

Ecological studies of the Psocids *Liposcelis brunnea*, *L. rufa*, *L. pearmani*, and *Lepinotus reticulatus*

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Abstract

Psocids (*Psocoptera*) are an emerging problem in grain storages, grain processing facilities, and product warehouses in the United States and many other countries. Development of effective pest management programs for psocids is dependent on having sound knowledge of their ecology. Given the limited information available on the ecology of psocids, we conducted ecological studies of four psocid species namely, *Liposcelis brunnea* (Liposcelididae), *Liposcelis rufa*, *Liposcelis pearmani* and *Lepinotus reticulatus* (Trogiidae). We conducted population growth studies of these four psocid species at different temperatures and relative humidities; development studies of *L. brunnea*, *L. rufa*, and *L. reticulatus* at different temperatures; and investigated the effects of temperature on reproductive parameters of *L. reticulatus*. Our studies provide important data on life history and reproductive parameters of four stored-product psocid pests. Because these parameters affect population dynamics, these data can be used in simulation models to predict psocid population dynamics and thereby aid in the development of more effective management strategies.

1. Introduction

Psocids are an emerging problem in stored grain and in food facilities such as mills, processing plants, and warehouses (Rees and Walker, 1990). Before the 1990s in Australia and China and 2000s in the United States, psocids were not considered serious pests of stored products (Phillips and Throne, 2010). However, in some countries such as Australia, they have now become the most frequently encountered stored-product pest in some areas (Rees, 2003). In other countries such as Britain, Denmark, and The Netherlands, psocids (*Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae)) are major household pests of farinaceous products (Turner, 1986).

Prior to 2008, many detailed studies had been conducted on management of psocid pests of stored products (e.g., Leong and Ho, 1994; Ho and Winks, 1995; Santoso et al., 1996; Wang et al., 1999a; Ding et al., 2002), but few detailed studies had been conducted on their biology (Fahy, 1971; Khalafalla, 1990; Wang et al., 1999b; Wang et al., 2000; Wang et al., 2001). Wang et al. (1999b; 2000) conducted life history studies on *L. bostrychophila* and developed predictive models. Sinha (1988) determined temporospatial distribution of psocids in stored wheat in Canada. The recognition of psocids as pests of stored grain and grain processing facilities in the United States (Phillips and Throne, 2010) and the limited amount of published information on their biology prior to the 2000s led to the USDA-ARS Center for Grain and Animal Health Research (CGAHR), Manhattan, KS, USA initiating ecological studies of psocids infesting stored commodities in the United States in 2004. The Stored-Product Entomology Laboratory at Oklahoma State University, Stillwater, OK, USA has since joined CGAHR in conducting psocid research in the United States.

The fact that psocids were considered mere nuisance pests until the 1990s was probably partly responsible for the limited amount of published information available on their biology. The small size of psocids (1 mm) and the difficulty handling and identifying them could also be other contributing factors. Furthermore, the techniques used to conduct biological studies on psocids prior to 2004 were laborious, imprecise, and not user friendly. Therefore, to facilitate ecological studies of stored-product psocids, new techniques for studying their biology had to be developed. This paper provides information on the new, faster, and more user-friendly techniques developed for studying psocid biology and presents data on ecological studies conducted on the psocids *Liposcelis brunnea* Motschulsky, *L. rufa* Broadhead,

L. pearmani Lienhard, and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae) using these techniques.

2. Materials and methods

2.1. Effects of Temperature and Relative Humidity on Population Growth

We determined effects of temperature and relative humidity on increase in number of *L. reticulatus* over a 46-d period at six temperatures (22.5, 25.0, 27.5, 30.0, 32.5, and 35.0°C) and four relative humidities (32, 43, 55, and 75%); *L. brunnea* and *L. pearmani* 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%); and *L. rufa* over a 30-d period at eight temperatures (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C) and four relative humidities (43, 55, 63, and 75%). The top third of the inner surface of vials was coated with Fluon® (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids from escaping, and 5 g of psocid diet were placed in each vial. Psocid diet used for *L. reticulatus* was a mixture of 97% cracked hard red winter wheat (*Triticum aestivum* L.), 2% rice krispies, and 1% brewer's yeast and for the other three species was cracked hard red winter wheat. A screen (US #40 mesh) was placed in the snap-cap lid to allow air movement. For *L. reticulatus*, vials were randomly placed in each of four plastic boxes (40 x 27.5 x 16 cm high) containing saturated solutions of MgCl₂, K₂CO₃, NaBr, and NaCl below perforated false floors to maintain r.h. of 32, 43, 55, and 75% (Greenspan 1977), respectively, and the diet in the vials was equilibrated at room temperature for 4 wk. For *L. brunnea*, *L. rufa*, and *L. pearmani*, saturated solutions of K₂CO₃, NaBr, NaNO₂, and NaCl were used to maintain r.h. of 43, 55, 63, and 75%, respectively, during equilibration.

Five 1 to 2-wk-old adult females, obtained using the protocol described in Opit and Throne (2008, 2009), were added to vials containing equilibrated diet, which were then incubated at each temperature-r.h. combination. Incubators were set at desired temperatures, and four plastic boxes (20 x 12.5 x 10 cm high) containing saturated solutions of the desired relative humidities were placed into each incubator. Six vials containing diet equilibrated at room temperature and each relative humidity were randomly assigned to the corresponding relative humidity box in each incubator. Four locations were established in each incubator for the boxes to occupy. Every 7 d (11 d for *L. reticulatus*), the boxes in each incubator were shuffled so that each box spent a total of at least 7 or 11 d in each location 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 HOBO temperature and r.h. sensor. Live insects in each vial were counted after 30 or 46 d, depending on the species, 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 psocids using a moist brush under a dissecting microscope. For all species, the experimental design was a randomized complete block (RCBD) with subsampling.

2.2. Effects of Temperature on Development

Three species were investigated; *L. brunnea*, *L. rufa*, and *L. reticulatus*. The procedures for obtaining and setting up eggs for the experiment were similar to those used by Opit and Throne (2008, 2009). Thirty centrifuge caps containing eggs were then randomly placed in each of 6 or 8 plastic boxes (30 x 23 x 9 cm high) that were painted black and contained saturated NaCl solution to maintain 75% r.h. The number of plastic boxes used depended on the number of temperatures that were under investigation (six for *L. brunnea* and *L. reticulatus* and eight for *L. rufa*). One box was placed in each of six or eight incubators set to maintain the desired treatment temperatures. The procedures for monitoring egg and nymphal development were similar to those used by Opit and Throne (2008) where psocids were marked using fluorescent powder. The experiment for each species had three temporal replications.

In the determination of the effects of temperature on the duration of development for each of the psocid species, data for male and female psocids were analyzed separately (*L. reticulatus* has only females). For both data sets, the design used for analysis was a RCBD with subsampling.

2.3. Effects of Temperature on Reproductive Parameters

Only *L. reticulatus* was investigated. One newly emerged adult female was placed in each 35-mm Petri dish containing five pieces of cracked wheat and 20 mg of colored diet. Twenty Petri dishes were placed in each of six plastic boxes (28 x 19 x 9 cm high) containing saturated NaCl below their false floors to maintain 75% r.h.; the plastic boxes, containing newly emerged adults and 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. 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 (due to egg removal), 20 mg were added. Replenishment occurred only once. During the checking of Petri dishes for eggs, psocid excrement was also removed using a moist brush in order to keep the Petri dishes clean.

This experiment had four temporal replications. The experimental design was a randomized complete block (RCBD) with subsampling. PROC GLM was used for analysis of variance (ANOVA) 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.

3. Results and discussion

3.1. Effects of Temperature and Relative Humidity on Population Growth.

Liposcelis brunnea, *L. rufa*, *L. pearmani*, and *L. reticulatus* will not survive at 43% r.h. (Fig. 1) At 55% r.h., *L. reticulatus* will not survive; *L. rufa* and *L. pearmani* will survive between 22.5 and 30°C; and *L. brunnea* between 22.5 and 35°C (Fig. 1).

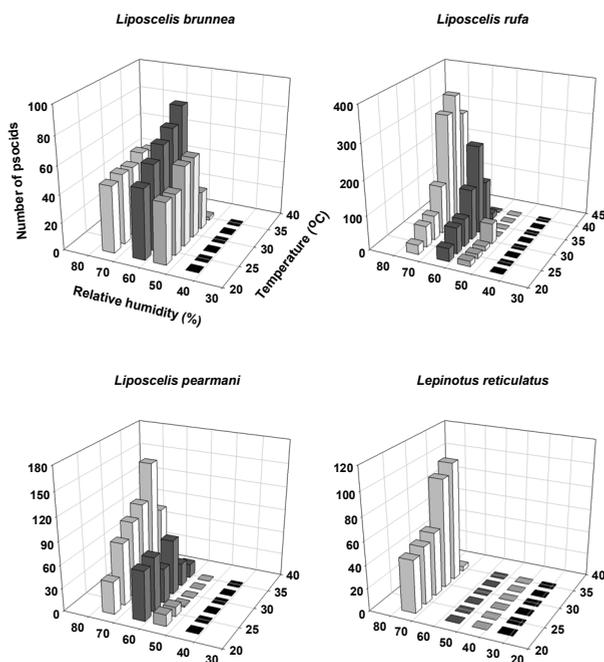


Figure 1 Numbers of psocids found at different relative humidity and temperature combinations. *L. brunnea*, *L. rufa*, and *L. pearmani* populations were allowed to increase over a 30-day period; *L. reticulatus* over a 46-day period.

At 63% and 75% r.h., *L. pearmani* and *L. brunnea* will not survive above 35°C. *L. rufa* will not survive at 40°C and 63% r.h. but will survive at 40°C and 75% r.h. Of these four species, *L. reticulatus* appears to survive under the narrowest set of conditions and appears suited to cooler and more humid conditions. *L. pearmani* and *L. brunnea* appear capable of surviving under a much wider range of conditions ranging

from 22.5 to 35°C and 55% to 75% r.h. The ability of *L. rufa* to multiply at 55% r.h., at temperatures of 22.5, 25, 27.5, and 30.0°C may allow it to thrive under conditions of low relative humidity where other *Liposcelis* species may not.

In addition, its ability to multiply rapidly at high temperatures of 35 and 37.5°C and 75% r.h. may allow it to thrive at temperatures too high for most *Liposcelis* species. Therefore, *L. rufa* appears to have the widest distribution of these four species. Optimal breeding conditions for *L. brunnea*, *L. rufa*, *L. pearmani*, and *L. reticulatus* were 32.5°C and 63% r.h.; 35°C and 75% r.h.; 32.5°C and 75% r.h.; and 30 and 32.5°C and 75% r.h., respectively. Starting from an initial population of five females each, populations of these psocid species grew by 17-, 73-, 31-, and 21-fold, respectively, under optimal conditions (*L. reticulatus* populations increased over a 46-d period whereas those of the other three species was over a 30-d period). Among these species, *L. rufa* populations grew fastest. Based on our data, the predicted size of the range of the four species in declining order would be: *L. rufa*, *L. brunnea* and *L. pearmani*, and *L. reticulatus*.

3.2. Effects of Temperature on Development.

Temperature had no effect on egg viability of *L. rufa*, *L. brunnea*, and *L. reticulatus*. Average percentages of viable eggs across all temperatures were 90, 87, and 80%, respectively. Nymphal survivorship averaged 78, 63, and 36%, respectively. The low nymphal survivorship for *L. brunnea* and *L. reticulatus* may be due to the susceptibility of nymphs to handling or that the relative humidity in which the development studies were conducted (75%) was not the optimal r.h. for these species. The fact that *L. brunnea* populations were higher at 63% r.h. than at 75% r.h. appears to support this explanation. The shortest development times for the egg and combined nymphal and combined immature stages of *L. rufa* females generally occurred at higher temperatures compared to *L. brunnea* and *L. reticulatus* (Table 1). This observation further shows that *L. rufa* is adapted to surviving in relatively high temperature environments. Prior to our ecological studies on *L. rufa*, the only two *Liposcelis* species that were known to survive well under relatively high temperature were *Liposcelis paeta* (Wang et al., 2009) and *L. decolor* (Tang et al., 2008).

Table 1 Shortest development times for the egg and combined nymphal and combined immature stages of female psocids, and the corresponding temperatures at which they occurred.

Species Egg	Combined nymphal	Development time (d) [temperature (°C)]	
		Combined immature	
		stage	stage
<i>Liposcelis rufa</i>	4.5 (40.0)	15.9 (32.5)	21.6 (37.5)
<i>Liposcelis brunnea</i>	6.0 (32.5)	15.9 (32.5)	21.6 (35.0)
<i>Lepinotus reticulatus</i>	6.4 (32.5)	16.6 (32.5)	22.9 (32.5)

In its development from egg to adult, *L. reticulatus*, which is a parthenogenetic species, has four instars (Table 2). We found exuviae consumption after molting to be quite common in *L. reticulatus*. In the case of *L. rufa* and *L. brunnea*, which are described from both males and females, there were at least three different numbers of instars for each sex (Table 2); exuviae consumption in these species was not as common as in *L. reticulatus*. In *L. reticulatus* where exuviae consumption was common, the general trend was that development was slower for psocids that did not eat exuviae. The possible reason for this could lie in the nutritional status of exuviae. Lipids and nitrogenous compounds (protein and chitin) can account for as much as 4.4% (Nelson and Sukkestad, 1975) and 87% (Mira, 2000), respectively, of the total weight of insect exuvia. Therefore, eating exuviae would be beneficial to psocids.

Table 2 Mortality of N1 and N2 instars as a percentage of total instar mortality and variation by gender of the total number of instars and the observed percentage of each number.

Species	N1 and N2 Mortality (%)	Variation in total instar number (observed % of each number)	
		Males	Females
		<i>Liposcelis rufa</i>	64
<i>Liposcelis brunnea</i>	94	2, 3, and 4 (13, 82, and 5, respectively)	3, 4, and 5 (18, 78, and 4, respectively)
<i>Lepinotus reticulatus</i>	83		4 (100)

3.3. Effects of Temperature on Reproductive Parameters.

All reproductive parameters varied with temperature (Table 3). 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* (Pearman) (Tang et al., 2008), *L. paeta* Pearman (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 temperatures for intrinsic rate of increase, *L. reticulatus* has the highest potential for population growth among these psocid species.

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

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

N, number of females in the analysis; r, intrinsic rate of population increase; Ro, net reproductive rate; T, generation time (d); and t, population doubling time (d).

All reproductive parameters varied with temperature (Tables 4 and 5). Regression equations described the relationship between temperature and each of the parameters preoviposition period, oviposition period, postoviposition period, oviposition rate (eggs/female/wk), and longevity quite well (Table 5). We found that *L. reticulatus* oviposition period and longevity declined with increasing temperature (Tables 4 and 5). 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 (Papaj, 2000; Jarvis et al., 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; Jarvis 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, for example, resources could be diverted to maintenance of body functions other than reproduction.

Table 4 Effects of constant temperatures on *Lepinotus reticulatus* preoviposition period (mean ± SE), oviposition period, postoviposition period, longevity, fecundity, and the percentage of adult lifespan spent in oviposition.

Temperature (°C)	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Longevity (d)	Fecundity (eggs/♀)	Percentage of lifespan 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
25.0	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
30.0	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
35.0	2.7 ± 0.23	18.4 ± 2.1	2.8 ± 0.02	23.8 ± 2.2	21.3 ± 2.0c	75.2 ± 1.70c

ANOVA 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 lifespan 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 (LSD) test.

Table 5 Parameters describing the effects of constant temperatures on *Lepinotus reticulatus* preoviposition period, oviposition period, postoviposition period, oviposition rate (eggs/female/wk), and longevity.

Subject	Maximum R2	R2	F	a	b	c
Preoviposition period	0.43	0.38	13.7	1.39 ± 0.60	1646.19 ± 444.30	--
Oviposition period	0.90	0.87	152.7	-8.33 ± 4.05	36971.45 ± 2992.18	--
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	-2951.27 ± 701.70	--
Longevity	0.87	0.86	134.1	-13.76 ± 5.64	48203.12 ± 4162.70	--

In the case with an asterisk (*), $df = 2,21$; equation is of the type $y = a + bx + cx^2$ with an adjusted R2 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.

We found post-oviposition periods for temperatures of 22.5, 25, and 27.5°C to be longer than pre-oviposition periods; at temperatures of 30, 32.5, and 35°C they were either similar or shorter (Table 4). Pre-oviposition period declined with temperature most probably due to already stated reasons related to resource allocation, egg production, and egg maturation. Post-oviposition also showed the same trend except there was an increase in the post-oviposition period at 35°C for the same reasons.

Our studies provide important data on life history and reproductive parameters of four stored-product psocid pests. Because these parameters affect population dynamics, these data can be used in simulation models to predict psocid population dynamics and thereby aid in the development of more effective management strategies.

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