis*, *L. brunnea*, cannot only survive but also multiply rapidly at relative humidities <60%. Weng (1986) showed that mortality of adult female *L. entomophila* increased sharply at humidities <56%. This does not seem to be the case for *L. brunnea*, which we found capable of achieving a 12-fold population increase at 27.5 and 30°C and 55% RH, over a 30-d period. According to Devine (1982), psocids maintain body water levels by absorbing atmospheric water vapor when RH is 60% or above; however, below this level, more water is lost than gained resulting in dehydration and death. Therefore, we suggest that it is likely that *L. brunnea* is adapted in such a way that it is able to absorb atmospheric water vapor at a relative humidity as low as 55%.

We found *L. brunnea* population growth was higher at 63% RH than at 75% RH. This is contrary to the common belief that higher relative humidities are conducive for the population growth of *Liposcelis* species because of high levels of mold. In fact, Semple (1986) suggested that generally psocid infestations are more serious in commodities with high moisture content because they are contaminated by mold. A possible reason for the lower population growth at 75% RH could be that the levels of mycotoxins produced when fungal populations are high are toxic to psocids (Frisvad 1995). The fact that we found *L. brunnea* population growth at temperatures of 22.5–32.5°C and 75% RH to be similar seems to support the suggestion that low fungal growth at low temperatures promotes



**Fig. 2.** Development of male *L. brunnea* at constant temperatures and 75% RH: (A) first- and (B) third-instar nymphs.

**Table 4.** Duration (mean ± SE) of immature stages of female *L. brunnea* at six constant temperatures and 75% RH for individuals with four nymphal instars

Temperature (°C)	n	Duration (d)						
		Egg	N1	N2	N3	N4	Nymphs	Eggs + nymphs
22.5	9	12.9 ± 0.4	11.6 ± 0.7	6.8 ± 0.5a	7.6 ± 0.6	10.8 ± 1.0	36.7 ± 1.6	49.6 ± 1.6
25	18	9.9 ± 0.3	8.6 ± 0.5	5.7 ± 0.3ab	7.2 ± 0.4	7.5 ± 0.8	29.2 ± 1.1	39.1 ± 1.1
27.5	19	8.3 ± 0.3	8.2 ± 0.5	6.1 ± 0.3a	6.7 ± 0.4	7.5 ± 0.8	28.6 ± 1.1	36.8 ± 1.1
30	16	6.6 ± 0.3	7.3 ± 0.6	5.9 ± 0.4a	6.4 ± 0.4	6.3 ± 0.8	26.1 ± 1.2	32.7 ± 1.2
32.5	10	6.0 ± 0.4	6.5 ± 0.7	5.9 ± 0.5a	5.8 ± 0.6	5.7 ± 1.0	24.4 ± 1.5	30.5 ± 1.5
35	7	6.3 ± 0.5	6.1 ± 0.7	4.6 ± 0.5b	4.3 ± 0.7	6.6 ± 1.1	21.5 ± 1.7	27.7 ± 1.7

Means for N2 followed by different letters are significantly different.

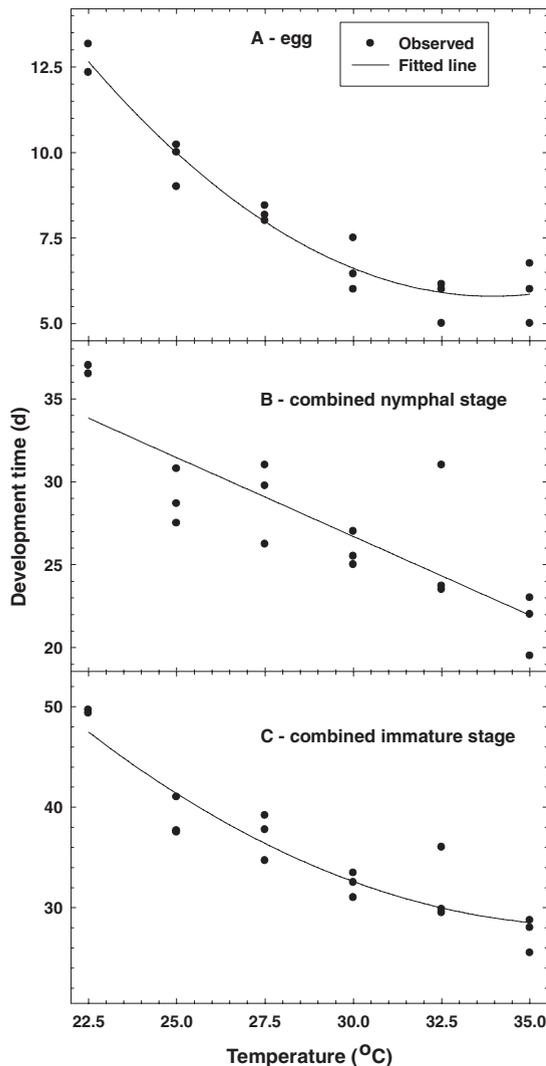
ANOVA results for egg, N1, N2, N3, N4, combined nymphal, and combined immature stages were  $F = 44.8, P < 0.01$ ;  $F = 8.9, P = 0.01$ ;  $F = 2.0, P = 0.2$ ;  $F = 3.7, P = 0.04$ ;  $F = 4.9, P = 0.01$ ;  $F = 11.6, P < 0.01$ ; and  $F = 25.7, P < 0.01$ , respectively; in all cases,  $df = 5,10$ .

higher psocid population growth and that greater fungal growth at higher temperatures might inhibit psocid population growth.

We also found that 35°C has a detrimental effect on the survival and reproduction of *L. brunnea*. Although 58–77% of nymphs survived to adulthood within the 22.5–32.5°C temperature range, only 33% of the nymphs survived to adults at 35°C. This may partly explain the retarded population growth of *L. brunnea* at 35°C. It is possible that at 35°C and lower relative humidities, the inability to replace lost water fast enough may be what limits population growth; however, at higher relative humidities, increased levels of mycotoxins could be a key factor limiting population growth. During development, we found that 87–100% of the total mortality was caused by N1 and N2 mortality. A similar result was reported by Opit and Throne (2008), who found that 80–100% of the total mortality in *L. reticulatus* was caused by N1 and N2 mortality. Rees and Walker (1990) also showed that 35°C temperature was detrimental to *L. bostrychophila* and *L. entomophila*. According to their study, only *L. paeta* was able to survive at temperatures >36°C.

We found that the mean developmental period of female *L. brunnea* was longer than that of males. This can be attributed to the generally greater number of instars in females. According to Mockford (1993), insects in the order Psocoptera usually have four to six nymphal stages. However, in this study, we showed that male *L. brunnea* have two to four instars, and the percentages of males with two, three, and four instars were 13, 82, and 5%, respectively. We have also shown that female *L. brunnea* have three to five instars, and the percentages of females with three, four, and five instars were 18, 78, and 4%, respectively. Compared with *L. entomophila* (Leong and Ho 1995) and *L. bostrychophila* (Wang et al. 2000), *L. brunnea* has a much longer life cycle. At 30°C, for example, female *L. brunnea* require 33 d to complete development, which is 11 d longer than females of *L. entomophila* and *L. bostrychophila*. This suggests that *L. brunnea* may be a less serious pest of stored wheat than either of these species. However, the ability of *L. brunnea* to multiply rapidly at 55% RH may allow it to thrive at grain moisture contents below the survival thresholds of other *Liposcelis* species.

With the exception of the second-instar stage of both male and female *L. brunnea*, generally the trend is for duration of the egg, nymphal, combined nymphal, and combined immature stages to decrease



**Fig. 3.** Development of female *L. brunnea* at constant temperatures and 75% RH: (A) egg, (B) combined nymphal stage, and (C) combined immature stage.

**Table 5.** Parameters ± SE for linear or quadratic equations describing the duration of the egg, individual nymphal, combined nymphal, and combined immature stages of female *L. brunnea* at constant temperatures

Subject	Maximum R <sup>2</sup>	Adjusted R <sup>2</sup>	F	a	b	c
Egg duration	0.95	0.93	116.3	66.1 ± 8.23	-3.55 ± 0.575	0.0523 ± 0.00990
N1 duration	0.82	0.73	25.5	38.2 ± 12.4	-1.74 ± 0.870	0.0234 ± 0.0150
N3 duration	0.70	0.50	10.0	-7.04 ± 11.4	1.17 ± 0.800	-0.0237 ± 0.0138
N4 duration	0.60	0.41	7.5	58.9 ± 19.5	-3.34 ± 1.37	0.0529 ± 0.0235
Nymphal duration <sup>a</sup>	0.83	0.70 <sup>b</sup>	35.2	55.2 ± 4.72	-0.951 ± 0.160	—
Egg + nymphal duration	0.93	0.84	46.5	155 ± 35.5	-6.88 ± 2.48	0.0933 ± 0.0428

N1, N3, and N4 represent the first, third, and fourth nymphal instars, respectively.

Lack-of-fit *P* values for the duration of the egg, N1, N3, N4, combined nymphal, and combined immature stages were 0.78, 0.51, 0.29, 0.56, 0.15, and 0.07, respectively.

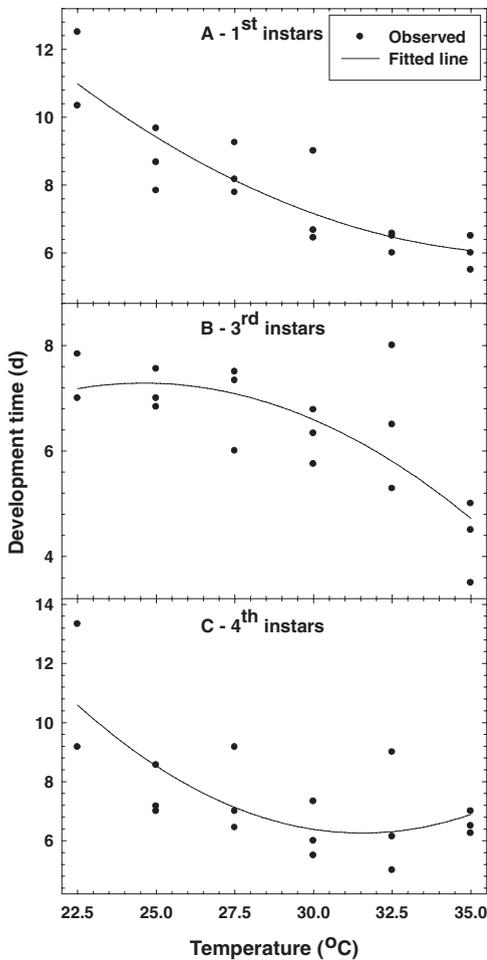
<sup>a</sup> *df* = 1,15 and *P* < 0.001. In all other cases, *df* = 2,14 and *P* < 0.001.

<sup>b</sup> Coefficient of determination (*R*<sup>2</sup>).

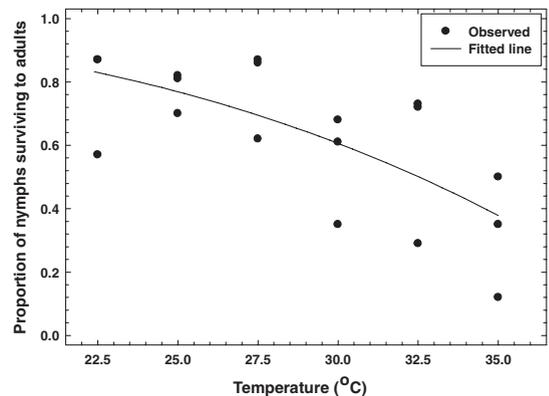
with temperature between 22.5 and 35°C or for duration to decrease with temperature up to a minimum after which development time starts to increase. A similar trend has been reported for all developmental stages of *L. bostrychophila* (Wang et al. 2000) and *L.*

*reticulatus* (Opit and Throne 2008). The temperature-dependent equations for the development of *L. brunnea* eggs, individual nymphal, combined nymphal, and combined immature stages and nymphal survivorship can provide valuable information for elucidating the population dynamics of this species (Summers et al. 1984), despite the fact that this psocid does not live in environments with constant temperatures, and can be used to develop effective management strategies for it. In both male and female *L. brunnea*, the second-instar stage did not show any clear trends in response to temperature. The reasons for this are not clear, but it is possible that if more frequent observations had been made, we might have found a relationship between temperature and development time.

According to Nayak and Collins (2008), *L. bostrychophila* is more tolerant to phosphine at their optimum environmental relative humidity of 70% than at a suboptimal 55% RH. They found that this effect was more pronounced at low temperatures than at higher temperatures because air at a given relative humidity holds more water vapor at higher temperatures than at lower temperatures (ASAE Standards 1994). Based on the results of this study, it is likely that *L. brunnea* would be difficult to control at even 55%



**Fig. 4.** Development of female *L. brunnea* at constant temperatures and 75% RH: (A) first-, (B) third-, and (C) fourth-instar nymphs.



**Fig. 5.** Effects of constant temperatures on *L. brunnea* nymphal survivorship. The equation  $y = 0.99 - 1.4x^3$  describes the relationship well (maximum *R*<sup>2</sup> = 0.58; *R*<sup>2</sup> = 0.49; *F* = 15.6; *P* = 0.001; Lack-of-fit test *P* = 0.68).

RH because they do not seem to be stressed by this low level of relative humidity.

Our work showed that *L. brunnea* can reproduce at 55% RH and that it reproduces more rapidly at 63% RH than at 75% RH. We also showed that *L. brunnea* males have two to four instars, whereas females have three to five instars. Because of a relatively longer life cycle, *L. brunnea* may not be as formidable a stored product pest as other psocids of the genus *Liposcelis*. Finally, we developed temperature-dependent developmental equations plus a nymphal survivorship equation that can be used to understand better *L. brunnea* population dynamics and to develop effective management strategies.

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