LIPOSCELIS OBSCURUS BROADHEAD (PSOCOPTERA: LIPOSCELIDIDAE) ECOLOGY AND DEHUMIDIFICATION FOR PSOCID MANAGEMENT

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LIPOSCELIS OBSCURUS BROADHEAD (PSOCOPTERA: LIPOSCELIDIDAE)

ECOLOGY AND DEHUMIDIFICATION

FOR PSOCID MANAGEMENT

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Abstract: Psocids (Psocoptera) have become more economically important as serious pests of stored-products worldwide in the last two-to-three decades. However, knowledge on their ecology and biology which is crucial for the development of effective management strategies is lacking. In this study, I investigated the effects of constant temperatures and relative humidities (RH) on the population growth and development of *L. obscurus*. I also investigated the effects of low RH on the survival of four psocid species. This research shows that *L. obscurus* can survive and multiply at a low relative humidity of 55% at temperatures of 22.5–27.5°C and a high temperature of 42.5°C at 75% RH. The optimal conditions for multiplication for this species are 40.0°C and 75% RH where population growth was a 215-fold from an initial population of five adults. The optimum temperature for development is 40.0°C and requires 15.8 d to develop from egg to adult. *L. obscurus* had three to five nymphal instars. Temperature had significant effect on development time for all developmental stages. I developed temperature-dependent equations for *L. obscurus* developmental stages which can be used to elucidate its population dynamics. Also, my data from the effects of low RH on psocid survival demonstrated that psocids can be managed using dehumidification (a physical control method). At 43 or 50% RH, at least 8–16 d will be required to control all developmental stages of *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* depending on the species. My data on *L. obscurus* ecology and the effects of low RHs on the survival of psocids will facilitate the development of strategies that can play a significant role in the integrated management of psocids.

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CHAPTER I

INTRODUCTION

A number of insect and mite species are classified as stored-product pests; they consistently infest items such as foodstuffs, grains, and many value-added food products (Phillips and Throne 2010). Most stored product pests are found around the world partly due to international trade and transportation systems (Phillips and Throne 2010). Studies indicate that the quantity of stored grain lost to insect damage is 5–10% in advanced countries and up to 35% in developing countries (Campbell et al. 2004). Contamination of packaged food products and reduced aesthetic value of food resulting from stored-product pest infestation leads to market rejection (Phillips and Throne 2010). Stored product pests also contaminate food products with their presence, alive or dead, and waste products—some of which are toxic, allergenic, or repulsive (Rees 2004) and some serve as potential mechanical vectors for human pathogens (Foil and Gorham 2000). These pests are usually controlled with insecticides. However, government regulations on the use of insecticides and the development of resistance to insecticides of these insects call for inclusion of non-chemical approaches to manage these pests (Philips and Throne 2010, Opit et al. 2011).

Beetles (Order: Coleoptera) and moths (Order: Lepidoptera) are often the most encountered economically important stored-product pests (Phillips and Throne 2010). *Rhyzopertha dominica* (F) (Coleoptera: Bostrichidae) and *Sitophilus oryzae* (L) (Coleoptera: Curculionidae) are two examples of internal feeders that usually cause damage to stored grains.

Therefore, research to mitigate the effects of stored product beetles have focused on internally- feeding grain insects (Phillips and Throne 2010). However, psocids (Psocoptera: Liposcelididea), formerly known as secondary pests, also play a significant role in directly damaging stored products.

Psocids belong to a relatively small order of insects and around 5,500 species described (Ahmedani et al. 2010). Severe psocid infestations have been encountered in diverse places such as 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). The four most economically important psocid species with worldwide distribution are *Liposcelis entomophila* (Enderlein) (Psocoptera: Liposcelididae), *Liposcelis decolor* (Pearman), *Liposcelis bostrychophila* Badonnel, and *Liposcelis paeta* Pearman (Nayak et al. 2014). In the United States, *Liposcelis* and *Lepinotus* are two genera of psocids that are the most economically important. For example, *Liposcelis corrodens* (Heymons), *L. brunnea* Motschulsky, *L. obscurus* Broadhead, *L. rufa* Broadhead, and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae), have been found infesting stored commodities (Mockford 1993, Lienhard and Smithers 2002, Opit and Throne 2008, Gautam et al. 2010).

Psocids have risen to prominence over the last two-to-three decades as serious pests of stored products. Some explanations for the sudden rise of psocids to prominence include the fact that they quickly develop resistance to contact insecticides and the fumigant phosphine. For example, delayed egg development and hatching in the presence of phosphine compromises efficacy of the fumigant phosphine (Nayak et al. 2014). The notoreity of psocids has become more evident because psocids thrive on a variety of food products, and cause deterioration of stored products due to their presence, exuviae, feces, and cadavers (Obr 1978, Opit and Throne

2008, Athanassiou et al. 2010. They also feed on whole grain kernels and cause damage to grain germ and endosperm, leading to significant grain weight loss and germination failure (Kučerová 2002, Gautam et al. 2013). Psocid natural ecology, including short generation times, allows them to rapidly colonize new habitats and to quickly proliferate given the right environmental factors (Guedes et al. 2008a). Lastly, consumers are increasingly rejecting commodities infested with psocids, causing economic losses (Opit et al. 2011).

Liposcelis obscurus has been found in large numbers infesting peanut warehouses in Oklahoma, US (Opit, unpublished data). *L. obscurus* is an obligate parthenogen (Mockford 1993). The only ecological study conducted on *L. obscurus* investigated its biology with focus on its reproductive parameters affected by temperature and food (Khalafalla 1990). Detailed ecological studies have been conducted on a number of psocid species, including *L. reticulatus* (Opit and Throne 2008), *L. pearmani* (Aminatou et al. 2011), *L. fusciceps* (Gautam et al. 2015), *L. bostrychophila* (Rees and Walker 1990, Turner 1994, Wang et al 2000), *L. brunnea* (Opit and Throne 2009), *L. decolor* (Tang et al. 2008), *L. entomophila* (Rees and Walker 1990, Wang et al. 1998), and *L. paeta* (Rees and Walker 1990, Wang et al. 2009). Apart from the study by Khalafalla (1990), there are no other published studies on the ecology and population dynamics of *L. obscurus*. However, to effectively manage any pest, in-depth knowledge of its ecology is required. Given the lack of information on the ecology of *L. obscurus*, studies on the population growth and development of *L. obscurus* were initiated to provide an experimental basis for developing management strategies for this pest.

Psocids are usually controlled using contact insecticides such as the fumigant phosphine. However, because they may quickly develop resistance to insecticides, non-insecticide alternatives are needed. From previous ecological studies, relative humidites (RHs) below 60%

are detrimental to pscoid survival (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Conversely, *L. brunnea, L. rufa*, *L. fusciceps*, and *L. pearmani* reproduced at 55% RH at 22.5ºC. However, population increase was extremely slow and at ≤43% RH, psocids did not survive (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). To date, there are no published data on using low RH as a management tool for psocids. Given the detrimental effects of low RHs on psocid survival, studies were also initiated to investigate the effects of 43 or 50% RH on the survival of *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta.*

Results obtained from the study of *L. obscurus* ecology and the effects of low RHs (dehumidification) on the survival of four psocid species are expected to help develop ecological strageties that could play a significant role in the integrated management of psocids.

Objectives

Over the last two to three decades, the pest status of psocids has changed from nuisance pests to important pests of stored products (Gautam et al. 2015). To effectively manage any pest, in-depth knowledge of its biology is required. Before 2004, techniques used to conduct psocid biological studies were not user-friendly (Opit and Throne 2008). Lately, detailed biological studies have been conducted on several species of psocids because new techniques have been developed (Opit and Throne 2008). However, there is no published data on the ecology and biology of *L. obscurus.*

Standard practices of disinfestation against psocids are less effective compared to beetle pests. Psocids are relatively more tolerant to chemical treatments, and alternatives to insecticides are needed (Opit et al. 2011). From previous ecological studies, psocids multiply in

environments with RHs ≥63% but do not survive below 55% (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). However, there are no published studies on using low RH (dehumidification) as a physical control to manage psocids.

The objectives of my thesis are:

Objective 1: Determine the effects of constant temperatures and RHs on the population growth of *L. obscurus*.

Objective 2: Determine the effects of constant temperatures on the development of *L. obscurus*.

Objective 3: Determine the effects of low RH on the survival of four psocid species (*L. bostrychophila*, *L. decolor*, *L. peata*, and *L. entomophila*).

CHAPTER II

LITERATURE REVIEW

Psocoptera

Identification

Psocoptera is a small order of insects with over 5,500 species from 41 families and three subfamilies identified across the world (Mockford 1993, Turner 1994, Ahmedani et al. 2010). Psocids and lice (Phthiraptera: Pediculidae) are related and similar in morphology (Lyal 1985, Kučerová 2002, Light et al. 2010). Although not parasitic like lice, psocids are often associated with mammals because they live in their nests, burrows, fur, or feathers (Lyal 1985). Psocids are small (~ 1–6 mm), soft-bodied insects. They have large heads compared to the rest of the body; protruding black eyes, long, filiform antennae that bends back on their abdomen, and small thoraxes (Mockford 1971). Psocids have stocky bodies, and their body color varies with many being pale yellow with brown abdominal bands (Mockford 1971). The eggs of psocids are smooth and ovoid shaped and eggs are laid singly or in groups (Baz 2008). Nymphs of psocids are colorless, and their size can increase rapidly until the nymphs mature into adults (Turner and Bishop 1998). Psocids are commonly called booklice because they inhabit old books and feed on binding glues. They are also called bark lice because some species that inhabit the bark of trees (Turner 1987).

Key characteristics

Knülle and Spadafora (1969) observed that a feature critical to the survival of psocids is their ability to actively absorb water from the atmosphere; psocid numbers can grow exponentially given the right ambient humidity (>70%). Contrary to popular belief, psocids survive and thrive on a variety of food products found in conditions that are not conducive to mold growth (Rees and Walker 1990, Opit and Throne 2008, Athanassiou et al. 2010). The small body size of psocids gives them the ability to exploit cracks and crevices and to remain unnoticed (Nayak et al. 2014). They can survive adverse conditions, such as lack of food, for relatively long periods of time (Turner and Maude-Roxby 1988). Moreover, some species such as *L. bostrychophila*, *L. reticulatus*, and *L. obscurus* are parthenogenetic (Mockford 1971, Lienhard and Smithers 2002). Parthenogenesis, a form of reproduction where new individuals develop from unfertilized eggs allows for rapid colonization of new habitats, is common in almost all insect orders and it is very extensive in Psocoptera (Yusuf and Turner 2004, Ahmedani et al. 2010). Psocids that are found outside have well-developed wings—outdoor psocid species. They feed on the bark of trees, dead leaves, and molds, hence causing little problems as pests. Some psocid species are found and prefer to live within buildings and are pests—indoor psocid species (Turner 1994). Psocid species of the genus *Liposcelis* (Liposcelididae) and *Lepinotus* (Trogiidea) cause problems in domestic structures and stored grains, stored-product storage facilities, and museums (Baz and Monserrat 1999, Rees et al. 2003, Throne et al. 2006).

Distribution of Psocids

Stored product pests, including psocids, are found all over the world partly due to the transportation of grains (Philips and Throne, 2010). The psocid species found in the US are *L. reticulatus*, *L. bostrychophila*, *L. rufa*, *L. fusciceps*, *L. pearmani*, *L. brunnea*, *L. corrodens*, *L.*

decolor, *L. entomophila*, and *L. paeta* (Sinha 1988, Mockford 1993, Lienhard and Smithers 2002, Gautam et al. 2010, Aminatou 2011 et al., Gautam et al. 2015). *Liposcelis bostrychophila* is the most studied species, and it has a worldwide distribution (Lienhard and Smithers, 2002). *L. bostrychophila* is usually found infesting unprocessed and processed dry foods in households, granaries, and warehouses (Broadhead 1954, New 1971, Turner 1994). In the US, large numbers of *L. entomophila* and *L. reticulatus* were found infesting wheat silos (Arbogast et al. 2000, Throne et al. 2006). Also, *L. bostrychophila*, *L. decolor*, *L. paeta*, *L. rufa*, *L. brunnea*, and *L. corrodens* have been found in food-processing facilities and flour mills (Mockford 1993, Lienhard and Smithers 2002, Gautam et al. 2010). Severe infestations have also been reported in Australia where *L. decolor* was mostly found in the cooler areas and only infested central and on-farm grain structures while *L. entomophila* and *L. bostrychophila* were frequently found in central storage structures and mills (Rees et al. 2003). *Liposcelis* spp. are recognized as a major pest of rice storage facilities in Indonesia (Santoso et al. 1996). *L. entomophila* was found in tobacco-processing facilities in Zimbabwe (Mashaya 1999) and railway vans used in conveying grains in Canada (Smith 1985). Heavy infestations have been found in food-processing facilities, feed and flour mills in Italy (Trematerra and Fiorilli 1999). Kučerová et al. (2006) identified psocids in Portugal, and Stejskal et al. (2003) also identified psocids in the Czech Republic. Turner (1994) reported the presence of psocids (*L. bostrychophila*) in households in the UK and Islam and Dey (1992) reported the presence of psocids in Bangladesh. In Pakistan, psocids were identified in provincial reserve centers of Jehlum and Faisalab (Ahmedani et al. 2007).

Economic Importance of Psocids

Why have psocids risen to become pests of substance?

Psocids show varied response to chemical treatments, and this has contributed to the rise of their pest status. For example, psocid numbers increased after grains were treated with permethrin, possibly because psocids had a higher tolerance to this insecticide compared to other stored product pest species (Pranata et al. 1983). Psocids are also known to benefit from the decrease of predators and competitors such as *Tribolium castaneum* (H) (Coleoptera: Tenebrionidae) after insecticide applications (Pranata et al. 1983). Another reason for the upsurge of psocids in the 1990s is associated with industry transitioning from the extensive use of contact insecticides to phosphine fumigation (Rees 1998). According to Nayak et al. (2003), the egg stage of psocids is the most tolerant to phosphine fumigation, which may explain the rise of control failures in countries in South and Southeast Asia. Psocid populations recover more rapidly from poorly conducted phosphine fumigations than beetle pests (Roesli et al. 1998). In Australia, the development of resistance to phosphine in psocids has increased their pest status and has put them in the same category as beetle pests (Collins et al. 2001). The physiological and behavioral characteristics of psocids make their management more difficult. For example, psocids disperse from grain facilities to absorb moisture during fumigation which probably reduces the efficacy of fumigants against them in open top silos (Guedes et al. 2008a). Also, the parthenogenetic mode of reproduction of some psocid species such as *L. bostrychophila*, *L. reticulatus*, and *L. obscurus* allows them to colonize new habitats rapidly and to proliferate (Nayak et al. 2014); they can also survive for reasonably long periods without food (Turner and Maude-Roxby 1988). Lastly, markets increasingly view psocids as contaminants (Kučerová 2002, Nayak 2006).

Significance of psocids to human and animal health

Large psocid infestations have substantial effects on human and animal health and safety (Nayak et al. 2014). Psocid species such as *L. bostrychophila* is commonly found in homes, but species such as *L. brunnea* and *L. decolor* are seldom found infesting homes (Baz and Monserrat 1999). Psocids are sometimes found to be associated with house dust, and this could probably increase dust allergy in humans (Spieksma and Smits 1974, Rijckaert et al. 1981). Turner et al. (1996) found that at least 5% of allergy patients showed strong positive skin reactions to the psocid antigen. In 2004, *L. bostrychophila* was reported to have caused a woman's toenail to be infected by onychomycosis; a fungal infection of the nail (Lin et al. 2004). Also, psocids may serve as intermediate hosts for tapeworms by ingesting their eggs, harboring their larvae in their gut and ultimately spread these parasites in the environment through their fecal matter (Allen 1959). The excreted tapeworm may be ingested by grazing animals (Baker 2007). Fungi and bacteria remain viable in the feces of *Liposcelis spp* after digestion and may be transmitted to other organisms (Turner 1994).

Economic impact of psocid infestations to stored grains

Psocid infestations lead to significant weight losses in stored grains (Kučerová 2002). Pike (1994) recorded weight loss of up to 2.9% in lightly milled rice after 3.5 months of *L. paeta* infestation. An average weight loss of 9.7% of broken wheat kernels due to infestations of *L. bostrychophila* over a three-month period has been recorded (Kučerová 1999). In cases of grain shipments for export, psocid infestations can lead to significant financial losses. According to Nayak et al. (2014), markets are increasingly rejecting commodities infested with psocids. Psocids can empty the kernels of grains by feeding on the soft endosperm of damaged or cracked uninfected grains (Gautam et al. 2015). They feed on the germ, by first gaining access via the

damaged grain testa caused by harvesting, handling or by the attack of stored grain beetle pests (Ahmedani et al. 2010). Kučerová (2002) and Gautam et al. (2013) observed that psocid infestations do not only cause a considerable loss in weight of wheat but also result in significant germination failure. The presence of large psocid populations in stored grain can increase grain temperature and humidity, which may eventually lead to grain decay (Ahmedani et al. 2010).

Management of Psocids

Use of chemicals and resistance problems

The use of insecticides to manage pest problems is common around the world. Stored-product psocids are difficult to control, and they have high natural tolerance to many categories of insecticides used, despite the fact that these chemicals are successful in controlling stored-product beetle pests (Athanassiou et al. 2015). Moreover, with the limited amount of information available on the ecology of psocids until recently, management of these pests has mainly focused on *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* (Nayak et al. 2014). Organophosphates such as fenitrothion and diazinon are highly effective against psocids (Turner 1988). However, pyrethroids and carbamate insecticides are not (Turner 1994). Pyrethroids are reported to be relatively ineffective against *Liposcelis* species (Guedes et al. 2008a). Bio-pesticides, such as spinosad, also seem ineffective in controlling psocids. However, a mixture of spinosad and natural pyrethrum provide up to three months of protection against infestations of *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* (Guedes et al. 2008a). A combined treatment of spinosad 1 mg kg^{-1} plus chlopyrifos-methyl 10 mg kg^{-1} can control all the four *Liposcelis* species, but the high application rate of 10 mg kg^{-1} of chlopyrifos methyl may restrict its use to seed treatments only (Nayak and Daglish 2007). Some insect growth regulators such as fenoxycarb seem to be effective against *L. bostrychophila* when applied to their diet (Buchi

1994). However, pyriproxyfen, applied as a surface treatment on concrete is not effective against *L. bostrychophila*, *L. decolor*, and *L. paeta* (Athanassiou 2011). Chlorfenapyr, which belongs to a group of microbially-produced compounds called halogenated pyrroles, is effective as a surface treatment (Guedes et al. 2008b). The use of alternating controlled atmospheres (35% CO_2 and 1% O_2) and organophosphate insecticides (e.g. dichlorvos) delays the development of resistance by psocids and also provides a significant increase in mortality compared to using these tactics individually (Wei et al. 2002).

Phosphine fumigation is a popular strategy to manage stored product pests. However, the use of phosphine is a major challenge because psocids may be naturally tolerant or have developed high levels of resistance (Nayak et al. 2002). Nayak et al. (2003) stated that the egg stage of psocids is the most tolerant to phosphine fumigation. Also, psocid populations recover more rapidly from poorly conducted phosphine fumigations than beetle pests (Roesli 1998). Phosphine together with high temperature and low RH manipulation are needed to provide the shortest fumigation period to control resistant psocid species (*L. bostrychophila*) (Nayak and Collins 2008). Methyl bromide is more effective at managing all life stages of *L. entomophila*, *L. decolor*, *L. bostrychophila*, *L. paeta* than sulfuryl fluoride (Athanassiou et al. 2015), but the former insecticide has been phased out of use in mills and warehouse in the US.

Physical Control Methods

The difficulties encountered in managing psocids with chemical insecticides have inspired research into tactics that could be used as alternatives or used to support chemical application which forms part of integrated pest management techniques (Phillips and Throne 2010). Heat treatment can be employed as an alternative to insecticides to manage psocids (Opit et al. 2011). Beckett and Morton (2003) investigated the effect of moderately elevated

temperatures on three psocid species—*L. bostrychophila*, *L. decolor*, and *L. paeta* (≈ 45 to 55ºC) and found out that psocid adults were more vulnerable while eggs were relatively more tolerant to heat disinfestation. Additionally, psocid species show a variable response to heat treatment and are more susceptible to heat disinfestation than *R. dominica* or *S. oryzae* (Beckette and Morton 2003). Although heat treatment can be effectively used to control psocids, it may not be practical to directly apply heat to stored food commodities and heat sensitive equipment in facilities (Phillips and Throne 2010). Heat treatment can alter the nutrient composition of some food products. Cold treatment, an ecologically based technique, can be used to manage all life stages of *L. entomophila*, *L. paeta*, *L. bostrychophila*, and *L. decolor*—with the exception of *L. bostrychophila* eggs, complete mortality of psocids is attained when exposed to -18ºC for 24 h (Arthur et al. 2017). The use of diatomaceous earth (DE) is another way of controlling stored-product insect pests, and it is used in systems with lower RH (Korunic et al. 1996). DE absorbs hydrocarbons from cuticles of insects initiating lethal dehydration (Phillips and Throne 2010). Athanassiou et al. (2009) demonstrated that DE, when used alone, does not reduce progeny production of *L. entomophila*, *L. reticulatus*, and *L. decolor*. Psocids multiply in environments with RHs ≥63%, but do not survive below 55% (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010, Gautam et al. 2015). Therefore, low RH (dehumidification) can be used as a physical control to manage psocids (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Sanitation is one of the most important and fundamental management practices that is used to exclude pests from food packages and storage areas because it limits the resources pests need for their survival and reproduction (Phillips and Throne 2010).

Ecology of Psocids

From the many species of psocids described worldwide, in only few cases has the biology of these species been explored (Fahy 1971, Khalafalla 1990, Wang et al. 2000, Wang et al. 2001, Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015) and most of these studies have focused on *L. bostrychophila.* These studies have mostly investigated the effects of environmental conditions on the development and population dynamics of psocids. Temperature and RH are factors known to affect the rate of psocid population growth (Nayak et al. 2014). The development of psocids from egg through to adult is paurometabolous: simple, incomplete metamorphosis involving several nymph stages (Nayak et al. 2014). Psocids, like many other insects, are ectothermic—they depend on ambient temperature for their growth and survival. However, beyond the required temperature range, temperature adversely affects biological processes, resulting in increased development time (Kingsolver et al. 2013).

The bodies of psocids contain water which is directly proportional to the humidity in the surrounding environment. An environment containing <60% RH is regarded as a dry and critical atmosphere for psocids; they actively transport water vapor into their bodies, enabling them to replace transpired water and maintain body weight even in the absence of food that contains moisture (Knülle and Spadafora 1969, Devine 1982). In high humidity environments, psocid lifespans relatively range from six months to one year (Broadhead and Hobby 1944). Their reproduction and population growth can be stopped by lowering the humidity in the environment as well as grain moisture content (Knülle and Spadafora 1969). To facilitate making pest management decisions and predicting the potential geographical distribution of psocids, an in-

depth understanding of their biology and the factors that influence their population growth is required (Opit and Throne 2008).

Effects of Temperature and Relative Humidity on Population Growth

According to literature, *L. reticulatus, L. brunnea, L. rufa, L. fusciceps* and *L. pearmani* survived at all temperatures within the 22.5ºC to 40ºC range at 75% RH. Ideal population growth conditions for *L. reticulatus, L. brunnea, L. rufa, L. fusciceps* and *L. pearmani* were; 32.5°C and 75% RH, 32.5°C and 63% RH; 35°C and 75% RH, 30ºC and 75%; 32.5°C and 75% RH, respectively. From an initial number of five adult females each, populations of these psocid species increased by 21- (*L. reticulatus*), 17- (*L. brunnae*), 73- (*L. rufa*), 16- (*L. fusciceps*), and 31-fold (*L. pearmani*), under optimum conditions. *L. reticulatus* populations increased over a 46-d period whereas those of the other four species increased over a 30-d period (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). *Lepinotus reticulatus* has a limited set of conditions for survival (22.5 to 32.5ºC at 75% RH), and it appears that they may multiply under lower temperatures and more humid environments (Opit and Throne 2008). None of the five species studied survived at 43% RH at all the temperatures tested (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Rees and Walker (1990) also stated that none of the three psocid species they investigated (*L. bostrychophila, L. entomophila,* and *L. paeta*) survived at RHs below 60%. The optimum temperature and RH for the survival and reproduction of *L. entomophila* and *L. bostrychophila* were 30°C and 70–80% RH, but none survived at temperatures ≥ 36°C (Rees and Walker 1990). However, *L. peata* reproduced more rapidly at 33–36°C and 70% RH.

Effects of temperature on development

Temperature did not have any effect on egg viability of *L. reticulatus*, *L. rufa*, *L. brunnea*, *L. fusciceps*, and *L. pearmani* (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). However, the viability of eggs of *L. bostrychophila*, *L. badia*, *L. decolor*, *L. paeta*, *L. tricolor*, and *L. yunnaniensis* was affected by temperature (Wang et al. 2000, Dong et al. 2007, Jiang et al. 2008, Tang et al. 2008, Wang et al. 2009, Hassan et al. 2011). As expected, most studies show that incubation time decreased with increasing temperature (Gautam et al. 2015). For all the species studied, lower and higher temperatures proved to be detrimental to nymphal survival and mortality occurred at the early instar stages. Optimal developmental temperatures of 35, 35, 35, 35, 37.5 and 37.5ºC have been found for *L. brunnea*, *L. fusciceps*, *L. decolor*, *L. entomophila*, *L. paeta*, and *L. rufa*, respectively, and this suggests that these species are likely to occur in relatively warm areas. However, Gautam et al. (2015) reported that *L. fusciceps*, although having an optimum developmental temperature between 35.0 and 37.5ºC, had lower population growth compared to *L. entomophila*, *L. paeta*, and *L. rufa*. The lower population growth of *L. fusciceps* compared to *L. entomophila*, *L. paeta*, and *L. rufa* suggests that it may have a narrower ecological distribution and may not be a major pest, particularly in warm areas. Females of *L. rufa*, *L. fusciceps*, and *L. pearmani* are reported to have two to five instars while males have two to four (Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). *L. reticulatus* and *L. obscurus* (species found in Egypt) have four instars (Khallafala 1990, Opit and Throne 2008). *L. brunnea* females have three to five instars while the males have two to four instars (Opit and Throne 2009). The mean developmental period of females is usually longer than that of males because females generally have one more instar than the males (Gautam et al. 2015). Exuviae consumption was found to

occur more commonly in *L. reticulatus* than in other sored-product psocid species. Development was found to be slower for *L. reticulatus* individuals that did not consume their exuviae (Opit and Throne 2008). Exuviae contain lipids and nitrogenous compounds that account for 4.4% (Nelson and Sukkestad 1975) and 87% (Mira 2000), respectively, of the total weight of insect exuviae. Therefore, the consumption of exuviae seems to be beneficial to psocid development.

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CHAPTER III

POPULATION GROWTH AND DEVELOPMENT OF *LIPOSCELIS OBSCURUS* BROADHEAD (PSOCOPTERA: LIPOSCELIDIDAE) AT CONSTANT TEMPERATURES AND RELATIVE HUMIDITIES

Abstract

The effects of nine temperatures (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, 40.0, and 42.5°C) and four RHs (43, 55, 63, and 75%) on the population growth and development of the parthenogenetic *Liposcelis obscurus* Broadhead (Psocoptera: Liposcelididae) were investigated in laboratory studies. Results showed that *L. obscurus* did not survive at 43% RH at all temperatures tested. At 55% RH, *L. obscurus* survived at 22.5, 25, and 27.5°C; none survived at 42.5°C and ≤63% RH. Population growth was highest at 40.0°C and 75% RH, where population increase was a 215-fold from an initial population of five adult females. *L. obscurus* has three-to-five nymphal instars, and the percentages of third, fourth, and fifth instars were 52, 41, and 7%, respectively. Temperature-dependent developmental equations were developed for *L. obscurus* eggs, individual nymphal, combined nymphal, and combined immature stages. *L. obscurus* populations grew faster at 30–42.5°C and 75% RH. These data provide a better understanding of *L. obscurus* population dynamics, and can be used to develop effective management strategies for this psocid.

KEY WORDS psocid, stored-product, population growth, development rate, *Liposcelis obscurus*

Introduction

Psocids of the genus *Liposcelis* (Psocoptera: Liposcelididae) have emerged as important pests of stored products worldwide over the last two-to-three decades (Nayak et al. 2014). Psocids are mostly found in grain food stores, food processing facilities, and they thrive on a variety of food products (Opit and Throne 2008a, Athanassiou et al. 2010). Psocid infestations do not only affect grain weight loss but also cause significant germination failure by feeding on the germ and endosperm (Kučerová 2002, Gautam et al. 2013). Psocids have a short generation time at elevated temperatures which allows them to rapidly colonize new habitats (Nayak et al. 2014). The economic importance of psocids in a commodity is not just limited to direct feeding and contamination but also the fact that their presence can lead to rejection of infested commodities from domestic and international markets (Nayak 2006). Psocids are difficult to control using standard practices of protection and disinfestation (Wang et al. 1999, Beckett and Morton 2003, Athanassiou et al. 2009, Huang et al. 2009).

In the US, *Liposcelis* and *Lepinotus* are two genera of psocids that are found in large numbers in grain storages and are of economic importance (Gautam 2010, Opit et al. 2011). Four *Liposcelis* species of notable economic importance worldwide are *L. bostrychophila* Badonnel, *L. entomophila* (Enderlein), *L. decolor* (Pearman), and *L. paeta* Pearman, but examples of the other species with limited significance include *L. corrodens* Heymons, *L. brunnea* Motschulsky, *L. obscurus* Broadhead, and *L. rufa* Broadhead (Gautam et al. 2010, Lienhard and Smithers 2002).

The number of studies that have been conducted on the biology of psocids has been steadily increasing over the last 15 yr (Knülle and Spadafora 1969, Khalafalla 1990, Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al.

2015). These studies investigated the effects of physical conditions (temperature and RH) on the development and population growth of psocids; they showed that psocids survive at RHs ≥55% and thrive at optimum temperatures of 30–37.5°C. Development of an effective management program for any pest depends on sound knowledge of its ecology. Increased knowledge of a pest's ecology helps to develop effective integrated pest management (IPM) programs to mitigate its economic impact.

L. obscurus is an obligate parthenogen (Mockford 1993). The only ecological study conducted on *L. obscurus* published in the scientific literature investigated its biology; the effects of temperature and food on the reproductive parameters of *L. obscurus* (Khalafalla 1990). Studies were initiated on the population growth and development of *L. obscurus* to provide data for the development of management strategies for this pest. Objectives were to determine the effects of constant temperatures and RHs on the population growth of *L. obscurus* and to quantify the effects of temperature on the development of *L. obscurus.*

Materials and Methods

Insects. Cultures of *L. obscurus* used in this study were started using insects collected from peanut (*Arachis hypogaea*) warehouses in Oklahoma. Voucher specimens of 100 *L. obscurus* preserved in 95% ethyl alcohol that were used in this study were deposited at the K.C. Emerson Entomology Museum at Oklahoma State University under lot numbers 119 (females). Psocids were reared on a mixture of 93% cracked wheat (*Triticum aestivum* L.) (Duster variety), 5% Rice Krispies (Kellogg North America Company, Battle Creek, MI), and 2% wheat germ (The Quaker Oats Company, Chicago, IL) (wt/wt; referred to as psocid diet hereafter) in 360-ml glass canning jars with mite-proof lids (Opit and Throne 2008b). The top one-third of the inner surface of each jar was coated with Fluon (polytetrafluoroethylene; Northern Products,

Woonsocket, RI) to prevent psocids from accessing and gathering on the inside of the lid. Cultures were placed inside a growth chamber maintained at 30.0 ± 1°C in plastic boxes (42 x 29 x 24 cm high) painted black, which had saturated NaCl solution beneath perforated false floors to maintain a RH of 75 ± 5% RH. The boxes were painted black to mimic dark conditions in which psocids are typically found.

Effects of Temperature and Relative Humidity on Population Growth. The effects of nine temperatures (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, 40.0, and 42.5^{o}C) and four RH (43, 55, 63, and 75%) on the population growth of *L. obscurus* over a 30-d period were determined. The inner sides of 108 Petri dishes (100 x 25-mm high) were coated with Fluon to prevent psocids from escaping. Into each Petri dish, 5 g of red colored diet, 1 g of cracked duster wheat, and 0.5 g wheat germ (hereafter referred to as diet) were placed. The mixture of red colored diet, cracked duster wheat, and wheat germ was used as diet because *L. obscurus* did not survive on the usual cracked wheat diet. The plastic Petri dish lids were replaced. Red colored diet was made by mixing 100 g of Rice Krispies with a solution of 5 ml of red food dye (Global Chem Sources Inc., Cedar Grove, NJ) in 300 ml of water, drying the mixture in a mechanical convection oven (model HTM 85, Precision Scientific, Inc., Chicago, IL) for 6 h, and then grinding the dried mixture in a Wiley Mill. A U.S. Standard #20 sieve (0.85-mm openings) (Scientific Apparatus, Philadelphia, PA) was used to sieve the diet. Petri dishes with diet were randomly put in four plastic boxes (42 x 29 x 24 cm high) containing each of the saturated solutions of K_2CO_3 (43%), NaBr (55%), $NaNO_2$ (63%), and NaCl (75%) (Greenspan 1977) beneath perforated false floors to maintain the required RH. Petri dishes were kept at the four RHs to equilibrate the diet in them at room temperature for 4 wk. Each box had 27 Petri dishes.

To obtain 1- to 2-wk-old *L. obscurus* adult females required for the experiment, 300 female late-instar nymphs of *L. obscurus* were picked from culture jars and placed in six 9-cm Petri dishes with Fluon-coated sides. Each Petri dish had 5 g of colored psocid diet, 1 g of cracked duster wheat, and 0.5 g of wheat germ in it. The Petri dishes were placed on perforated false floors of one black Rubbermaid plastic box (32 x 18 x 13 cm). The late instar nymphs were maintained at 75 ± 5% RH.

After 4 wk of diet equilibration, five 1- to 2-wk-old adult *L. obscurus* were placed in each of the 108 Petri dishes containing equilibrated diet. Nine incubators (Thermo Fisher Scientific; Waltham, MA) were set at temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, 40.0, and 42.5^{o}C, where four plastic boxes (17 x 17 x 12 cm high) containing saturated solutions of K_2CO_3, NaBr, $NaNO_2$, and NaCl were placed. Three Petri dishes containing diet, equilibrated at room temperature and each RH, were randomly assigned to the corresponding RH box in all incubators. Four locations were established in every 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 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; this was done by making sure that the desired amounts of the solute and solution of the saturated solution were present in each box. Environmental conditions in each incubator were monitored using a temperature and RH sensor (HOBO U12, Onset Computer Corporation, Bourne, MA). Live insects in each Petri dish 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 inner walls, and removing all motile *L. obscurus* using a moist brush under a stereomicroscope (Zeiss Stemi 2000-C; Thornwood, NY).

The experiment had three temporal replications, and the experimental design was a randomized complete block design (RCBD) with subsampling. Statistical procedures were done by using Statistical Analysis System software version 9.4 (SAS Institute 2014). PROC MIXED was used for analysis of variance (ANOVA) to determine the effects of temperature and RH on the number of psocids in the Petri dishes. These were transformed using the square root transformation to stabilize variances before analysis. Untransformed means and standard errors are reported for straightforward interpretation. We used the least significant difference (LSD) test to determine differences among mean numbers of psocids produced at the various temperatures and RHs despite the quantitative independent variables, because we were not able to quantify the relationship using a biologically meaningful equation (TableCurve 3D) (Systat Software, Inc. 2002a). A mathematical expression that adequately describes the relationship in a biologically meaningful way (in this case, relationship between temperature and RH to psocid population increase) is known as a biologically meaningful equation.

Effects of Temperature on Development. Eggs were obtained by placing 1 g of red colored diet, 5 particles of wheat germ, and 30 adult female psocids of unknown age from our psocid cultures in each of eighty 35-mm-diameter Petri dishes (Greiner Bio-One, Kaysville, UT), which had a coat of Fluon on the sides. Procedures used to obtain the red colored diet were similar to those described above for the effects of temperature and RH on population growth of *L. obscurus*. Red colored diet was used because psocids prefer to lay eggs between diet particles. Additionally, the red colored diet made it easy to see eggs and helped us to assess whether numbers of eggs were sufficient for the experiment. The Petri dishes were placed in two black Rubbermaid plastic boxes (30 x 23 x 9 cm high) that contained saturated NaCl solution (75% RH) beneath a perforated false floor. Boxes were placed in an incubator maintained at 40 ± 1^{o}C.

After 2 d, adult females were taken off, and the diet in each Petri dish was examined for eggs by using a dissecting microscope at 25x magnification. Each egg was carefully transferred into a flat cap of 1.5-ml centrifuge cup (LabSource Inc., Willowbrook, IL) with the help of a moist camel's-hair brush. The centrifuge cap was then placed inside a 25-mm diameter vial cap. The inner sides of centrifuge caps, vial caps, and 35-mm Petri dishes were coated with Fluon. The vial cap had three cracked wheat kernel (with a centrifuge cap inside it) and was placed inside a 35-mm Petri dish; a cracked wheat kernel was placed in the centrifuge cap. One egg transferred from the colored diet was placed on the floor of each of the 270 centrifuge caps, and the 35-mm Petri dish lids replaced. Thirty centrifuge caps (associated with vial caps and Petri dishes) were randomly placed in each of nine Rubbermaid plastic boxes (37 x 22 x 13-cm high; 270 centrifuge caps total) that were painted black and contained saturated NaCl solution to maintain 75% RH. One box was placed in each of the nine incubators set to maintain treatment temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, 40.0, and 42.5°C. Temperatures above 42.5°C were not tested because preliminary experiments had shown that *L. obscurus* eggs do not hatch at temperatures above 42.5^{o}C. The experiment had two temporal replications.

To estimate the incubation period of eggs, development of eggs was monitored daily with the aid of a dissecting microscope at 25x magnification. To mark insects after egg hatch to determine when one developmental stage ended and the next began, rocket red fluorescent powder (Day-Glo Color Corp., Cleveland, OH) was used. A fine camel's-hair brush altered by decreasing the number of hairs on it to one, and further shortening the length of that hair to 7 mm was used to apply the powder on the insects. The single hair of the modified camel's-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 an amount of powder as possible, and the powder on the brush was gently rubbed against the body of each psocid under observation.

After egg hatch, either the abdomen, thorax or both of each first instar (N1) was dusted with fluorescent powder. N1 psocids were not transferred to the vial caps until they had molted into second instar (N2). At the N2 stage, psocids were strong enough to endure handling. Each N2 was then transferred from the centrifuge cap into the larger vial cap, and the centrifuge cap together with the cracked wheat particle in it was removed. Nymphs in vial caps were examined daily, using a dissecting microscope at 25x magnification, to monitor development. The absence of fluorescent powder on the abdomen, thorax, or both on the nymphs indicated a molt had occurred. After each molt, psocids were immediately marked again. Additionally, vial caps were examined daily for exuvium to determine when a molt had occurred and whether the exuvium had been consumed or not. Any exuvium found was removed from the vial cap immediately. The psocid was not removed from the vial cap throughout the marking process. Any fluorescent powder that dropped on the vial cap floor and or on any cracked grain was completely cleaned up using a moist camel's-hair brush.

In the determination of the effects of temperature on the duration of development of *L. obscurus*, PROC MIXED was used for analysis of variance (ANOVA). The experimental design for the analysis of the proportions of viable eggs and nymphs that developed to the adult stage was an RCBD. Regression (TableCurve 2D; Systat Software 2002b) was used to describe the relationship between temperature and development time for the egg, individual nymphal, combined nymphal, and combined immature stages. Fitting curves with nonlinear regression showing the relationship between temperature and development time for the individual developmental stages were constructed using SigmaPlot version 10.0 (Systat Software 2006).

The selection of an equation used to describe the data was based on the magnitude and pattern of residuals, lack-of-fit tests, and whether the curve had a reasonable shape to describe the data. In the analysis of the proportions of viable eggs and nymphs that developed to the adult stage, the design for analysis was a RCBD. To analyze the proportions of viable eggs and nymphs, PROC MIXED was used for ANOVA after arcsine square-root transformation to stabilize variances.

The lower developmental threshold for *L. obscurus* was determined by fitting a linear equation to development rate (reciprocal of development time) and temperature data using TableCurve 2D (Systat Software Inc. 2002b). The upper developmental thresholds were obtained by fitting the appropriate equation to all the development rate and temperature data and by using the "EVALUATION" procedure in TableCurve 2D (Systat Software Inc. 2002b).

Results

Effects of Temperature and Relative Humidity on Population Growth. The nine temperatures and four RHs tested affected *L. obscurus* population growth (Table 1). No live *L. obscurus* were found at 43% RH for all temperatures; at 55% RH and 30–42.5C; and 63% RH at 42.5°C. Numbers of *L. obscurus* at 35 and 37.5°C and 75% RH were very similar—approximately a 143-fold increase in population, in 30 d, for each temperature. Population growth was highest at 40.0°C and 75% RH, where population increase was 215-fold (Table 1). At 42.5°C and 75% RH, *L. obscurus* populations declined.

Effects of Temperature on *L. obscurus* Development. *Eggs*. Incubation varied with temperature and the relationship between temperature and incubation time was well described by a quadratic equation (Fig. 1A; Tables 2 and 3). The optimal incubation temperature is 40.0°C, and development is completed in 4.1 d. The predicted optimal incubation temperature is 39.7°C and development is completed in 39.7 d, based on the quadratic equation.

Nymphal and *Combined Nymphal Stages*. Duration of the nymphal and combined nymphal stages varied with temperature (Fig. 1B–E; Tables 2 and 3). Quadratic equations described the relationship between temperature and development time well for individual nymphal and combined nymphal stages (Table 3). Temperature had a significant effect on development time for N1 (first instar), N2 (second instar), and N3 (third instar) (Fig. 1B–D); where development time decreased with increasing temperature. Based on analysis of data for all nymphs that developed to adults, combined nymphal development time averaged 28.6 d at 25ºC and declined to 11.6 d at 40.0ºC. However, developmental time increased slightly at 42.5ºC and development is completed in 11.8 d, respectively (Table 2). Based on the quadratic equation for the combined nymphal stages, the predicted optimal developmental temperature is 41.1ºC and development is completed in 11.7 d.

Combined Immature Stages. The analysis of data for all individuals that developed to adults showed that temperature had a significant effect on total developmental time from egg to adult (Table 2), and a quadratic equation fit the data well (Fig. 1F; Table 3). Total developmental time from egg to adults averaged 42.7 d at 25°C and declined to 15.8 d at 40.0°C. However, developmental time increased slightly at 42.5 and development is completed in 16 d, respectively (Table 2). Based on the quadratic equation for total developmental time, the predicted optimal incubation temperature is 41.7°C and development was completed in 11.8 d. The upper developmental threshold was estimated as 43.9°C. The lower developmental threshold was estimated as 13.2ºC using a linear equation that best described the development rate and temperature relationship. Based on this study, *L. obscurus* has three to five nymphal instars, and the percentages of third, fourth, and fifth instars were 52, 41, and 7%, respectively.

Effects of Temperature on Egg Viability and Nymphal Survivorship. Temperature affected egg viability (F = 3.8; df = 7, 7; P = 0.049), which ranged from 83% to 100% and averaged 91.5% for all temperatures. Temperature had no effect on nymphal survivorship (F = 1.0; df = 1, 1; P = 0.50). Proportions of nymphs surviving to adults at the nine different temperatures ranged from 65-73%.

Discussion

Results from this study show that *L. obscurus* did not survive at 43% RH at any of the temperatures tested; at 55% RH and 30.0–42.5ºC; and at 63% RH and 42.5ºC. The optimal temperature and RH for population growth of is *L. obscurus* are 40.0ºC and 75% RH. *Lepinotus reticulatus, L. brunnea, L. rufa, L. pearmani,* and *L. fusciceps* have also been reported not to survive at 43% RH (Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Although *L. obscurus* survived and barely multiplied at 55% RH and 22.5–27.5ºC over 30 d, data indicate it will not thrive at this low RH. At 63% RH, a low temperature of 22.5ºC results in limited increase in population, and a high temperature of 42.5ºC kills all psocids. At 75% RH, a low temperature of 22.5°C results in limited increase in *L. obscurus* population. Rees and Walker (1990) observed that *L. bostrychophila, L. entomophila,* and *L. paeta* did not survive at low RHs (<60%). Knulle and Spadora (1969) stated that below the equilibrium RHs of psocids, death occurs. According to Devine (1982), high atmospheric water vapor of ≥60% RH is necessary for psocids to maintain body water levels by absorption; however, below this level, more moisture is lost than gained, which results in dehydration and death. At 30.0°C and 55% RH, *L. obscurus* did not survive, but *L. brunnea, L. rufa,* and *L. fusciceps* populations grew, although growth was slow (Opit and Throne

2009, Gautam et al. 2010). *L. brunnea*, *L. rufa*, and *L. fusciceps* are probably well adapted in a manner that enables them to absorb atmospheric water vapor even when RH is as low as 55%.

The highest population growth for *L. obscurus* occurred at 40.0ºC and 75% RH. RH of 75% has also been found to be optimal for the population growth of *L. reticulatus*, *L. rufa*, *L. pearmani*, and *L. fusciceps* but 63% RH was optimal for *L. brunnea*. Optimum temperatures for these species were 30.0C° for *L. fusciceps;* 32.5°C for *L. reticulatus*, *L. pearmani, and L. brunnea;* and 35.0°C for *L. rufa* (Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Optimal RH for *L. brunnea* (63%) explains why it mainly occurs in the relatively drier parts of US compared with other species (Gautam et al. 2010). However, its distribution may be limited by high temperatures of 35.0°C or higher (Opit and Throne 2009). Rees and Walker (1990) showed that the optimum conditions for *L. bostrychophila*, *L. entomophila*, and *L. paeta* are 30.0°C and 80% RH, 30°C and 70% RH, and 33°C and 70% RH, respectively. *L. rufa* barely survives at 40.0°C (Gautam et al. 2010). Therefore, higher temperatures may limit *L. rufa* distribution although it reproduces relatively well at lower RHs and temperatures (55% RH and 22.5–30.0ºC) compared to *L. obscurus*. The optimum conditions for *L. obscurus* (40.0ºC and 75% RH) imply that it is expected to have a broader distribution than *L. rufa*, and be more abundant in hot and humid areas. Based on this study, *L. obscurus* is capable of surviving and multiplying at moderately high rates at 42.5°C.

Temperature affected *L. obscurus* egg viability, and the percentage of viable eggs averaged 91.4% across all temperatures. Temperature also affected egg viability of species such as *L. bostrychophila*, *L. tricolor* Badonnel, *L. badia* Wang, Wang, and Lienhard, *L. decolor*, *L. paeta*, and *L. yunnaniensis* Li & Li; these species were geographical strains from China (Wang et al. 2000, 2009, Dong et al. 2007, Jiang et al. 2008, Tang et al. 2008, Wang et al. 2009, Hassan et

al. 2011). Temperature did not affect the egg viability of *L. reticulatus* (87%), *L. brunnea* (80%), *L. rufa* (90%), *L. pearmani* (86%), and *L. fusciceps* (91%); these species were geographical strains from the US (Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015).

RHs of ≤63% RH and 25 and 27.5^{o}C had a detrimental effect on the survival and population growth of *L. obscurus.* Temperatures >40^{o}C at both 63 and 75% RH are detrimental to *L. obscurus.* Previous studies have also shown that both low and high temperatures are detrimental to psocid nymphal survival and development in the cases of *L. reticulatus*, *L. brunnea*, *L. rufa*, *L. pearmani*, and *L. fusciceps* (Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015).

L. obscurus has three to five nymphal instars, and the percentages of third, fourth, and fifth instars were 52, 41, and 7%, respectively. *L. brunnea* females were also found to have three to five nymphal instars with a higher percentage having four nymphal instars (78%) compared with *L. obscurus* which has a higher percentage of insects with three nymphal instars. However, Khalafalla (1990), reports that the *L. obscurus* strains found in Egypt have exactly four instars. Opit and Throne (2008b), report that *L. reticulatus* (a parthenogenetic species) also has four nymphal instars. Males and females of bisexual *Liposcelis* species are found to have two to four and two to five nymphal instars, respectively (Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Due to the additional number of instars female psocids have, the developmental period of females is longer than that of males. The evolution of a variable number of *Liposcelis* instars may be to prolong their survival in adverse conditions (Aminatou et al. 2011). According to Mockford (1993), psocids usually have four to six nymphal stages.

The optimal temperature for *L. obscurus* development from egg to adult was 40.0ºC and development was completed in 15.8 d. The optimal temperature for development of female *L. badia*, *L. bostrychophila*, *L. reticulatus*, *L. pearmani*, and *L. tricolor* was 32.5ºC and development were completed between 17 and 31 d (Wang et al. 2000, Dong et al. 2007, Jiang et al. 2008, Opit and Throne 2008, Aminatou et al. 2011). For *L. brunnea*, *L. entomophila*, *L. decolor*, and *L. fusciceps*, the optimal temperature for development was 35.0°C and development were completed in 23.6, 21.7, 16.1, and 19.0 d, respectively; also, *L. paeta* and *L. rufa*'s development were completed in 11.5 and 21.6 d, respectively, at 37.5°C (Tang et al. 2008, Wang et al. 2008, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). At the optimal temperature of 40.0°C, development of *L. obscurus* from eggs to adult takes a slightly shorter time compared to other psocids that have been studied.

Liposcelis decolor, *L. entomophila*, *L. paeta*, and *L. rufa* have higher optimal temperatures for development. Guedes et al. (2008) found *L. entomophila* to have higher variability and greater tolerance to heat shock stress than *L. reticulatus*. Although heat shock protein of 70 kDa (HSP 70) was not identified, small heat-inducible proteins (23 and mainly 27 kDa) having a common epitope with HSP 70 were found. The higher optimal temperatures for development for *L. decolor*, *L. entomophila*, *L. paeta*, and *L. rufa* may be due to the presence of small heat-inducible proteins which enable heat tolerance; this may explain why these species are commonly found in large numbers during the summer and fall months of the year when temperatures are high in grain storage structures compared to *L. reticulatus* (Opit et al. 2011). By inference, *L. obscurus* with the highest optimal temperature (40.0°C) for development among psocids so far studied would be expected to have higher levels of heat shock proteins or small heat-inducible proteins which enable heat tolerance.

Based on this study, *L. obscurus* is predicted to be more abundant and a major pest in hot and humid areas of the world. That being said, to the best of our knowledge *L. obscurus* has only been reported twice—it was found infesting a peanut warehouse in Oklahoma, US and in stored rice in Egypt. Possible reasons for why *L. obscurus* has not been frequently reported may be due to lack of research or misidentification of this species. Research needs to be conducted on the heat shock proteins of *L. obscurus.*

Temperature-dependent equations for the development of *L. obscurus* eggs, individual nymphal, combined nymphal, and combined immature stages developed in this study describe the relationship between temperature and development time for these life stages well. This study shows that the predicted optimal temperatures for eggs, combined nymphal, and combined immature development were 39.7, 41.1, and 41.7^{o}C, respectively. At these temperatures, development is completed in 4.4, 11.7, and 11.8 d, respectively. Based on the developed equations, predicted time for development of *L. obscurus* decreased with increasing temperature and similar relationships have been developed for other *Liposcelis* species (Opit and Throne 2008b, Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015).

Based on our data, the upper and lower developmental thresholds for *L. obscurus* combined immature stages were 43.9^{o}C and 13.2^{o}C, respectively. The upper developmental threshold of *L. obscurus* was higher than that *L. bostrychophila, L. rufa, L. pearmani, L. yunnaniensis, L. paeta, L. tricolor,* and *L. decolor* whose upper developmental thresholds were 38.8, 38.7, 33.1, 40.52, 42.0, 38.98, and 42.04^{o}C, respectively (Wang et al. 2000, 2009, Dong et al. 2007, Tang et al. 2008, Gautam 2010, Aminatou 2011, Hassan et al. 2011). The lower developmental threshold of *L. obscurus* was lower than that of *L. bostrychophila* (15.5^{o}C), *L. paeta* (20.2^{o}C), and *L. pearmani* (13.9^{o}C). However, the lower developmental threshold of *L.*

obscurus was greater than that of *L. rufa* (8.5^{o}C), *L. badia* (10.0^{o}C), *L. tricolor* (11.3^{o}C), *L. fusciceps* (11.9^{o}C), *L. decolor* (13.0^{o}C), and *L. yunnaniensis* (13.02^{o}C) (Wang et al. 2000, 2009, Dong et al. 2007, Jiang et al. 2008, Tang et al. 2008, Gautam et al. 2010, Hassan et al. 2011, Aminatou et al. 2011). The temperature-dependent equations for the development of *L. obscurus* developed in this study can be used to provide valuable information for explaining the population dynamics of this species (Summers et al. 1984) and can be used to optimize management strategies for it.

This study demonstrates how temperature and RH affect *L. obscurus* population growth and development. *L. obscurus* is not expected to be a serious pest in grain storages where temperatures are 27.5°C or less. Given that *L. obscurus* had a relatively higher population growth over a 30-d period compared to other *Liposcelis* species at higher temperatures of 35–42.5°C and 75% RH, we expect it to be (or become) a predominant pest in hot and humid areas. Finally, the temperature dependent equations developed for this species could be used to understand *L. obscurus* population dynamics and to develop effective management strategies.

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Table 1. Number (±SE) of motile *Liposcelis obscurus* present in Petri dishes after 30 d (n = 9).

Temp (°C)	Relative humidity (%)			
	43	55	63	75
22.5	0.0 ± 0.0 i	5.89 ± 0.70 i	9.33 ± 1.44 i	6.78 ± 0.76 i
25.0	0.0 ± 0.0 i	13.67 ± 2.73 i	31.89 ± 3.65 hi	25.0 ± 3.09 i
27.5	0.0 ± 0.0 i	16.56 ± 4.9 i	47.67 ± 9.02 ghi	51.67 ± 7.0 ghi
30.0	0.0 ± 0.0 i	0.0 ± 0.0 i	112.0 ± 16.11 fgh	81.44 ± 9.3 ghi
32.5	0.0 ± 0.0 i	0.0 ± 0.0 i	180.11 ± 22.95 ef	293.44 ± 40.51 d
35.0	0.0 ± 0.0 i	0.0 ± 0.0 i	430.67 ± 80.0 c	714.56 ± 95.1 b
37.5	0.0 ± 0.0 i	0.0 ± 0.0 i	223.67 ± 41.55 de	714.67 ± 65.85 b
40.0	0.0 ± 0.0 i	0.0 ± 0.0 i	122 ± 41.57 fg	1077.89 ± 79.36 a
42.5	0.0 ± 0.0 i	0.0 ± 0.0 i	0.0 ± 0.0 i	281.33 ± 50.54 d

ANOVA results for temperature and relative humidity interaction were $F = 34.5$; df = 24, 70; $P < 0.0001$. Means within a column or row followed by the same letter(s) are not significantly different ($P > 0.05$).

Table 2. Duration (d ± SE) of immature stages of female *L. obscurus* at eight constant temperatures and 75% RH

		Duration (d)						
Temp (°C)	*n*	Eggs	N1	N2	N3	N4[a]	Nymphs	Eggs + nymphs
25.0	16	14.3 ± 0.23	8.6 ± 0.86	6.4 ± 0.61	7.6 ± 0.58	5.4 ± 1.03	28.6 ± 1.44	42.7 ± 1.49
27.5	21	10.3 ± 0.17	7.7 ± 0.52	5.1 ± 0.51	5.2 ± 0.37	3.0 ± 0.53	21.0 ± 0.43	29.2 ± 1.55
30.0	44	7.9 ± 0.08	6.4 ± 0.36	5.1 ± 0.30	3.8 ± 0.35	3.0 ± 0.55	16.9 ± 0.64	24.7 ± 0.63
32.5	38	6.5 ± 0.11	5.4 ± 0.25	5.9 ± 0.59	3.6 ± 0.29	3.1 ± 0.47	16.7 ± 0.77	22.8 ± 0.77
35.0	40	6.0 ± 0.08	5.6 ± 0.26	3.8 ± 0.28	3.3 ± 0.28	3.2 ± 0.68	14.5 ± 0.76	20.5 ± 0.75
37.5	37	4.8 ± 0.09	3.9 ± 0.27	4.2 ± 0.36	3.5 ± 0.28	2.0 ± 0.59	12.0 ± 0.51	16.7 ± 0.55
40.0	40	4.1 ± 0.05	4.0 ± 0.22	3.5 ± 0.25	3.1 ± 0.22	1.8 ± 0.35	11.6 ± 0.43	15.8 ± 0.43
42.5	36	4.5 ± 0.12	3.6 ± 0.17	3.9 ± 0.22	3.0 ± 0.18	3.0 ± 0.52	11.8 ± 0.51	16.0 ± 0.50

ANOVA for: eggs, N1, N2, N3, N4, combined nymphs, and combined immature stages were $F = 245.8$, $P < 0.0001$; $F = 11.6$, $P = 0.0022$; $F = 2.05$, $P = 0.1818$; $F = 12.3$, $P = 0.0019$; $F = 2.8$, $P = 0.0978$; $F = 46.6$, $P = 0.0001$; and $F = 85.0$, $P < 0.0001$, respectively. In all cases, df = 7, 7.

[a] Values of *n* for N4 at 25, 27.5, 30, 32.5, 35, 37.5, 40, and 42.5 were 13, 16, 20, 21, 19, 8, 20, and 11, respectively.

Table 3. Parameters (±SE) for quadratic equations ($y = a + b/x + c/x^2$) describing the duration of the egg, individual nymphal, combined nymphal, and combined immature stages of female *Liposcelis obscurus* at constant temperatures

Subject	Max. R^2	Adjusted R^2	*F*	a	b	c
Egg duration	0.99	0.98	505.3	20.87 ± 3.94	-1466.0 ± 255.2	32482.4 ± 4025.7
N1 duration	0.88	0.85	47.2	-2.52 ± 6.69	220.22 ± 432.97	1493.9 ± 6831.3
N2 duration	0.47	0.34	5.72	0.33 ± 9.89	127.5 ± 639.8	544.0 ± 10095.3
N3 duration	0.88	0.85	49.4	19.94 ± 5.49	-1266.9 ± 355.5	23825.1 ± 5609.3
N4 duration	0.61	0.52	10.3	13.4 ± 7.38	-821.9 ± 477.5	15300.2 ± 7534.1
Nymphal duration	0.94	0.93	103.8	35.9 ± 14.38	-2215.7 ± 929.9	50458.7 ± 14672.1
Egg + nymphal duration	0.95	0.94	130.0	62.64 ± 19.87	-4025.7 ± 1285.1	87232.9 ± 20275.9

N1, N2, N3, and N4 represent the first, second, third, and fourth instar, respectively.

In all cases, df = 2, 13 and $P = 0.000$ except for N2 and N4 where $P = 0.017$ and 0.002, respectively.

Lack-of-fit *P* values for the duration of the egg, N1, N2, N3, N4, combined nymphal, and combined immature stages were 0.38, 0.73, 0.76, 0.68, 0.12, 0.31, and 0.08 respectively.

Figure Caption

Fig. 1. Development of female *L. obscurus* at constant temperatures and 75% RH: (A) eggs, (B) second, (C) third, and (D) fourth instars, and (E) combined nymphal and (F) combined immature stages.

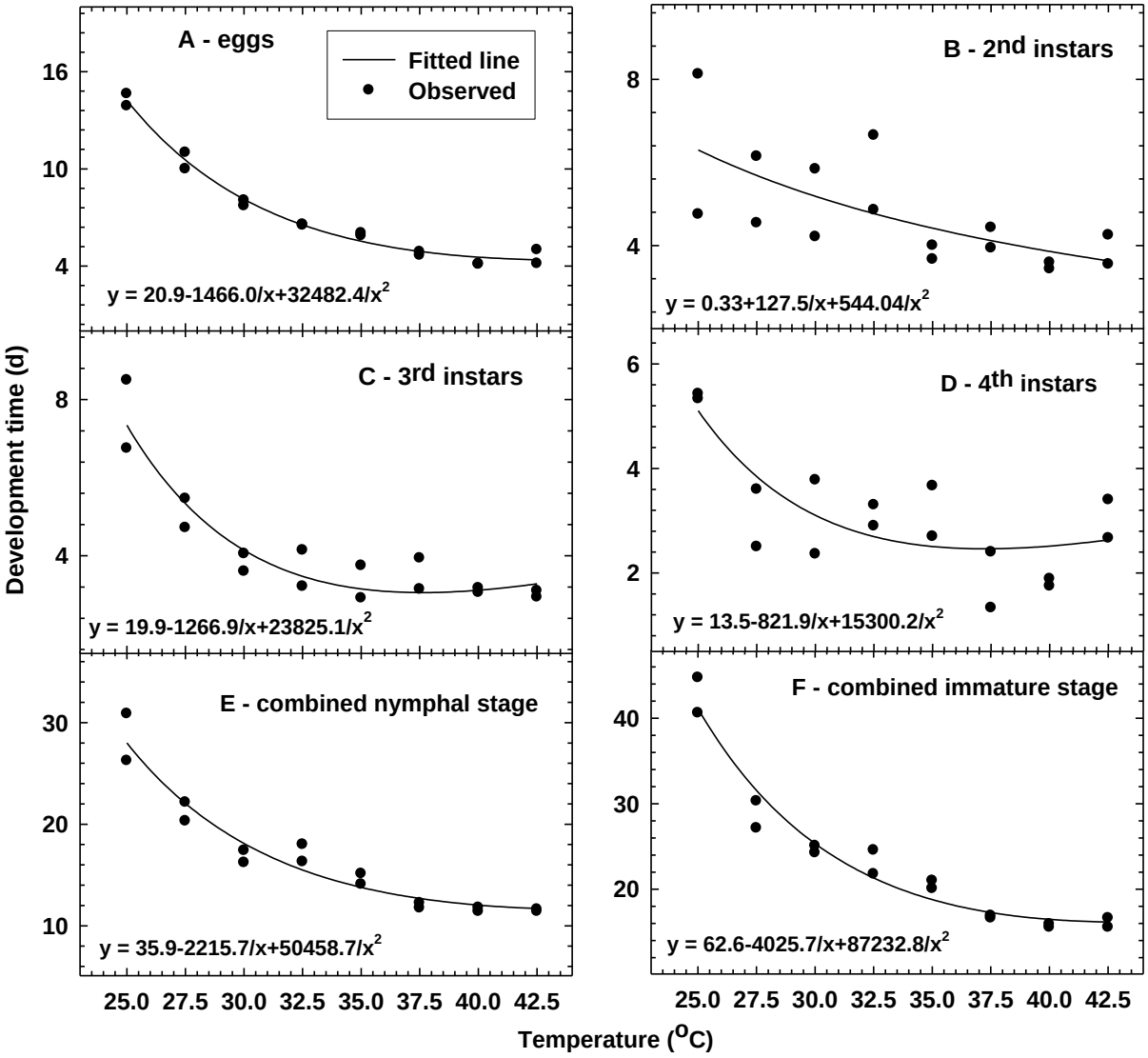
A - eggs
Fitted line
Observed
y = 20.9-1466.0/x+32482.4/x2
B - 2nd instars
y = 0.33+127.5/x+544.04/x2
C - 3rd instars
y = 19.9-1266.9/x+23825.1/x2
D - 4th instars
y = 13.5-821.9/x+15300.2/x2
E - combined nymphal stage
y = 35.9-2215.7/x+50458.7/x2
F - combined immature stage
y = 62.6-4025.7/x+87232.8/x2
Development time (d)
Temperature (OC)
25.0 27.5 30.0 32.5 35.0 37.5 40.0 42.5

Fig. 1

CHAPTER IV

EFFECTS OF LOW RELATIVE HUMIDITIES ON THE SURVIVORSHIP OF FOUR PSOCID SPECIES

Abstract

Psocids (Psocoptera) are important stored-product pests. In the present study, eggs and early instar nymphs, adults, and all life stages of *Liposcelis entomophila*, *Liposcelis decolor*, *Liposcelis bostrychophila*, and *Liposcelis paeta* were subjected to 43, 50, and 75% (control) relative humidities (RHs) for 2, 4, 6, 8, 10, 12, 14, and 16 d at 30.0ºC. All adults of four species were killed in 8 d at 43 and 50% RH except *L. bostrychophila* where 12 d were required at 50%. For all life stages and eggs and early instar nymphs, maximum survival times at 43 or 50% RH for *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta* were 8 and 10 d, 8 and 12 d, 10 and 14 d, and 12 and 16 d, respectively. Over the 30-d period of this experiment, numbers of nymphs and adults of all species increased at 75% RH. Data show that species and life stages of psocids respond to 43 and 50% RH differently. At 43 and 50% RH, time required to kill all stages of the four psocid species is 8–12 d and 10–16 d, respectively. Data indicate potential of low RH for psocid control in certain scenarios.

KEY WORDS Booklice, integrated pest management, stored-product, *Liposcelis*, dehumidification, physical control.

Introduction

Psocids (Psocoptera) are major pests of stored-products that cause economic losses in stored grains (Nayak et al. 2014). Severe psocid infestations have been encountered in grain storages 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). Globally, the four most economically important psocid species are *Liposcelis entomophila* (Enderlein), *Liposcelis decolor* (Pearman), *Liposcelis bostrychophila* Badonnel, and *Liposcelis paeta* Pearman (Nayak et al. 2014). In the U.S.A., *Liposcelis corrodens* (Heymons), *L. brunnea* Motschulsky, *L. rufa* Broadhead, and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae), have also been found infesting stored commodities (Mockford 1993, Lienhard and Smithers 2002, Gautam et al. 2010).

Over the last two-to-three decades, the economic importance of psocids have increased and this can be attributed to the variable response of psocides to standard management strategies compared to stored-product beetle pests (Nayak et al. 2014); their ability to thrive on a variety of food products (Opit and Throne 2008) and increased resistance to residual insecticides and the fumigant phosphine (Nayak et al. 2003). Furthermore, they feed on whole grain kernels and cause damage to grain germ and endosperm—leading to significant grain weight loss and germination failure (Kučerová 2002b, Gautam et al. 2013).

Physical control measures such as heat and cold treatments (Beckett and Morton 2003, Opit et al. 2011, Arthur et al. 2017); controlled atmospheres (Wang 1999); manipulation of environmental conditions (temperature and RH) (Nayak et al. 2014); and the use of DE (Athanassiou et al. 2009) are available for psocid management but are ineffective when used alone and are not well developed. These physical control measures are needed as a basis for

integrated management strategies for psocids (Nayak et al. 2014). However, the susceptibility of psocids to insecticides and physical control measures depends on the treatment, environmental conditions, species and exposure substrate because, infestations of psocids often consist of more than one species and each responds differently to treatment (Nayak et al. 2014, Gautam et al. 2015, Arthur et al. 2017).

The effect of RH on the population growth and development of psocids have been studied (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). RHs in the 63–75% range favor stored-product psocid survival, whereas RHs below 60% are detrimental (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Although *L. brunnea*, *L. rufa*, *L. fusciceps*, and *L. pearmani* are capable of reproducing at an RH of 55% at 22.5ºC, population increase is extremely slow (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015). Psocids usually do not survive at RH ≤43% RH (Opit and Throne 2009, Gautam et al. 2010, Aminatou et al. 2011, Gautam et al. 2015).

To date, there are no published data on using low RH as a management tool for psocids. Given the detrimental effects of low RH to psocid survival, low RHs could play a significant role in the integrated management of psocids. Therefore, the objective of the present study was to investigate the effects of RHs of 43 and 50% on psocid 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 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 on a mixture 93% cracked duster wheat, 5% Rice Krispies (Kellogg Company, Battle Creek, MI), and 2% wheat germ (wt/wt; referred to as psocid diet below) in 360-ml glass canning jars with mite-proof lids (Opit and Throne 2008), and the top 3 cm of the inner surface of each jar was coated with Fluon (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids accessing and gathering on the inside of the lid. Cultures were maintained at 30.0 ± 1°C and 75 ± 5% RH.

Effects of 43% Relative Humidity on the Survival of all Life Stages of Psocids. The top third of the inner surface of 27 vials were coated with Fluon to prevent the escape of psocids. Each vial had a snap-cap lid with a screen (US Standard #40 mesh with 0.42-mm openings) on it to allow air movement. In each vial was added 1.0 g of *L. decolor*, diet from the cultures of this species; diet contained eggs, nymphs, and adults. Another 0.1 g of wheat germ was also added to each vial. Vials were randomly assigned to 9 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 x 18 x 13 cm high) were prepared, and each contained a saturated solution of K_2CO_3 below a perforated false floor to maintain an RH (RH) of 43%. 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. Three other black plastic boxes (32 x 18 x 13 cm high) were prepared, but these contained a saturated solution of NaCl below a perforated false floor to maintain 75% RH. 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 9 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); three boxes with 43% RH and another three with 75% RH. All boxes were placed in an incubator maintained at 30.0°C. Environmental conditions (temperature and RH) in each box were monitored using a temperature and RH sensor (HOBO U12, Onset Computer Corporation, Bourne, MA). Vials in the 43% RH boxes were checked to determine presence or absence of *L. decolor* nymphs and adults before they were transferred to the boxes with 75% RH. Vials transferred to the boxes with 75% RH were again checked after 7 d for presence or absence of live nymphs and adults, but insects were not counted. The numbers of nymphs and adults in the three vials transferred to boxes with 75% RH were determined 14 d after each group of 3 vials had been placed in the boxes with 75% RH. 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 dishes whose sides were 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 with *L. decolor* psocids 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 vials) except that there were only three boxes. 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. Steps involving checking for the presence or absence of nymphs and adults, and counting of live psocids described above—in relation to 7 and 14 ds—were conducted at times corresponding to those of similarly labeled vials in the 43% RH treatment.

The protocol used for *L. decolor* as described above was repeated for *L. entomophila, L. bostrychophila,* and *L. paeta* separately. Therefore, there were 36 vials assigned to each "A", "B", and "C" box in the 43% RH treatment at the start of the experiment. For 75% RH treatment boxes, 36 vials assigned to each "A", "B", and "C" box as described in 43% RH treatment.

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 hole in the center to allow air flow was used to cover each of the vials. One gram of psocid diet was placed in each vial. Forty mixed-sex adults of *L. decolor* were added to the diet. The procedures for randomization and replication of vials, monitoring, counting of nymphs and adults were similar to those described above for all life stages.

A second treatment with *L. decolor* psocid 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 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 protocol used for *L. decolor* as described above was repeated for *L. entomophila*, *L. bostrychophila*, and *L. paeta* separately. Forty mixed-sex adults (20 each) were used for *L. entomophila* and *L. paeta.* However, only female adults (40) of *L. bostrychophila* were used for this experiment because it is a parthenogenetic species.

Effects of 43% RH on the Survival of Psocid Eggs and Early Instar Nymphs. The inner sides of 27 Petri dishes (35 mm diameter) 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; Greiner Bio-One, Kaysville, UT). Colored diet was made by mixing 100 g of Rice Krispies with a solution of 5 ml of red food dye (Global Chem Sources Inc., Cedar Grove, NJ) in 300 ml of water. Drying of the mixture was done in a mechanical convection oven (model HTM 85, Precision Scientific, Inc., Chicago, IL) for 6 h, and then grinding the dried mixture in a Wiley Mill and using a #20 sieve (0.85-mm openings) (Scientific Apparatus, Philadelphia, PA). Because psocids prefer to lay eggs in between diet particles, their eggs can be easily seen on colored diet. Colored diet also 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 x 18 x 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 duster wheat 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, counting of nymphs and adults were similar to those described above for all life stages.

A second treatment 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, assessment of eggs and early nymphs, adult survival, and counting 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.

Data Analysis. Each experiment had three replications, and the experimental design was a randomized complete block (RCBD) with three spatial replications. All statistical procedures were accomplished using Statistical Analysis System software version 9.4 (SAS Institute 2014). We used PROC GLM for the analysis of variance (ANOVA) to determine the effects of RH and

duration of exposure period on the survival of the psocids. The least significant difference (LSD) test was used to establish differences among mean numbers of psocids.

Results

L. entomophila. RH and exposure period had a significant effect on survival of *L. entomophila* adults, all life stages, and eggs and early instar nymphs (Figs. 1A–F; Table 1). No live psocid nymphs and adults were found after ≥8 d exposure of adults, all life stages, or eggs and early instar nymphs to 43% RH (Figs. 1A–C). 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 after 16 d of exposure it reached 473.67 ± 19.95, 846.0 ± 42.76, and 75.67 ± 5.24, respectively (Figs. 1A–C). No live psocid nymphs and adults were found after ≥8 d exposure of adults to 50% RH (Fig. 1D). 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 (Figs. 1E and F). 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 639.67 ± 45.58, 831.0 ± 29.50, and 187.67 ± 10.40, respectively (Figs. 1D–F).

L. decolor. RH and exposure period had a significant effect on survival of *L. decolor* adults, all life stages, and eggs and early instar nymphs (Figs. 2A–F; Table 2). No live psocid nymphs and adults were found after ≥8 d exposure of adults, all life stages, or eggs and early instar nymphs to 43% RH (Figs. 2A–C). 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 after 16 d of exposure it reached 605.0 ± 47.96, 1050.0 ± 178.50, and 309.67 ± 3.67, respectively (Figs. 2A–C). No live psocid nymphs and

adults were found after ≥8 d exposure of adults to 50% RH (Fig. 2D). 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 (Figs. 2E and F). 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 426.33 ± 23.90, 1938.67 ± 176.97, and 250.0 ± 24.27, respectively (Figs. 2D–F).

L. bostrychophila. RH and exposure period had a significant effect on survival of *L. bostrychophila* adults, all life stages, and eggs and early instar nymphs (Figs. 3A–F; Table 3). No live psocid nymphs and adults were found after ≥8 d exposure of adults to 43% RH (Fig. 3A). In the case of all life stages and eggs and early instar nymphs, no live nymphs and adults were found after ≥10 d exposure of adults to 43% RH (Figs. 3B and C). 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 after 16 d of exposure it reached 636.67 ± 43.34, 1162.0 ± 339.79, and 256.67 ± 8.82, respectively (Figs. 3A–C). No live psocid nymphs and adults were found after ≥10 d exposure of adults to 50% RH (Fig. 3D). 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 (Figs. 3E and F). 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 605.0 ± 49.57, 2371.0 ± 293.60, and 257.67± 30.19, respectively (Figs. 3D–F).

L. paeta. RH and exposure period had a significant effect on survival of *L. paeta* adults, all life stages, and eggs and early instar nymphs (Figs. 4A–F; Table 4). No live psocid nymphs and adults were found after ≥8 d exposure of adults to 43% RH (Fig. 4A). In the case of all life

stages and eggs and early instar nymphs, no live nymphs and adults were found after ≥12 d exposure of adults to 43% RH (Figs. 4B and C). 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 735.67 ± 45.44, 2945.0 ± 381.63, and 157.0 ± 6.81, respectively (Figs. 4A–C). No live psocid nymphs and adults were found after ≥8 d exposure of adults to 50% RH (Figs. 4D). 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 (Figs. 4E and F). 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 488.33 ± 10.7, 2407.00 ± 233.84, and 166.67 ± 18.21, respectively (Figs. 4D–F).

Discussion

Data 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 and all life stages combined. Based on data from this study, at 43% RH, 8–12 d are required to control all developmental stages of the four species investigated, depending on species. Data also show that at 50% RH, 8–16 d are required to control all developmental stages of the four species investigated, depending on species.

The tolerance of eggs may relate to their physical structure. Kucerova (2002a) 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 hence may be responsible for the 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 control method, psocid eggs have also been shown to be tolerant to heat, cold, phosphine, and controlled atmospheres that are targeted at them for management (Beckett and Morton 2003, Nayak et al. 2003, Nayak and Collins 2008, Arthur et al. 2017). Eggs of *L. paeta* have also been found to be quite relatively 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, in addition to being relatively more tolerant to sulfuryl fluoride and heat (Beckett and Morton 2003, Athanassiou et al. 2012); this may mean that *L. paeta* eggs could possess certain structural and compositional aspects that could be could be contributing to tolerance.

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 (Turner 1988) but carbamates and pyrethroid insecticides are not (Turner 1994). However, β-cyfluthrin, which is an enriched isomer of 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 of up to 40 weeks (Nayak et al. 2003). Nicotinoids such as imidacloprid are effective against *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* (Nayak and Daglish 2007), but the high application rate of 10 mg kg^{-1} required makes it more suitable as a seed treatment rather than a grain protectant. Spinosad is a newly developed bacterium-derived protectant that can be effectively used to manage

Rhyzopertha dominica and *Cryptolestes ferrugineus* (Subramanyam et al. 2007). The downside to spinosad is that it is not effective against *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* in wheat (Nayak and Daglish 2007) but these are the major four liposcelids infesting wheat. A combined treatment of spinosad 1 mg kg^{-1} plus chlopyrifos-methyl 10 mg kg^{-1} can control all the four *Liposcelis* species, but the high application rate of 10 mg kg^{-1} of chlopyrifos methyl may restrict its use to seed treatments only (Nayak and Daglish 2007). Some insect growth regulators such as fenoxycarb seem to be effective against *L. bostrychophila* when applied to food (Buchi 1994). However, pyriproxyfen, applied as a surface treatment on concrete is not effective against *L. bostrychophila*, *L. decolor*, and *L. paeta* (Athanassiou 2011). Chlorfenapyr, which belongs to a group of microbially-produced compounds called halogenated pyrroles, is effective as a surface treatment (Guedes et al. 2008b).

Physical control measures such as heat and cold treatment (Beckett and Morton 2003, Opit et al. 2011, Arthur et al. 2017); controlled atmosphere (Wang 1999); manipulation of environmental conditions (temperature and RH) (Nayak et al. 2014); and the use of DE (Athanassiou et al. 2009) have been used for psocid management but are not well developed and are less effective when used alone. For example, treatments with DE showed 50% mortality of psocid adults after 7 d; its effect could be improved when used together with low atmospheric moisture of ≤60 RH (Nayak et al. 2014). Controlled and modified atmosphere of carbon dioxide and nitrogen are effective against *L. entomophila* and *L. bostrychophila* but require up to at least 3 wks to achieve complete control (Nayak et al. 2014).

Many studies indicate that high and low RHs have a significant effect on the population growth and development of stored-product psocids (Gautam et al. 2015 and references therein). Psocids thrive at RHs ≥60%, but below this critical level, water loss is higher than gained 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 below 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, Aminatou et al. 2011, Gautam et al. 2015). 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.

Based on data from this study, control of psocids using disinfestation 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 control of infestation. It is critical that the warehouses or items being disinfested are clean in order to increase the efficacy of the dehumidification. Dehumidification is commonly used in homes in the United States to control pests such as mites (Arlian 2001). Similarly, commercial or industrial dehumidifiers can be used to disinfest empty stores or warehouses and items such as pallets of psocids. Research needs to be conducted on the cost benefit analysis of disinfesting large warehouses using dehumidification. To the best of our knowledge, this is the first published study on use of dehumidification for psocid control. Data from this study show that dehumidification or low RH (43 and 50%) treatment can be used to disinfest warehouses and items such as pallets of stored-product psocids. Therefore, dehumidification is an additional tool in the arsenal for psocid management using IPM strategies.

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Table 1. Results for number of *Liposcelis entomophila* nymphs and adults surviving after exposure to 43%, 50% or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14 or 16 d.

Parameter	Source	43%			50%		
		df	F	P	df	F	P
Adults	RH	1	1914.30	<0.0001	1	4915.61	<0.0001
	Exposure period	8	17.79	<0.0001	8	19.67	<0.0001
	RH*Exposure period	8	79.19	<0.0001	8	169.93	<0.0001
All life stages	RH	1	2159.61	<0.0001	1	1202.30	<0.0001
	Exposure period	8	17.10	<0.0001	8	6.98	<0.0001
	RH*Exposure period	8	93.72	<0.0001	8	58.26	<0.0001
Eggs	RH	1	2159.61	<0.0001	1	1202.30	<0.0001
	Exposure period	8	17.10	<0.0001	8	6.98	<0.0001
	RH*Exposure period	8	93.72	<0.0001	8	58.26	<0.0001

Table 2. Results for number of *Liposcelis decolor* nymphs and adults surviving after exposure to 43%, 50% or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14 or 16 d.

Parameter	Source	43%			50%		
		df	F	P	df	F	P
Adults	RH	1	520.50	<0.0001	1	2159.51	<0.0001
	Exposure period	8	4.63	<0.0001	8	3.73	0.0032
	RH*Exposure period	8	35.17	<0.0001	8	91.28	<0.0001
All life stages	RH	1	228.40	<0.0001	1	684.02	<0.0001
	Exposure period	8	1.39	0.2369	8	2.62	0.0238
	RH*Exposure period	8	9.91	<0.0001	8	40.50	<0.0001
Eggs	RH	1	583.44	<0.0001	1	602.99	<0.0001
	Exposure period	8	15.44	<0.0001	8	12.81	<0.0001
	RH*Exposure period	8	55.19	<0.0001	8	63.61	<0.0001

Table 3. Results for number of *Liposcelis bostrychophila* nymphs and adults surviving after exposure to 43%, 50% or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14 or 16 d.

Parameter	Source	43%			50%		
		df	F	P	df	F	P
Adults	RH	1	1388.59	<0.0001	1	1597.85	<0.0001
	Exposure period	8	11.35	<0.0001	8	2.64	0.0229
	RH*Exposure period	8	67.65	<0.0001	8	76.98	<0.0001
All life stages	RH	1	183.80	<0.0001	1	1075.29	<0.0001
	Exposure period	8	1.18	0.3376	8	1.67	0.1408
	RH*Exposure period	8	11.70	<0.0001	8	38.87	<0.0001
Eggs	RH	1	923.75	<0.0001	1	1085.18	<0.0001
	Exposure period	8	6.84	<0.0001	8	6.44	<0.0001
	RH*Exposure period	8	72.41	<0.0001	8	88.58	<0.0001

Table 4. Results for number of *Liposcelis paeta* nymphs and adults surviving after exposure to 43%, 50% or 75% relative humidity (RH) for 0, 2, 4, 6, 8, 10, 12, 14 or 16 d.

Parameter	Source	43%			50%		
		df	F	P	df	F	P
Adults	RH	1	2221.48	<0.0001	1	1281.62	<0.0001
	Exposure period	8	4.00	0.0020	8	13.49	<0.0001
	RH*Exposure period	8	84.80	<0.0001	8	59.15	<0.0001
All life stages	RH	1	469.05	<0.0001	1	396.73	<0.0001
	Exposure period	8	3.97	0.0028	8	2.85	0.0155
	RH*Exposure period	8	22.10	<0.0001	8	20.92	<0.0001
Eggs	RH	1	588.82	<0.0001	1	663.17	<0.0001
	Exposure period	8	24.59	<0.0001	8	39.39	<0.0001
	RH*Exposure period	8	54.19	<0.0001	8	68.74	<0.0001

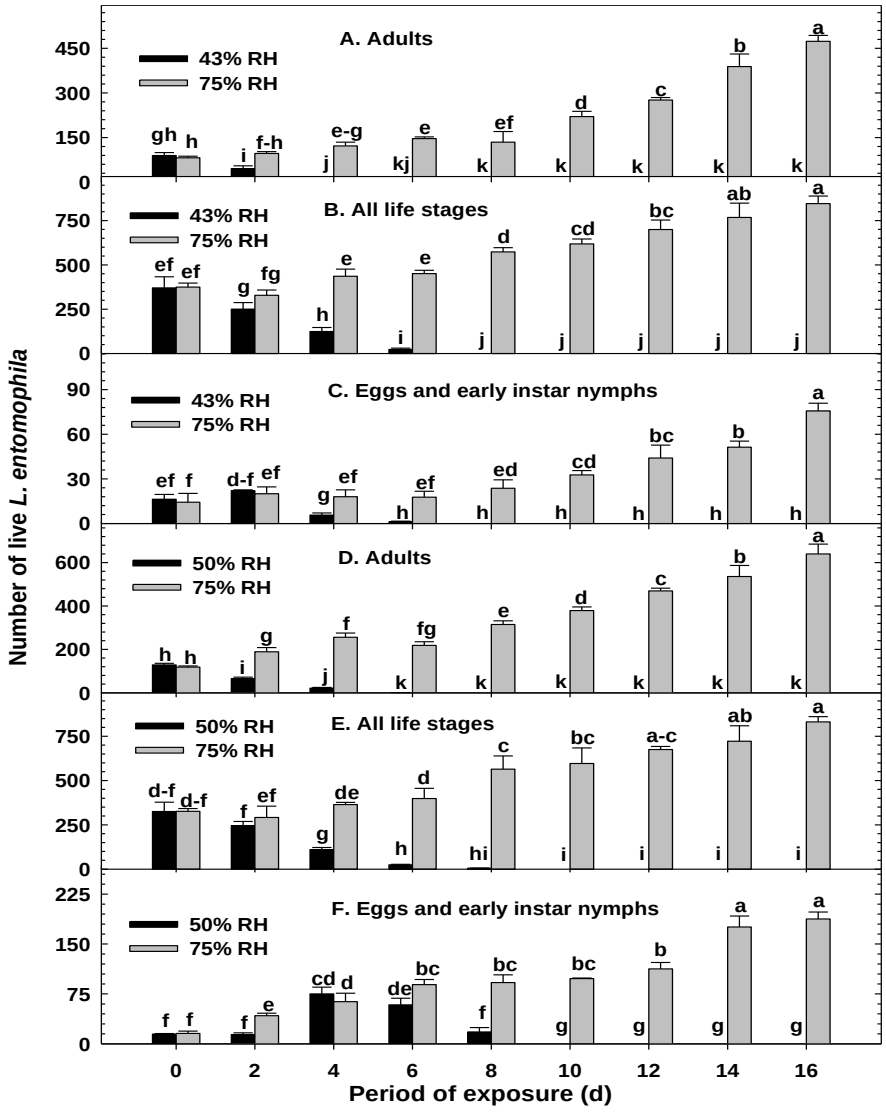
Figure Captions

Fig. 1. Survival (mean ± SE) of *Liposcelis entomophila* exposed to 43 or 75% RH for adults (A), all life stages (B), and eggs and early nymphs (C); for *L. entomophila* exposed to 50 or 75% RH for adults (D), all life stages (E), eggs and early nymphs (F). Means with different lowercase letters are significantly different ($P < 0.05$).

Fig. 2. Survival (mean ± SE) of *Liposcelis decolor* exposed to 43 or 75% RH for adults (A), all life stages (B), and eggs and early nymphs (C); for *L. decolor* exposed to 50 or 75% RH for adults (D), all life stages (E), eggs and early nymphs (F). Means with different lowercase letters are significantly different ($P < 0.05$).

Fig. 3. Survival (mean ± SE) of *Liposcelis bostrychophila* exposed to 43 or 75% RH for adults (A), all life stages (B), and eggs and early nymphs (C); for *L. bostrychophila* exposed to 50 or 75% RH for adults (D), all life stages (E), eggs and early nymphs (F). Means with different lowercase letters are significantly different ($P < 0.05$).

Fig. 4. Survival (mean ± SE) of *Liposcelis paeta* exposed to 43 or 75% RH for adults (A), all life stages (B), and eggs and early nymphs (C); for *L. paeta* exposed to 50 or 75% RH for adults (D), all life stages (E), eggs and early nymphs (F). Means with different lowercase letters are significantly different ($P < 0.05$).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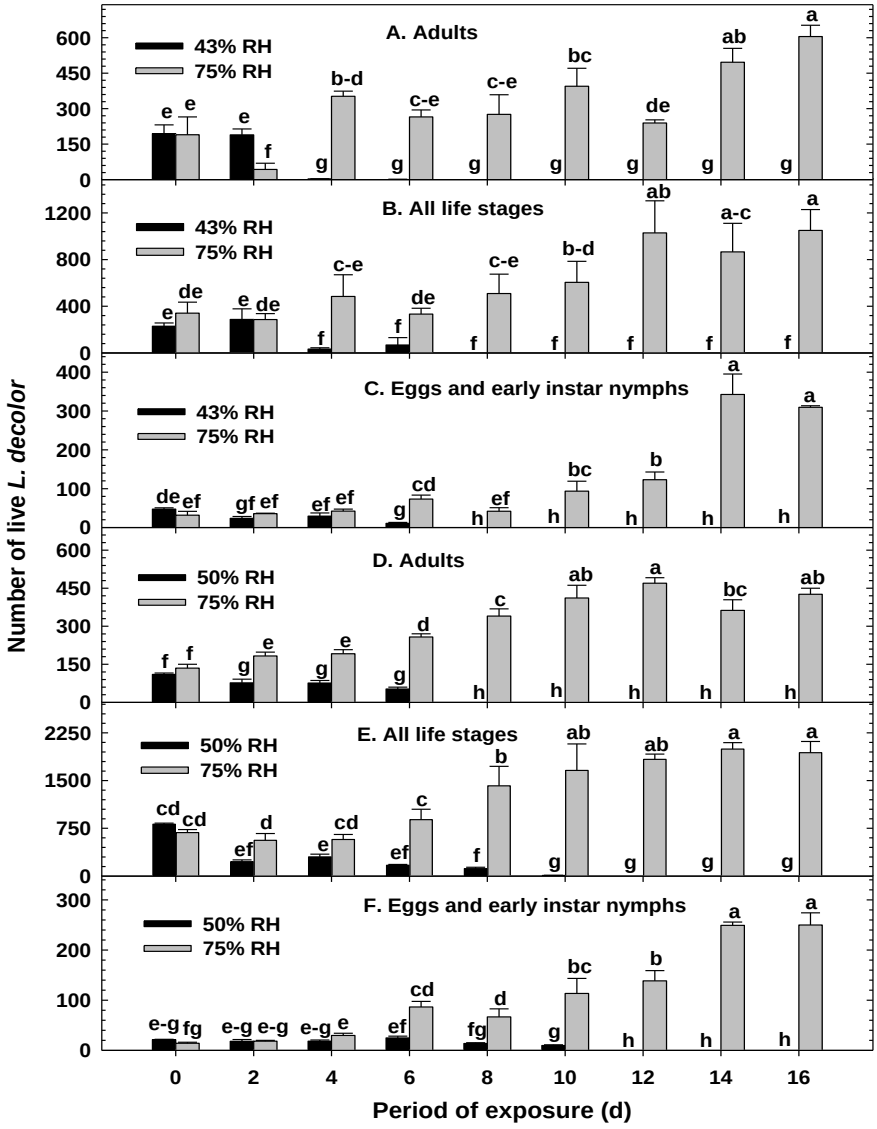
43% RH
75% RH
B. All life stages
43% RH
75% RH
C. Eggs and early instar nymphs
43% RH
75% RH
D. Adults
50% RH
75% RH
E. All life stages
50% RH
75% RH
F. Eggs and early instar nymphs
50% RH
75% RH
Number of live L. entomophila
Period of exposure (d)

Fig. 1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43% RH
75% RH
B. All life stages
43% RH
75% RH
C. Eggs and early instar nymphs
43% RH
75% RH
D. Adults
50% RH
75% RH
E. All life stages
50% RH
75% RH
F. Eggs and early instar nymphs
50% RH
75% RH
Number of live L. decolor
Period of exposure (d)

Fig. 2

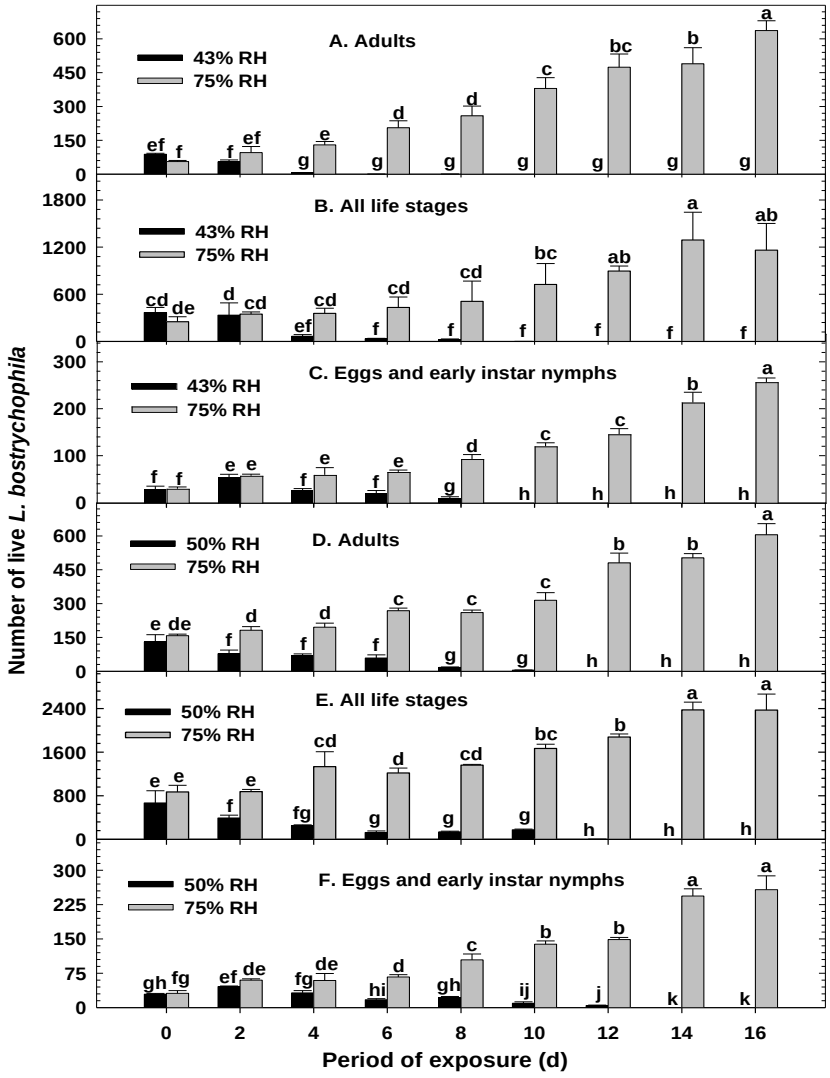
A. Adults
43% RH
75% RH
B. All life stages
43% RH
75% RH
C. Eggs and early instar nymphs
43% RH
75% RH
D. Adults
50% RH
75% RH
E. All life stages
50% RH
75% RH
F. Eggs and early instar nymphs
50% RH
75% RH
Number of live L. bostrychophila
Period of exposure (d)

Fig. 3

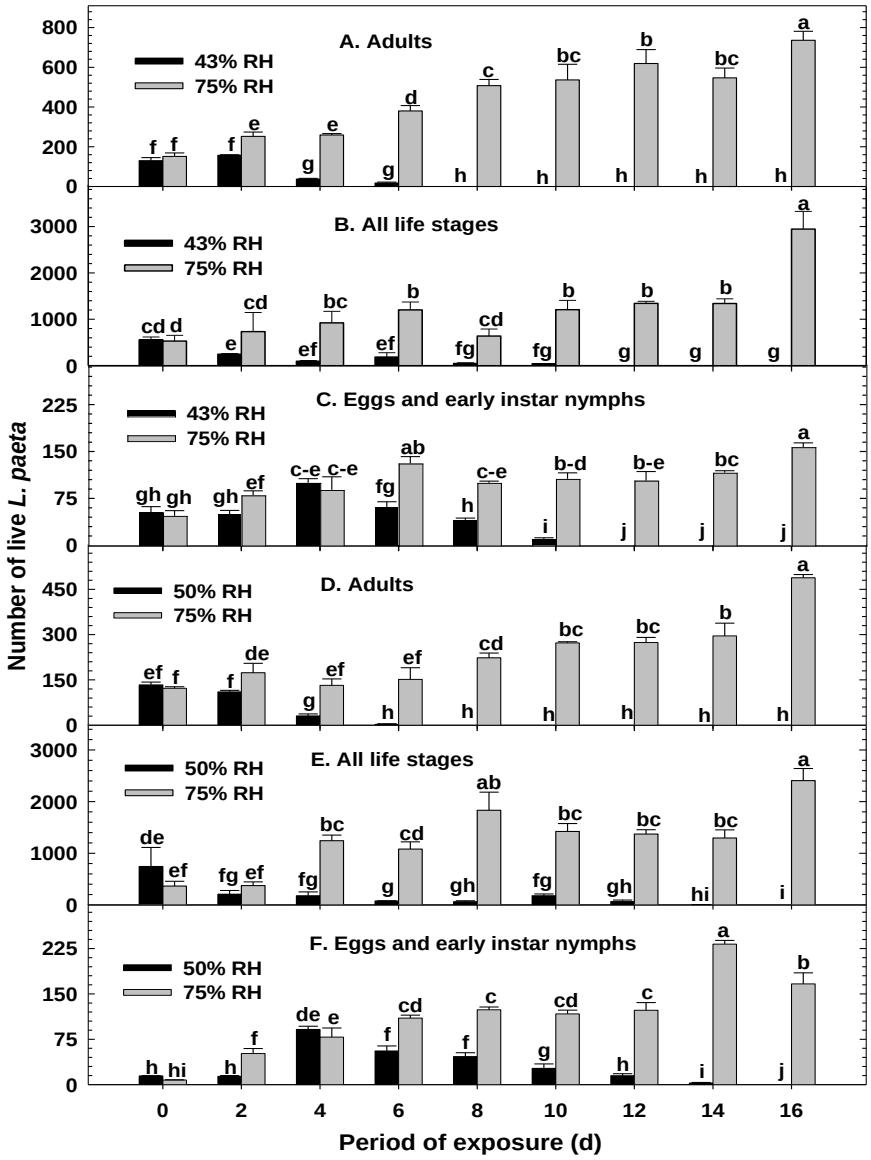
A. Adults
43% RH
75% RH
B. All life stages
43% RH
75% RH
C. Eggs and early instar nymphs
43% RH
75% RH
D. Adults
50% RH
75% RH
E. All life stages
50% RH
75% RH
F. Eggs and early instar nymphs
50% RH
75% RH
Number of live L. paeta
Period of exposure (d)

Fig. 4

CHAPTER V

CONCLUSIONS

Psocids have emerged as important pests of stored products all over the world, including the US, in the last two-to-three decades. Psocid natural ecology, including short regeneration time, allows them to rapidly colonize and proliferate in new habitats given the optimal RH >60% and optimal temperatures. Moreover, consumers increasingly reject commodities infested with psocids, causing economic losses.

Despite the economic importance of psocids, available knowledge on the biology and ecology of psocids is not plentiful. However, to effectively manage any pest, a good understanding of its ecology is critical. Given the lack of information on *Liposcelis obscurus* (a parthenogenetic psocid), I initiated experiments to study *L. obscurus* ecology. I investigated the effects of nine constant temperatures (22.5, 25, 27.5, 30, 32.5, 35, 37.5, 40, and 42.5°C) and four RHs (43, 55, 63, and 75%) on the population growth and the effects of nine constant temperatures and 75% RH on the development of *L. obscurus*. The nine temperatures and four RHs tested had effects on *L. obscurus* population growth. No live *L. obscurus* were found at 43% RH for all temperatures tested. Population growth was slow at 55% RH and 22.5–27.5°C. The optimal conditions for population growth were 40.0°C and 75% RH, where population increase was a 215-fold from an initial population of five females in 30 d. The optimal temperature range for population growth of *L. obscurus* is 32.5–40.0°C. At 42.5°C and 75% RH, *L. obscurus*

populations declined. The ability of *L. obscurus* rapidly multiply at higher temperatures (32.5–42.5°C) and high RH (75%) implies that this species may have a broader ecological distribution compared to other psocid species and thrives in warm and humid areas. The data from my study on of effects of temperature on *L. obscurus* development show that *L. obscurus* females have three to five instars. The percentage of females with third, fourth, and fifth instars were 52, 41, and 7%, respectively. The shortest development period occurred at 40.0°C; at this temperature, development was completed in 15.8 d. Temperature had a significant effect on the developmental time for all life stages of *L. obscurus*. However, temperature affected egg viability and nymphal survivorship. I have developed temperature dependent equations which can be used to predict developmental periods of *L. obscurus*. The lower and upper developmental thresholds for *L. obscurus* were estimated as 13.2 and 43.9°C, respectively. My research is the first study conducted on *L. obscurus* ecology and has provided significant information that improves our understanding of *L. obscurus* ecology. Information from my research can be used to elucidate *L. obscurus* population dynamics.

Psocids are difficult to control using standard practices of disinfestation compared to beetle pests. Psocids are relatively more tolerant to chemical treatments, and this calls for alternatives to pesticides. From previous ecological studies, psocids multiply in environments with RHs ≥63% but do not survive below 55%. However, there are no published studies on using low RH (dehumidification) as a physical control to manage psocids. This research represents one of the first studies investigating the effects of low RH on psocid survival. In this study, eggs and early instar nymphs, adults, and all life stages of *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta* were subjected to 43, 50, or 75% (control) RHs for 2, 4, 6, 8, 10, 12, 14, and 16 d at 30.0ºC. All adults of the four species were killed in 8 d at 43 and 50% RH except *L.*

bostrychophila where 12 d were required at 50% RH. For all life stages and eggs and early instar nymphs, maximum survival times at 43 and 50% RH for *L. entomophila*, *L. decolor*, *L. bostrychophila*, and *L. paeta* were 8 and 10 d, 8 and 12 d, 10 and 14 d, and 12 and 16 d, respectively. Over the 30-d period of this study, numbers of nymphs and adults of all species increased at 75% RH. My data show that different species and life stages of psocids respond differently to 43 and 50% RH. At 43 and 50% RH, time required to kill all stages of the four psocid species is 8–12 d and 10–16 d, respectively. Data on the use of low RHs (dehumidification) for psocid control can be used to facilitate physical control measures for effective disinfestations of psocids in empty warehouses and storage items such as pallets with the help of industrial dehumidifiers.

Psocids often infest stored commodities in on-farm facilities and product warehouses. However, measures such as sanitation, sealing of cracks, crevices and/or openings in storage structures, and close monitoring of storage conditions can reduce or prevent pest population outbreaks. Grain silos and product warehouses with high temperatures and RHs provide ideal environmental conditions for psocid survival and multiplication. High moisture in grains facilitates fungal growth and increase the RH of the storage environment. Therefore, drying grains to proper moisture content for long-term storage is important for the prevention of psocid infestation. Physical control measures that minimize psocid infestations of storage structures include proper sanitation of storage areas and equipment prior to harvest and bin sealing, cleaning, and disinfestation using either dehumidification, heat, or cold treatments. My data on *L. obscurus* ecology and the effects of low RHs on the survival of psocids will facilitate development of strategies that can play a significant role in the integrated management of psocids.

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