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Effects of Dehumidification on the Survivorship of Four Psocid Species

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Abstract

Psocids are damaging stored-product pests. In this study, eggs and early-instar nymphs, adults, and all life stages of *Liposcelis entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta* were subjected to 43, 50, or 75% (Control) relative humidity (RH) for 2, 4, 6, 8, 10, 12, 14, or 16 d at 30.0°C. All adults of these species died within 8 d at both 43 and 50% RH, except for *L. bostrychophila*, which required 12 d at 50% RH for 100% mortality to occur. For all life stages and eggs and early-instar nymphs, maximum survival times (times to 100% mortality) at 43 or 50% RH for *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta*, were 8 and 10 d, 8 and 12 d, 12 and 14 d, and 12 and 16 d, respectively. During this study, numbers of nymphs and adults of all species 14 d after the RH treatments increased within the 75% RH Control arenas. Different species and life stages responded differently to 43 and 50% RH, as time to kill all stages of the four psocid species was 8–12 and 10–16 d, respectively. Results indicate that using a specific RH environment may be effective in psocid management.

Key words: booklice, integrated pest management, humidity, *Liposcelis*, physical control

Psocids are stored-product pests that can cause unacceptable economic losses, mainly through costs of disinfestation to prevent damage and possible rejection of commodities (Phillips and Throne 2010, Nayak et al. 2014). Severe psocid infestations have been encountered in grain storage on farms, processed foods in warehouses, museums, and food processing facilities, particularly in warm and humid areas (Guedes et al. 2008a, Gautam et al. 2010, Nayak et al. 2014). Globally, the four most economically important psocid species are *Liposcelis entomophila* (Enderlein) (Psocoptera: Liposcelididae), *L. decolor* (Pearman), *L. bostrychophila* Badonnel, and *L. paeta* Pearman (Nayak et al. 2014). In the United States, *Liposcelis corrodens* (Heymons), *L. brunnea* Motschulsky, *L. rufa* Broadhead, *L. fusciceps* Badonnel, *L. pearmani* Lienhard, *L. corrodens* (Heymons), and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae) have also been found infesting stored commodities (Mockford 1993; Lienhard and Smithers 2002; Opit and Throne 2008; Gautam et al. 2010, 2016; Aminatou et al. 2011; Opit et al. 2011a). *Liposcelis obscura* Broadhead was found infesting stored peanuts in a warehouse in Golden, OK (Opit et al. 2018).

During the past three to four decades, economic importance of psocids has increased (Phillips and Throne 2010). This can be attributed to the variable response of psocids to standard management strategies compared with stored-product beetle pests, and their ability to thrive on a variety of food products (Nayak et al. 1998, Nayak and Collins 2008). They also show increased resistance to residual insecticides and the fumigant phosphine (Nayak et al. 2003, 2014). Furthermore, they feed on whole grain kernels, causing damage to the germ and endosperm, leading to significant weight loss and germination failure (Kučerová 2002a, Gautam et al. 2013).

Physical control measures such as heat or cold treatments (Beckett and Morton 2003, Opit et al. 2011b, Arthur et al. 2017), controlled atmospheres (Wang 1999), and manipulation of relative humidity (referred hereafter as RH) are useful for psocid management, but these methods are not well developed. If adequately researched and applied, physical control measures have good potential as tools for the management of psocids (Nayak et al. 2014, Lupo 2018). The susceptibility of psocids to insecticides and physical control measures depend on the treatment,

environmental conditions, species, and exposure, as infestations often consist of more than one species and species may respond differently to any given treatment (Nayak et al. 2014, Arthur et al. 2017).

The effects of RH on population growth and development of psocids have been studied (Gautam et al. 2016 and references therein). In general, RHs > 63% have been known to favor stored-product psocid population growth, whereas RH below 60% is detrimental (Rees and Walker 1990; Opit et al. 2009; Gautam et al. 2010, 2016; Aminatou et al. 2011; Nayak et al. 2014). Although *L. brunnea*, *L. rufa*, *L. fusciceps*, and *L. pearmani* can reproduce at 55% RH between 22.5–30°C, population increase is slow. No psocid has been reported to thrive at 43% RH (Opit and Throne 2009; Gautam et al. 2010, 2016; Aminatou et al. 2011).

Currently, little data are available on evaluating low RH as a management tool for psocids. Given the detrimental effects of low RH on psocid survival, it could play a significant role in integrated management of psocids. Therefore, the objective of our study was to evaluate effects of 43% RH, and 50% RH, on survival of *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta*.

Materials and Methods

Insects

Cultures of *L. bostrychophila* and *L. paeta* used in this study were started from insects originally collected from a grain elevator at the USDA-ARS Center for Grain and Animal Health Research (CGHAR), Manhattan, KS, whereas insects for starting cultures of *L. decolor* and *L. entomophila* were collected from steel bins containing wheat also at CGAHR. Voucher specimens of 100 female *L. bostrychophila, L. decolor*, *L. entomophila*, and *L. paeta* preserved in 95% ethyl alcohol that were used in this study were deposited at the K. C. Emerson Entomology Museum at Oklahoma State University (OSU) under lot numbers 106, 107, 110, and 111, respectively. Voucher specimens of 100 male *L. decolor*, *L. entomophila*, and *L. paeta* were deposited in the same location at OSU under lot numbers 108, 109, and 112, respectively. Psocids were reared in a laboratory at OSU on a diet and under conditions described in Gautam et al. (2016).

Effects of 43% RH on the Survival of all Life Stages of Psocids

The top third of the inner surface of 27 vials (3 cm in diameter × 6 cm high; Intrapac Inc., Plattsburgh, NY) were coated with Fluon to prevent the escape of psocids. Each vial had a modified snap-cap lid with a screen (US Standard #40 mesh with 0.42-mm openings) on it to allow air movement. In each vial, 1.0 g of diet infested with *L. decolor* was added from the stock cultures of this species; the diet contained an undetermined number of eggs, nymphs, and adults. In addition, 0.1 g of wheat germ was added to each vial. Vials were randomly assigned to nine groups of three vials each. Vials in each group were labeled as 1A, 1B, and 1C with the final group of vials marked as 9A, 9B, and 9C, respectively. Three black plastic boxes (32 × 18 × 13 cm high) were prepared, and each contained a saturated solution of K_2CO_3 below a perforated false floor to maintain an RH of 43% (Greenspan 1977). These boxes were designated as 'A', 'B', and 'C' boxes. All 'A' vials were placed in the 'A' box, and this was accordingly repeated for 'B' and 'C' vials as well. Black boxes were used to prevent light entry and to create dark conditions inside each box; this was done to mimic the natural living conditions for psocids. There were 27 total vials for 43% RH treatment for *L. decolor*, and these corresponded to the nine different exposure periods, replicated three times.

Three other black plastic boxes (32 × 18 × 13 cm high) were prepared, but these contained a saturated solution of NaCl below a perforated false floor to maintain 75% RH (Greenspan 1977). The 43% RH box containing 'A' vials had nine vials for *L. decolor.* Vial '1A' was transferred to a corresponding 'A' box with 75% RH before the 'A' box with 43% RH was placed in the incubator maintained at 30°C. Vials '1B' and '1C' were also transferred to boxes 'B' and 'C' with 75% RH before boxes 'B' and 'C' with 43% RH were placed in the incubator. Every 2 d, over a 16-d period one vial from each of the 'A', 'B', and 'C' boxes with 43% RH were accordingly transferred to the corresponding 'A', 'B', and 'C' boxes with 75% RH, i.e., the experiment had nine periods of exposure to 43% RH, 0, 2, 4, 6, 8, 10, 12, 14, and 16 d. Altogether, there were six boxes for testing the effects of 43% RH on *L. decolor* survival (hereafter referred to as the 43% RH treatment), i.e., three boxes with 43% RH and another three with 75% RH. In a nutshell, for day 0 treatment, Vial '1A' was transferred to the corresponding box with 75% RH before the boxes were put in the incubator. For all other exposure periods, 2, 4, 6, 8, 10, 12, 14, and 16 d, vials from each of the A, B, and C boxes with 43% RH were accordingly transferred to corresponding A, B, and C box with 75% RH, at the end of the respective exposure period. All boxes were placed in an incubator maintained at 30°C. Environmental conditions (temperature and RH) in each box were monitored using a temperature and RH sensor (HOBO U12, Onset Computer Corporation, Bourne, MA). The numbers of nymphs and adults in the three vials transferred to boxes with 75% RH, during each transfer event, were determined 14 d after each group of three vials had been placed in the boxes with 75% RH, that is to say, psocid numbers were counted 14 d after the RH treatment. Counting of nymphs and adults in each vial was accomplished by pouring small amounts of diet containing all life stages of psocids into a 9-cm Petri dish with sides coated with Fluon. Live psocids were counted using a stereo microscope (Zeiss Stemi 2000-C; Thornwood, NY) and with the aid of damp, horsetail painting brushes.

A second treatment (Control) with *L. decolor* was set up using only boxes containing a saturated solution of NaCl below perforated false floors to maintain 75% RH. The setup was similar to that described above (27 vials) except that there were only three boxes and no vial transfers. This was the Control treatment. The numbers of nymphs and adults in these Control treatment vials were counted at the same time as those in the corresponding 'A', 'B', and 'C' vials and boxes from the 43% RH treatment described above. Counting of live psocids after 14 d was conducted at times corresponding to those of similarly labeled vials in the 43% RH treatment. The procedures for *L. decolor* as described above were repeated for *L. entomophila*, *L. bostrychophila*, and *L. paeta* separately.

Effects of 43% RH on the Survival of Psocid Adults

The top third of the inner sides of 27 vials were coated with Fluon as described above. A screen (US Standard #40 mesh with 0.42-mm openings), glued to a modified snap-cap lid, which had a 1-cm-diameter hole in the center to allow air flow was used to cover each of the vials. One gram of uninfested psocid diet was placed in each vial. Forty mixed-sex adults (20 of each sex) of *L. decolor* were added to the diet. The procedures for randomization and replication of vials, monitoring, and counting of nymphs and adults were similar to those described above for all life stages.

A second treatment (Control) with *L. decolor* adults was set up using only boxes containing a saturated solution of NaCl below

perforated false floors to maintain 75% RH. There were only three 75% RH boxes in this case and no vial transfers. One gram of uninfested psocid diet was placed in each vial. Forty mixed-sex adults of *L. decolor* were added to each vial. Assessment of *L. decolor* adult survival, and counting procedures were similar to those described above for all life stages of *L. decolor*.

The procedures for *L. decolor* described above were repeated for *L. entomophila*, *L. bostrychophila*, and *L. paeta* separately. Forty mixed-sex adults (20 of each sex) were used for *L. entomophila* and *L. paeta*. For *L. bostrychophila*, a parthenogenetic species, 40 female adults were used for the experiment.

Effects of 43% RH on the Survival of Psocid Eggs and Early-Instar Nymphs

The inner sides of 27 Petri dishes (35 mm in diameter; Greiner Bio-One, Kaysville, UT) were coated with Fluon. To obtain *L. decolor* eggs, 1 g of colored psocid diet, and 30 adult female psocids of unknown ages from the laboratory culture jars were placed in each of the 27 Petri dishes (35 mm in diameter). Colored diet was made as described in Opit and Throne (2008). Because psocids prefer to lay eggs in between diet particles, their eggs can be easily seen on colored diet. Therefore, colored diet permits the determination of whether there are sufficient numbers of eggs for the study. Petri dishes with adult female psocids were placed on false floors in a plastic box (32 × 18 × 13 cm high) painted black that contained saturated NaCl solution beneath the false floor to maintain 75% RH. Adult females were kept in an incubator at 30°C for 3 d to lay eggs. After 3 d, adult females were removed from the diet leaving only eggs in the Petri dishes. Ten particles of cracked wheat (Duster variety) were added to each of the Petri dishes with eggs. The cracked wheat particles were added to the colored diet containing eggs after removal of adults because psocids hide in cracked wheat and their removal after egg laying becomes difficult. The procedures for randomization and replication of Petri dishes, monitoring, and counting of nymphs and adults at the end of the experiment were similar to those described above for all life stages. Over the 0- to 16-d period, when eggs were held at 43 and 50% RH, at the point of transfer of the vials to the 75% RH boxes there were likely both eggs and nymphs in the vials.

A second treatment (Control) with *L. decolor* psocid eggs was set up using only boxes containing a saturated solution of NaCl below perforated false floors to maintain 75% RH. The set up was similar to that described above (27 Petri dishes) except that there were only three 75% RH boxes and no Petri dish transfers. The procedures used to obtain eggs and counting to determine psocid survival were similar to those described for all life stages of *L. decolor*. The procedures described above were applied for *L. entomophila*, *L. bostrychophila*, and *L. paeta* separately.

Effects of 50% RH on the Survival of Psocids

All procedures for 50% RH for these four psocid species, for the different developmental stages, were the same as those described above for 43% RH experiments. However, a saturated salt solution of magnesium nitrate, $Mg(NO_3)_2$ (Greenspan 1977), was used to maintain 50% RH. The 43 and 50% RHs had separate 75% RH treatments.

Data Analysis

Each experiment had three replications, and the experimental design was a randomized complete block (RCBD) with three spatial replications. Data were analyzed by developmental stage of each species, and RHs of 43 and 75% and 50 and 75% were analyzed separately. Statistical analysis was performed with SAS Version 9.4 (SAS Institute, Cary, NC, 2014). The effects of exposure period and RH were assessed using analysis of variance methods (PROC MIXED). Data were transformed using square root transformation before analysis. Untransformed means are reported to simplify interpretation.

The simple effects of exposure period at a given RH were assessed with protected planned contrasts (SLICE option in an LSMEANS statement). Additionally, the SLICE option was used to assess simple effects of RH in a given exposure period. We used a least significant difference test to determine differences among mean number of psocids surviving different RH and exposure periods.

Results

Liposcelis entomophila

RH and exposure period had a significant effect on survival of *L. entomophila* adults, all life stages, and eggs and early-instar nymphs (Table 1). No live psocid nymphs and adults were found after ≥8 d of exposure of adults, all life stages, or eggs and early-instar nymphs to 43% RH (Table 2). However, the number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d steadily increased until at 16 d of exposure it reached

Table 1. Analysis of variance (ANOVA) results for number of *Liposcelis entomophila* nymphs and adults surviving at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50, or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Source	43%		50%	
		F	*P*	*F*	*P*
Adults	RH	1,318.3	<0.001	4,454.8	<0.001
	Exposure period	12.1	<0.001	19.1	<0.001
	RH × Exposure period	55.1	<0.001	152.7	<0.001
All life stages	RH	2,185.7	<0.001	1,259.7	<0.001
	Exposure period	17.3	<0.001	7.3	<0.001
	RH × Exposure period	94.9	<0.001	61.0	<0.001
Eggs and early-instar nymphs	RH	516.5	<0.001	823.9	<0.001
	Exposure period	7.7	<0.001	22.4	<0.001
	RH × Exposure period	34.9	<0.001	73.2	<0.001

The 43 and 50% relative humidities had separate 75% RH treatments. In all cases, df for RH, exposure period, and RH and exposure period interaction are 1,36; 8,36; and 8,36, respectively. Psocid numbers reported are 14 d after the RH treatments.

Table 2. Mean number ± SE of surviving *Liposcelis entomophila* nymphs and adults at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50 or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Expo	43%	75%	50%	75%
Adults					
	0	89.7 ± 3.5aC	82.0 ± 5.3aA	128.7 ± 7.3aD	118.7 ± 5.0aA
	2	45.3 ± 2.2aB	96.7 ± 25.9bA	65.3 ± 6.9aC	189.0 ± 19.7bB
	4	4.3 ± 1.8aA	122.0 ± 18.8bAB	22.0 ± 3.1aB	255.7 ± 19.8bC
	6	0.3 ± 0.3aA	146.3 ± 28.5bB	0.3 ± 0.3aA	218.7 ± 16.5bBC
	8	0.0 ± 0.0aA	134.7 ± 8.8bB	0.0 ± 0.0aA	315.0 ± 16.5bD
	10	0.0 ± 0.0aA	244.0 ± 16.6bC	0.0 ± 0.0aA	379.0 ± 17.0bE
	12	0.0 ± 0.0aA	306.3 ± 56.2bC	0.0 ± 0.0aA	469.7 ± 12.4bF
	14	0.0 ± 0.0aA	388.7 ± 8.3bD	0.0 ± 0.0aA	535.7 ± 50.8bG
	16	0.0 ± 0.0aA	473.7 ± 37.5bD	0.0 ± 0.0aA	639.7 ± 45.6bH
All life stages	0	370.0 ± 63.0aE	374.7 ± 22.6aA	325.3 ± 52.9aD	326.3 ± 15.3aAB
	2	250.7 ± 36.7aD	328.7 ± 29.6bA	245.7 ± 23.2aD	291.3 ± 63.9aA
	4	124.0 ± 22.5aC	436.0 ± 39.9bB	110.3 ± 11.7aC	364.7 ± 12.2bAB
	6	22.7 ± 7.3aB	451.0 ± 18.5bB	24.3 ± 2.9aB	398.3 ± 57.4bB
	8	0.0 ± 0.0aA	573.0 ± 24.0bC	5.7 ± 0.3aAB	564.0 ± 75.0bC
	10	0.0 ± 0.0aA	618.3 ± 27.9bCD	0.0 ± 0.0aA	596.7 ± 87.5bCD
	12	0.0 ± 0.0aA	699.7 ± 53.8bDE	0.0 ± 0.0aA	675.0 ± 17.2bCDE
	14	0.0 ± 0.0aA	768.0 ± 80.3bEF	0.0 ± 0.0aA	722.3 ± 86.9bDE
	16	0.0 ± 0.0aA	846.0 ± 42.8bF	0.0 ± 0.0aA	831.0 ± 29.5bE
Eggs and early-instar nymphs	0	16.3 ± 3.2aC	14.3 ± 5.9aA	14.7 ± 0.9aB	15.7 ± 0.9aA
	2	22.0 ± 0.6aC	20.0 ± 4.6aA	14.0 ± 2.5aB	42.3 ± 3.8bB
	4	5.7 ± 1.5aB	18.0 ± 4.6bA	75.0 ± 10.1aC	63.3 ± 12.8aC
	6	1.0 ± 0.6aA	17.7 ± 4.1bA	58.7 ± 9.9aC	89.0 ± 7.8bD
	8	0.0 ± 0.0aA	23.7 ± 5.7bAB	18.0 ± 6.5aB	92.0 ± 11.8bD
	10	0.0 ± 0.0aA	32.7 ± 2.9bBC	0.0 ± 0.0aA	98.0 ± 1.0bD
	12	0.0 ± 0.0aA	44.0 ± 8.7bCD	0.0 ± 0.0aA	112.7 ± 9.6bD
	14	0.0 ± 0.0aA	51.3 ± 4.1bD	0.0 ± 0.0aA	175.7 ± 16.4bE
	16	0.0 ± 0.0aA	75.7 ± 5.2bF	0.0 ± 0.0aA	187.7 ± 10.4bE

Significant differences between relative humidities for each exposure period are denoted with different lower-case letters and differences among exposure periods for each RH are denoted by different upper-case letters ($P < 0.05$). Psocid numbers reported are 14 d after the RH treatments.

Table 3. Analysis of variance (ANOVA) results for number of *Liposcelis decolor* nymphs and adults surviving at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50, or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Source	43%		50%	
		F	*P*	*F*	*P*
Adults	RH	521.1	<0.001	2,142.1	<0.001
	Exposure period	5.0	<0.001	3.7	0.003
	RH × Exposure period	36.1	<0.001	90.6	<0.001
All life stages	RH	222.3	<0.001	605.1	<0.001
	Exposure period	1.4	<0.001	2.8	0.017
	RH × Exposure period	9.6	<0.001	35.3	<0.001
Eggs and early-instar nymphs	RH	608.3	<0.001	619.7	<0.001
	Exposure period	16.1	<0.001	12.6	<0.001
	RH × Exposure period	57.5	<0.001	63.8	<0.001

The 43 and 50% relative humidities had separate 75% RH treatments. In all cases, degrees of freedom (df) for RH, exposure period, and RH and exposure period interaction are 1,36; 8,36; and 8,36, respectively. Psocid numbers reported are 14 d after the RH treatments.

473.7 ± 37.5, 846.0 ± 42.8, and 75.7 ± 5.2, respectively (Table 2). No live psocid nymphs and adults were found after ≥8 d of exposure of adults to 50% RH (Table 2). However, in the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after ≥10 d of exposure (Table 2). The number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for the nine periods tested steadily increased until after 16 d of exposure it reached 639.7 ± 45.6, 831.0 ± 29.5, and 187.7 ± 10.4, respectively (Table 2).

Liposcelis decolor

RH and exposure period had a significant effect on survival of *L. decolor* adults, all life stages, and eggs and early-instar nymphs (Table 3). No live psocid nymphs and adults were found after ≥8 d of exposure of adults, all life stages, or eggs and early-instar nymphs to 43% RH (Table 4). However, the number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d generally steadily increased until after 16 d of exposure when it reached 605.0 ±

Table 4. Mean number ± SE of surviving *Liposcelis decolor* nymphs and adults at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50 or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Expo	43%	75%	50%	75%
Adults					
	0	194.3 ± 37.1aB	189.7 ± 75.7aB	110.7 ± 5.7aC	135.0 ± 15.4aA
	2	189.0 ± 25.3bB	43.3 ± 26.1aA	77.0 ± 14.1aB	183.0 ± 14.8bB
	4	3.0 ± 0.6aA	352.7 ± 21.4bCD	76.3 ± 9.8aB	191.7 ± 16.2bB
	6	1.3 ± 0.3aA	265.3 ± 29.2bBC	52.7 ± 7.2aB	257.7 ± 12.4bC
	8	0.0 ± 0.0aA	276.0 ± 82.8bBC	0.0 ± 0.0aA	340.3 ± 28.3bD
	10	0.0 ± 0.0aA	395.0 ± 75.9bCD	0.0 ± 0.0aA	411.3 ± 50.4bE
	12	0.0 ± 0.0aA	219.0 ± 18.1bB	0.0 ± 0.0aA	470.0 ± 21.4bE
	14	0.0 ± 0.0aA	496.7 ± 58.4bDE	0.0 ± 0.0aA	362.7 ± 41.7bD
	16	0.0 ± 0.0aA	605.0 ± 48.0bE	0.0 ± 0.0aA	426.3 ± 23.9bE
All life stages	0	229.0 ± 27.5aB	341.0 ± 93.9aA	814.3 ± 17.0aD	682.3 ± 49.1aA
	2	287.0 ± 90.5aB	285.7 ± 51.0aA	225.7 ± 28.7aBC	562.7 ± 105.7bA
	4	33.0 ± 10.6aA	483.3 ± 186.5bAB	300.7 ± 43.8aC	574.7 ± 78.5bA
	6	67.3 ± 62.9aA	332.3 ± 49.9bA	169.0 ± 13.0aBC	885.7 ± 164.3bA
	8	0.0 ± 0.0aA	509.0 ± 165.5bAB	117.3 ± 20.4aB	1,418.3 ± 306.2bB
	10	0.0 ± 0.0aA	604.3 ± 180.3bAB	9.3 ± 3.3aA	1,660.0 ± 416.0bB
	12	0.0 ± 0.0aA	1,029.0 ± 274.0bC	0.0 ± 0.0aA	1,518.3 ± 209.5bB
	14	0.0 ± 0.0aA	865.7 ± 245.3bBC	0.0 ± 0.0aA	1,995.0 ± 102.2bC
	16	0.0 ± 0.0aA	1,050.0 ± 178.5bC	0.0 ± 0.0aA	1,938.7 ± 177.0bC
Eggs and early-instar nymphs	0	47.3 ± 3.2aD	31.7 ± 9.8aA	21.0 ± 1.0aB	16.3 ± 0.7aA
	2	23.7 ± 4.7aBC	35.7 ± 1.2aA	18.0 ± 3.5aB	18.0 ± 1.7aA
	4	29.3 ± 8.1aCD	42.3 ± 5.0aA	18.3 ± 2.2aB	29.7 ± 4.4aA
	6	10.7 ± 2.4aB	73.0 ± 10.3bB	24.7 ± 3.7aB	86.3 ± 11.2bBC
	8	0.0 ± 0.0aA	42.0 ± 9.0bA	13.7 ± 1.7aB	66.7 ± 16.1bB
	10	0.0 ± 0.0aA	93.7 ± 25.4bBC	9.7 ± 1.3aB	113.3 ± 30.1bC
	12	0.0 ± 0.0aA	123.0 ± 19.8bC	0.0 ± 0.0aA	138.7 ± 20.3bC
	14	0.0 ± 0.0aA	342.7 ± 52.4bD	0.0 ± 0.0aA	249.3 ± 6.5bD
	16	0.0 ± 0.0aA	309.7 ± 3.7bD	0.0 ± 0.0aA	250.0 ± 24.3bD

Significant differences between relative humidities for each exposure period are denoted with different lower-case letters and differences among exposure periods for each RH are denoted by different upper-case letters ($P < 0.05$). Psocid numbers reported are 14 d after the RH treatments.

Table 5. Analysis of variance (ANOVA) results for number of *Liposcelis bostrychophila* nymphs and adults surviving at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50 or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Source	43%		50%	
		F	*P*	*F*	*P*
Adults	RH	247.9	<0.001	1,661.9	<0.001
	Exposure period	2.4	0.0036	2.7	0.018
	RH × Exposure period	12.0	<0.001	80.1	<0.001
All life stages	RH	179.3	<0.001	1,117.4	<0.001
	Exposure period	1.2	0.353	1.7	0.123
	RH × Exposure period	11.4	<0.001	40.4	<0.001
Eggs and early-instar nymphs	RH	950.1	<0.001	1,081.8	<0.001
	Exposure period	7.0	<0.001	6.5	<0.001
	RH × Exposure period	74.5	<0.001	88.4	<0.001

The 43 and 50% relative humidities had separate 75% RH treatments. In all cases, df for RH, exposure period, and RH and exposure period interaction are 1,36; 8,36; and 8,36, respectively. Psocid numbers reported are 14 d after the RH treatments.

48.0, 1,050.0 ± 178.5, and 309.7 ± 3.7, respectively (Table 4). No live psocid nymphs and adults were found after ≥8 d of exposure of adults to 50% RH (Table 4). However, in the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after ≥12 d of exposure (Table 4). The number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for the nine periods tested generally steadily increased until after 16 d of exposure it reached 426.3 ± 23.9, 1,938.7 ± 177.0, and 250.0 ± 24.3, respectively (Table 4).

Liposcelis bostrychophila

RH and exposure period had a significant effect on survival of *L. bostrychophila* adults, all life stages, and eggs and early-instar nymphs (Table 5). No live psocid nymphs and adults were found after ≥8 d of exposure of adults to 43% RH (Table 6). In the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after ≥12 and ≥10 d, respectively, of exposure to 43% RH (Table 6). However, the number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar

Table 6. Mean number ± SE of surviving *Liposcelis bostrychophila* nymphs and adults at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50, or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Expo	43%	75%	50%	75%
Adults					
	0	88.3 ± 4.4aB	55.7 ± 4.8aA	130.3 ± 31.6D	157.7 ± 6.8aA
	2	45.0 ± 2.1aB	95.3 ± 27.2aAB	78.0 ± 15.9aC	182.0 ± 16.1bA
	4	5.3 ± 1.2aA	129.7 ± 14.8bABC	69.7 ± 7.6aC	195.7 ± 17.7bA
	6	0.3 ± 0.3aA	205.7 ± 30.9bBC	58.7 ± 14.1aC	268.7 ± 11.3bB
	8	0.0 ± 0.0aA	259.0 ± 42.8bCD	17.0 ± 2.0aB	260.3 ± 10.8bB
	10	0.0 ± 0.0aA	380.0 ± 47.8bD	5.0 ± 0.6aB	314.7 ± 34.0bB
	12	0.0 ± 0.0aA	474.3 ± 58.7bF	0.0 ± 0.0aA	482.0 ± 42.1bC
	14	0.0 ± 0.0aA	424.5 ± 52.5bE	0.0 ± 0.0aA	503.0 ± 18.6bC
	16	0.0 ± 0.0aA	636.7 ± 43.3bG	0.0 ± 0.0aA	605.0 ± 49.6bD
All life stages	0	367.3 ± 64.7aB	250.0 ± 64.4aA	664.7 ± 225.6aD	868.3 ± 123.2aA
	2	333.7 ± 156.8aB	347.0 ± 28.0aAB	390.0 ± 53.7aC	876.0 ± 39.2bA
	4	64.3 ± 22.2aA	357.3 ± 65.4bAB	250.3 ± 15.5aBC	1,332.7 ± 274.0bB
	6	32.3 ± 7.4aA	432.3 ± 132.5bAB	123.7 ± 28.3aB	1,216.7 ± 91.3bB
	8	21.0 ± 9.6aA	509.7 ± 258.8bAB	135.0 ± 13.9aB	1,360.7 ± 13.9bBC
	10	0.3 ± 0.3aA	724.3 ± 266.4bBC	172.3 ± 15.3aB	1,668.0 ± 76.6bC
	12	0.0 ± 0.0aA	896.0 ± 63.2bCD	2.7 ± 0.3aA	1,877.7 ± 55.6bC
	14	0.0 ± 0.0aA	1,290.3 ± 354.1bD	0.0 ± 0.0aA	2,376.0 ± 141.2bD
	16	0.0 ± 0.0aA	1,162.0 ± 339.8CD	0.0 ± 0.0aA	2,371.0 ± 293.6bD
Eggs and early-instar nymphs	0	29.0 ± 6.0aC	29.7 ± 3.8aA	29.3 ± 1.8aD	31.3 ± 5.9aA
	2	53.7 ± 6.6aD	57.3 ± 3.2aB	46.0 ± 1.2aE	60.0 ± 3.1aB
	4	26.7 ± 3.3aC	59.0 ± 15.5bB	32.3 ± 5.0aD	59.3 ± 15.4bB
	6	20.3 ± 5.4aBC	65.3 ± 3.9bB	17.3 ± 2.3aD	67.0 ± 5.0bB
	8	9.7 ± 2.8aB	93.0 ± 9.3bC	22.0 ± 2.5aD	104.3 ± 12.8bC
	10	0.0 ± 0.0aA	120.0 ± 7.4bCD	10.0 ± 3.1aBC	138.7 ± 7.1bD
	12	0.0 ± 0.0aA	145.7 ± 11.9bD	4.7 ± 0.9aB	148.7 ± 4.8bD
	14	0.0 ± 0.0aA	213.3 ± 21.8bE	0.0 ± 0.0aA	244.0 ± 15.6bE
	16	0.0 ± 0.0aA	279.3 ± 38.0bF	0.0 ± 0.0aA	257.7 ± 30.2bE

Significant differences between relative humidities for each exposure period are denoted with different lower-case letters and differences among exposure periods for each RH are denoted by different upper-case letters ($P < 0.05$). Psocid numbers reported are 14 d after the RH treatments.

nymphs to 75% RH for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d generally steadily increased until after 16 d of exposure it reached 636.7 ± 43.3, 1,162.0 ± 339.8, and 279.3 ± 38.0, respectively (Table 6). No live psocid nymphs and adults were found after ≥12 d of exposure of adults to 50% RH (Table 6). However, in the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after ≥14 d of exposure (Table 6). The number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for the nine periods tested generally steadily increased until after 16 d of exposure it reached 605.0 ± 49.6, 2,371.0 ± 293.6, and 257.7 ± 30.2, respectively (Table 6).

Liposcelis paeta

RH and exposure period had a significant effect on survival of *L. paeta* adults, all life stages, and eggs and early-instar nymphs (Table 7). No live psocid nymphs and adults were found after ≥8 d of exposure of adults to 43% RH (Table 8). In the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after ≥12 d of exposure of adults to 43% RH (Table 8). The number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for the nine periods tested generally steadily increased until after 16 d of exposure it reached 735.7 ± 45.7, 2,945.0 ± 381.6, and 157.0 ± 6.8, respectively (Table 8). No live psocid nymphs and adults were found after ≥8 d of exposure of adults to 50% RH (Table 8). However, in the case of all life stages and eggs and early-instar nymphs, no live nymphs and adults were found after 16 d of exposure (Table 8). The number of nymphs and adults found after exposure of adults, all life stages, or eggs and early-instar nymphs to 75% RH for the nine periods tested generally steadily increased until after 16 d of exposure it reached 488.3 ± 10.7, 2,407.0 ± 233.8, and 166.7 ± 18.2, respectively (Table 8).

Discussion

Results from this study show that 43 and 50% RH are detrimental to eggs, nymphs, and adults of *L. entomophila*, *L. bostrychophila*, *L. decolor*, and *L. paeta*. Eggs and early-instar nymphs were more tolerant to 43 and 50% RH than adults. Based on our results, at 43% RH, 8–12 d is required to manage all developmental stages of the four species investigated, depending on the species. Results also show that at 50% RH, 8–16 d is required to manage all developmental stages of the four species investigated, depending on the species. Days to manage psocids here refers to number of days to 100% mortality.

The relative tolerance of eggs may be due to their physical structure. Kučerová (2002b) found that eggs of *Liposcelis*, *Dorypteryx*, and *Psyllipsocus* lack aeropyles. The absence of aeropyles on the chorion of eggs in psocids may suggest a slow conductance of water molecules (water vapor) across the chorion and hence may be responsible for the relative tolerance of eggs of *L. entomophila*, *L. bostrychophila*, *L. decolor*, and *L. paeta* to 43 and 50% RH. Although low RH is a different potential management method, psocid eggs have also been shown to be tolerant to heat, cold, phosphine, and controlled atmospheres evaluated for management (Beckett and Morton 2003, Nayak et al. 2003, Nayak and Collins

Table 7. Analysis of variance (ANOVA) results for number of *Liposcelis paeta* nymphs and adults surviving at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50 or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Source	43%		50%	
		F	*P*	*F*	*P*
Adults	RH	2,285.2	<0.001	1,322.6	<0.001
	Exposure period	4.1	0.002	13.9	<0.001
	RH × Exposure period	87.8	<0.001	61.0	<0.001
All life stages	RH	375.5	<0.001	434.3	<0.001
	Exposure period	3.0	0.010	3.2	0.007
	RH × Exposure period	17.7	<0.001	18.9	<0.001
Eggs and early-instar nymphs	RH	573.5	<0.001	667.4	<0.001
	Exposure period	24.0	<0.001	39.6	<0.001
	RH × Exposure period	52.8	<0.001	69.2	<0.001

The 43 and 50% relative humidities had separate 75% RH treatments. In all cases, degrees of freedom (df) for RH, exposure period, and RH and exposure period interaction are 1,36; 8,36; and 8,36, respectively. Psocid numbers reported are 14 d after the RH treatments.

Table 8. Mean number ± SE of surviving *Liposcelis paeta* nymphs and adults at the end of the experiment after exposure of adults, all life stages, and eggs and early-instar nymphs to 43, 50 or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14, or 16 d

Developmental stage	Expo	43%	75%	50%	75%
Adults					
	0	133.3 ± 14.9aC	151.3 ± 17.3aA	133.3 ± 9.4aC	122.3 ± 4.9aA
	2	157.3 ± 2.8aC	252.3 ± 20.8bB	110.3 ± 5.2aC	173.7 ± 31.2bBC
	4	37.0 ± 3.8aB	259.0 ± 7.2bB	30.7 ± 6.4aB	132.0 ± 21.1bB
	6	17.3 ± 4.9aB	380.0 ± 27.2bC	3.0 ± 1.7aA	151.7 ± 38.5bB
	8	0.0 ± 0.0aA	507.7 ± 31.2bD	0.0 ± 0.0aA	223.3 ± 15.6bC
	10	0.0 ± 0.0aA	536.3 ± 78.7bDE	0.0 ± 0.0aA	272.7 ± 3.7bCD
	12	0.0 ± 0.0aA	619.0 ± 70.0bE	0.0 ± 0.0aA	273.7 ± 17.1bCD
	14	0.0 ± 0.0aA	546.7 ± 49.6bDE	0.0 ± 0.0aA	295.7 ± 42.3bD
	16	0.0 ± 0.0aA	735.7 ± 45.7bF	0.0 ± 0.0aA	488.3 ± 10.7bE
All life stages	0	555.0 ± 62.7aC	529.7 ± 123.6aA	744.7 ± 366.6aC	585.7 ± 128.2aA
	2	245.7 ± 41.9aB	734.7 ± 411.0bA	207.3 ± 71.9aB	372.7 ± 73.8aA
	4	94.7 ± 14.5aB	923.3 ± 249.0bAB	178.3 ± 72.6aB	1,242.7 ± 109.2bB
	6	186.0 ± 91.0aB	1,200.3 ± 172.8bB	74.7 ± 4.4aB	1,080.0 ± 140.4bB
	8	47.7 ± 14.5aA	638.0 ± 150.1bA	61.3 ± 18.3aB	1,831.7 ± 350.1bB
	10	35.3 ± 5.2aA	1,206.7 ± 200.8bB	177.0 ± 35.0aB	1,420.3 ± 154.1bB
	12	0.0 ± 0.0aA	1,343.3 ± 45.2bB	65.3 ± 30.0aB	1,372.7 ± 83.7bB
	14	0.0 ± 0.0aA	1,339.7 ± 101.4bB	2.3 ± 2.3aA	1,294.3 ± 158.3bB
	16	0.0 ± 0.0aA	2,945.0 ± 381.6bC	0.0 ± 0.0aA	2,407.0 ± 233.8bC
Eggs and early-instar nymphs	0	52.7 ± 9.2aC	47.3 ± 8.1aA	14.3 ± 0.3aC	7.7 ± 0.3aA
	2	50.0 ± 5.9aC	80.0 ± 7.2bB	13.7 ± 1.3aC	51.3 ± 8.4bB
	4	100.0 ± 6.5aD	88.7 ± 20.9aBC	91.3 ± 5.2aF	78.7 ± 15.1aC
	6	60.7 ± 9.0aC	131.0 ± 10.8bD	55.7 ± 8.3aE	110.0 ± 4.9bD
	8	40.7 ± 2.9aC	100.0 ± 2.6bBC	46.3 ± 6.4aE	123.7 ± 4.6bD
	10	9.3 ± 2.6aB	106.3 ± 9.5bBCD	27.0 ± 7.2aD	117.0 ± 6.1bD
	12	0.0 ± 0.0aA	103.7 ± 14.2bBCD	14.7 ± 3.3aC	123.0 ± 12.7bD
	14	0.0 ± 0.0aA	116.3 ± 2.8bD	2.7 ± 0.9aB	232.3 ± 6.2bF
	16	0.0 ± 0.0aA	157.0 ± 6.8bE	0.0 ± 0.0aA	166.7 ± 18.2bE

Significant differences between relative humidities for each exposure period are denoted with different lower-case letters and differences among exposure periods for each RH are denoted by different upper-case letters ($P < 0.05$). Psocid numbers reported are 14 d after the RH treatments.

2008, Arthur et al. 2017). Eggs of *L. paeta* have been found to be tolerant to sulfuryl fluoride (Athanassiou et al. 2012). Eggs of *L. reticulatus* and *L. decolor* require 24 and 72 g/m^3 of sulfuryl fluoride, respectively, to attain 100% mortality, whereas survival of *L. paeta* eggs still occurred even at 96 g/m^3 treatment (Athanassiou et al. 2012). According to Beckett and Morton (2003), below 46°C, *L. paeta* eggs were more tolerant to heat than *L. decolor* and *L. bostrychophila* eggs. It is noteworthy that *L. paeta* eggs in this study were relatively more tolerant to 43 and 50% RH. The tolerance of *L. paeta* eggs to sulfuryl fluoride, heat, and 43 and 50% RH may mean that eggs of this psocid species could possess certain structural and compositional aspects that may be contributing to these observed tolerances to different management methods.

Variable response of psocids to current standard management strategies warrants the addition of an effective tool such as dehumidification. Phosphine has failed to control psocids in many instances (Rees 1998), as has methyl bromide (Ho and Winks 1995). Organophosphates such as fenitrothion and diazinon are highly

effective against psocids (Turner 1988) but carbamates and pyrethroid insecticides are not (Turner 1994). Beta-cyfluthrin is effective as a surface treatment (Guedes et al. 2008b). Combinations of carbamate and organophosphate insecticides applied as structural treatments can provide long-term protection (Nayak et al. 2003). At high applications rates, nicotinoids such as imidacloprid are effective against *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* (Nayak and Daglish 2007). Spinosad can be effectively used to manage *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) and *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae) (Subramanyam et al. 2007, Hertlein et al. 2011), but is generally not effective against psocids (Nayak and Daglish 2007). In some cases, *L. entomophila* resistant to chemical treatments such as organophosphates can be controlled using spinosad (Hertlein et al. 2011). Insect growth regulators may or may not be effective against psocids (Buchi 1994, Athanassiou et al. 2011). Application of chlorfenapyr as a surface treatment is effective against psocids (Guedes et al. 2008b). Diatomaceous earth treatments can result in 50% mortality of psocid adults, but can be more effective under low atmospheric moisture of ≤60% RH (Nayak et al. 2014).

Physical management measures such as heat and cold treatment (Beckett and Morton 2003, Opit et al. 2011b, Arthur et al. 2017), controlled atmosphere (Wang 1999), and manipulation of environmental conditions (temperature and RH; Nayak et al. 2014) have been used for psocid management but are not well developed and are less effective when used alone. Controlled and modified atmosphere of carbon dioxide and nitrogen are effective against *L. entomophila* and *L. bostrychophila* but require up to at least 3 wk to achieve complete disinfestation (Nayak et al. 2014).

Many studies indicate that high and low RH have a significant effect on the population growth and development of stored-product psocids (Gautam et al. 2016 and references therein). Psocids thrive at RHs ≥ 60%, but below this critical level, water loss is higher than gain, thus dehydration and death occur (Devine 1982). Rees and Walker (1990) demonstrated that *L. bostrychophila*, *L. entomophila*, and *L. paeta* do not survive at RHs < 60%. Contrary to the findings of Rees and Walker (1990), more recent studies show that *L. brunnea*, *L. rufa*, *L. pearmani*, and *L. fusciceps* can survive and reproduce at low to moderate rates even at 55% RH and temperatures ≤ 30°C, but none survived at 43% RH (Opit and Throne 2009; Gautam et al. 2010, 2016; Aminatou et al. 2011). The detrimental effects of low RH on psocids are confirmed by the present study where at 43 and 50% RH, 100% of all individuals, of all stages of *L. entomophila*, *L. bostrychophila*, *L. decolor*, and *L. paeta* were killed in 16 d or less.

Psocid infestations are often a serious problem in newly-constructed houses. Psocids brought in on construction materials during building usually rapidly proliferate in new houses due to the high RH found in them, which facilitates growth of both the psocids and fungi, with fungi (microscopic mold) serving as a food source for the psocids (Lupo 2018). Based on this study and several others (Gautam et al. 2016 and references therein), high RHs have a significant positive effect on population growth and development of stored-product psocids, and hence facilitate their proliferation. In this study, data show that management of psocids (disinfestation) can be accomplished using dehumidification for at least 8–12 d and 10–16 d at 43 and 50% RH, respectively. In fact, the use of dehumidifiers or air conditioners, accompanied by the use of fans to help increase air flow, in infested or potentially infested areas to reduce moisture to below 50% is a psocid management method used and/or prescribed by pest control operators (Lupo 2018).

Based on our results, control of psocids will require, at least 8–12 d and 10–16 d at 43 and 50% RH, respectively. Data from the present study also show that there are differences in psocid species response to dehumidification. Therefore, accurate identification of species is important because it would facilitate determination of how long the dehumidification should be conducted to achieve good psocid management. Because *L. paeta* is the most tolerant species, if psocid identification is not possible, it is prudent to conduct dehumidification using 43 and 50% RH for 12 and 16 d, respectively. It is critical that the warehouses or items being disinfested are clean in order to increase the efficacy of dehumidification when it is used as a management strategy for psocids. Commercial or industrial dehumidifiers can be used to disinfest empty storage areas, warehouses, or pallets. Research needs to be conducted on the cost–benefit analysis of disinfesting large warehouses using dehumidification. To our knowledge, this is the first published study containing quantitative data on use of dehumidification for psocid management. Data from this study show that dehumidification or low RH (43 and 50%) treatment has great potential for use in disinfesting warehouses and items such as pallets of stored-product psocids. Based on this study, dehumidification has potential to be an additional tool in the arsenal for psocid management using integrated strategies.

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