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A review of diapause and tolerance to extreme temperatures to dermestids (Coleoptera)

Department of Biological Sciences

1   **A REVIEW OF DIAPAUSE AND TOLERANCE TO EXTREME TEMPERATURES IN DERMESTIDS**
2   **(COLEOPTERA)**

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Abstract

Numerous species in Family Dermestidae (Coleoptera) are important economic pests of stored goods of animal and vegetal origin, and museum specimens. Reliance on chemical methods for of control has led to the development of pesticide resistance and contamination of treated products with insecticide residues. To assess its practicality as an alternate method of control, we review the literature on the tolerance of dermestids to extreme hot and cold temperatures. The information for dermestid beetles on temperature tolerance is fragmentary, experimental methods are not standardized across studies, and most studies do not consider the role of acclimation and diapause. Difficulties in determining the diapause status of dermestid larvae may explain the lack of studies. The few studies that do examine these factors show that they can greatly increase tolerance to cold temperatures. The use of extreme temperatures will need to target the most tolerant life stage, which for dermestids at cold temperatures will potentially be the cold-acclimated individuals in diapause. The development of effective protocols will be facilitated by studies that clearly and completely describe experimental and statistical methods, consider factors (life-stage, acclimation, diapause) that increase tolerance to extreme temperatures, and assess the mortality at various temperatures to develop mathematical models.

1. INTRODUCTION

Dermestid beetles (Coleoptera: Dermestidae) comprise a diverse group of more than 1200 described species in 45 genera. Most species are xerophilous necrophages; i.e., they develop on the desiccated tissues and hairs of dead animals (Háva & Nardi, 2004; Kiselyova & Mchugh, 2006; Zhantiev, 2009) (Table 1). Necrophagus species (e.g., *Dermestes* spp.) feed in animal carcasses and on dead insects (Kingsolver, 2002; Zhantiev, 2009). Nidicolous species (e.g., *Anthrenus* spp.) occur on mammals and in bird nests, where they feed on hair or feathers (Peacock, 1992; Háva, 2004; Zhantiev, 2009). A small number of species are predators and feed on wasp and bee larvae, and on spider eggs (Zhantiev, 2009). Feeding on plants is atypical for the family, but their tolerance to low humidity allows some dermestids (mainly *Trogoderma* spp. and *Attagenus* spp.) to develop solely on dried cereal products (Hinton, 1945; Kiselyova & Mchugh, 2006; Zhantiev, 2009).

A number of dermestids are of key economic importance. Some genera (*Trogoderma*, *Attagenus*) are pests of stored grains and stored grain products (Hinton, 1945; OEPP/EPPO, 2013). Other genera (*Attagenus* spp., *Anthrenus* spp.) are common in museums, where they damage preserved insect, bird, and mammal specimens, or items that contain plant or animal materials (Pinniger, 1991; Veer *et al*., 1991; Linnie, 1994). Species of *Anthrenus, Anthrenocerus* and *Dermestes* develop in products that contain wool, cotton, linen, synthetic fibres, and silk (Bennet *et al*., 1988; OEPP/EPPO, 2013). Species of *Attagenus* and *Dermestes* consume silkworm cocoons and prey on different life stages of silkworms (Kumar *et al.,* 1988; Veer *et al.,* 1996). About 28 species of *Dermestes* infest stored silkworm cocoons and *D. maculatus* is a reported vector of the microsporidian *Nosema bombycis* Nageli, which is the causative agent of pébrine disease in silkworms (Veer *et al.,* 1996). Dermestids also infest the packaging and containers used to ship stored products which, in combination with international commerce, have contributed to the cosmopolitan distribution of many dermestid species (Wildey & Wayman, 1979; Turner, 1986).

Given their economic importance, there is a large body of research describing measures to control dermestid infestations. Control, however, is complicated by the ability of some dermestids to undergo diapause. This ability is uncommon among stored-product insects and increases the tolerance of dermestids to extreme climatic conditions and insecticides (Bell, 1994).

65   **Table 1.** Biology and life history of the most economically important species of dermestids.

66

Species	Common name	Geographic distribution	Temperature (°C)[a]	RH (%)[a]	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
Anthrenus coloratus (Reitter 1881)	Asian carpet beetle	Southeast Europe, England, USA, Africa, Asia	33-35	70-80	6-9	115 -120 (univoltine)	-	Yes	Stored product and museum specimen pest	Ali (1997)
Anthrenus flavipes (LeConte 1854)	Furniture carpet beetle	Nearly cosmopolitan	35	90	18-20	246-248 (bivoltine)	-	Yes (obligate)	Animal products, museum pests	Griswold & Greenwald (1941); Ayappa *et al.,* (1957)
*Anthrenus sarnicus (*Mroczkowski 1963)	Guernsey carpet beetle	Europe	25	70	8	337	28	Yes (obligate)	Pest of dried animal collections in museums	Coombs & Woodroffe (1983); Armes (1988)
Anthrenus verbasci (Linnaeus 1767)	Varied carpet beetle	Cosmopolitan	20	70	3-5	192	27	Yes (obligate)	Pest of dried insect collections/silkworms pupae	Griswold & Greenwald (1941); Blake (1958)
Anthrenocerus australis (Hope 1843)	Australian carpet beetle	Europe and Australia	25	60-70	5-6	246	30	Yes (obligate)	Pest of dried dairy products, wool and other fabrics	Gerard & Ruf (1997)
Attagenus augustatus (Ballion, 1871)	-	China, Russia, middle east and India	29	-	-	730 (biennial)	150- 300	-	Pest of textiles, woolen fabrics and grains	Veer & Rao (1995)

Species	Common name	Geographic distribution	Temperature (°C)[a]	RH (%)[a]	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
Attagenus cyphonoides (Reitter 1881)	-	Nearctic, Oriental and Palaearctic regions	22-27	45-70	-	118-132 (univoltine)	10-14	Yes (obligate), larvae overwinter	Woolen and other animal products	Veer *et al.,* (1991)
Attagenus elongatulus (Casey 1900)	"yellow" black carpet beetle	Palaearctic region	27	50-70	-	90-95 days	18-20	Yes (crowded)	Infests plant and animal materials: woolens, felt and processed foods	Barak & Burkholder (1977)
Attagenus indicus (Kalik 1954)	-	India, Nepal	27	75	-	240-270 days (univoltine)	144-229	Hibernates as larvae or adult	Stored woolen fabrics and carpets	Veer & Rao (1995)
Attagenus unicolor (Brahm 1790)	Black carpet beetle	Cosmopolitan	28	65	5-11	> 326	3-35	Yes (obligate and larval crowding)	Pest of dead animal and vegetal materials	Back & Cotton (1938); Griswold & Greenwald (1941); Baker (1977, 1982)
Attagenus fasciatus (Thunberg 1795)	Banded black carpet beetle	Europe, nearly cosmopolitan	35	80	8-14	136 (bivoltine)	26-30	-	Attacks animal and vegetal products in storage	Ali *et al.,* (2011)
Attagenus lobatus (Rosenhauer 1856)	-	North Africa, South Europe, USA, Asia	25-27	65-70	-	253-287 (univoltine)	78-112	Overwinters as larvae or pupae	Woolen products	Veer *et al.,* (1991)
Attagenus scalaris (Pic 1893)	Black carpet beetle	Egypt, Libya	30	50	8-22	90-385	17-28	-	Stored textiles of animal origin	Abdel-Rahman, *et al.,* (1981)

Species	Common name	Geographic distribution	Temperature (°C)[a]	RH (%)[a]	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
Attagenus smirnovi (Zhantiev 1973)	Brown carpet beetle	Europe, Africa	20	65	-	22-32	20	Yes	Animal and vegetal museum collections	Hansen *et al.,* (2012)
Dermestes ater (Degeer 1774)	Black larder beetle	Cosmopolitan	25	40-80	-	64-77	100-200	-	Pest on raw animal products	Coombs (1981)
Dermestes haemorrhoidalis (Küster 1852)	Black larder beetle, sheepskin dermestid	Nearly cosmopolitan	25	65	-	95-112	110-194	-	Animal and vegetal products, insect collections	Coombs (1979)
Dermestes lardarius (Linnaeus 1758)	Larder beetle	Cosmopolitan	25	65	7	48-50	244	-	Scavengers/animal products	Coombs (1978); Jacob & Fleming (1984)
Dermestes maculatus (DeGeer 1774)	Leather (Hide) beetle	Cosmopolitan	33	-	6-8	34-40	14	Yes (crowded)	Stored produced of animal and vegetal origin	Osuji (1975); Cloud & Collison (1986)
Dermestes peruvianus (LaPorte de Castelnau 1840)	Peruvian larder beetle	South America, USA, Europe, Asia	25	65	-	65-73	33-192	-	Plant and animal material	Coombs (1979)

Species	Common name	Geographic distribution	Temperature (°C)[a]	RH (%)[a]	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
Trogoderma anthrenoides (Sharp 1902)	-	America, Europe, Asia	35	70	-	41-46	7-10	Yes (isolation)	Pest of plant and animal stored-products and museum specimens	Burges & Camell (1964)
Trogoderma variabile (Ballion 1878)	Warehouse beetle	Europe, Nearctic	32	70	5-6	30-46	14	Yes (isolation)	Pest of stored grain	Loschiavo (1960); Partida & Strong (1975)
Trogoderma granarium (Everts 1898)	Khapra beetle	Europe, Asia and Africa	35	73	4-7	24-36	12-14	Yes (crowded, isolation)	Major pest of animal and vegetal stored products (mainly grain and cereals)	Hinton (1945); Hadaway (1955); Burges (1962b)
Trogoderma versicolor (Creutzer 1799)	European larger cabinet beetle	Palaearctic region	30	73	-	30-43	12-16	-	Pest of dried animal and vegetal products/insect collections	Hadaway (1955)
Trogoderma inclusum (LeConte 1854)	Larger cabinet beetle	Nearly cosmopolitan	35	73	4-7	36-42	3-16	Yes (isolation)	Minor stored product pest	Strong (1975); Klein & Beck (1980)
Trogoderma angustum (Solier 1849)	Cabinet beetle	America, introduced to Asia and Europe	-	-	-	-	-	Yes (isolation)	Textiles and insect collections	Bell (1994)
Trogoderma sternale (Jayne 1882)	Cabinet beetle	Nearctic	-	-	-	-	-	Yes (isolation)	Minor stored product pest	Bell (1994)

Species	Common name	Geographic distribution	Tempe-rature (°C)[a]	RH (%)[a]	Larval stages (#)	Developmental time (days)	Adult longevity (days)	Diapause	Ecology	References
Trogoderma glabrum (Herbst 1783)	Glabrous carpet beetle	Holarctic region (temperate)	27-38	-	5-6	30-49	6-14	Yes (isolation)	Minor stored product pest	Beck (1971a); Archer & Strong (1975); Klein & Beck (1980)
Trogoderma ornatum (Say 1825)	Ornate cabinet beetle	Neartic region	-	-	-	-	-	Yes	Minor stored product pest	Bell (1994)
Trogoderma simplex (Jayne 1882)	Plain cabinet beetle	USA and Canada	32	50	5-6	63-77	10-22	Yes (isolation)	Minor stored product pest	Strong & Mead (1975)
Trogoderma grassmani (Beal 1954)	Tiny cabinet beetle	USA and Canada	-	-	-	-	-	Yes (isolation)	Minor stored product pest	Bell (1994)

*Blank cells represent unavailable information

[a] Temperature and humidity for the reported developmental time (days)

67   Control primarily has relied on fumigants and contact insecticides. Fumigants that have been

68   used to control dermestids include methyl bromide (Lindgren & Vincent, 1959; Linnie, 1994;

69   Fields & White, 2002; MBTOC, 2010), phosphine (Vincent & Lindgren, 1972; Bell *et al*., 1984;

70   Udeaan, 1990; Linnie, 1994; Bell & Wilson, 1995; Farooq *et al.,* 2000; Ahmedani *et al*., 2007),

71   naphthalene (Linnie, 1994), p-dichlorobenzene (Linnie, 1994), and sulfuryl fluoride (Su &

72   Scheffrahn, 1990; Rajendran *et al*., 2008; Sriranjini & Rajendran, 2008). Contact insecticides

73   used to control dermestids include malathion (Lindgren & Vincent, 1959; Singh & Yadav, 1994;

74   Khosla *et al.,* 2005), pyrethrins (Linnie, 1994), and chlorpyriphos (Singh & Yadav, 1994; Khosla *et*

75   *al.,* 2005; Eliopoulos, 2013). Use of fumigants and contact insecticides promote the

76   development of resistance, introduce residues into the environment, and can be detrimental to

77   the consumer's health (Cao *et al.,* 2002; Rajendran, 2002; Rajendran & Parveen, 2005). Methyl

78   bromide is an ozone-depleting substance. In accordance with the Montreal Protocol, its use has

79   been generally banned on a global basis with some exemptions (MBTOC, 2010) such as

80   quarantine. Phosphine is less effective than methyl bromide and some dermestids (e.g., *T.*

81   *granarium*) already have evolved phosphine resistance (Vincent & Lindgren, 1972; Bell *et al.,*

82   1984; Rajendran, 2002). These issues have led to examination of non-chemical methods of

83   control, varying with the nature of the infested product (Rajendran & Parveen, 2005).

84   Alternative methods include the use of controlled atmospheres (CO_2-rich, O_2-poor

85   atmospheres) (Khatoon & Heather, 1990; Reichmuth *et al*., 1993), vegetable oils (Traynier *et al*.,

86   1994), inert dust (Nakamoto, 1989), radiation (Khatoon & Heather, 1990), and extreme

87   temperatures (Fields & White, 2002; Wright *et al.,* 2002; Abdelghany *et al.,* 2015).

88   The use of extreme temperatures may provide the most viable alternative to chemical

89   applications. It has been used as an insect control method in North America since the early

90   1900s (Dean, 1911; Mathlein, 1961; Burges & Burrell, 1964), there are no reported cases of

91   insects developing resistance to heat or cold, there are no residues to harm consumers, and it

92   does not require registration, as do insecticides in most jurisdictions (Fields & White, 2002;

93   Eliopoulos *et al.,* 2011; Fields *et al*., 2012). However, adoption of extreme temperatures as a

94   treatment method has been hampered by an inability to increase or decrease temperatures

95   economically and quickly, as well as a lack of knowledge on the combination of temperature

96   and period of exposure that is needed to control different species of dermestids (Strang, 1992;

97   Bergh *et al.*, 2006). Some of the studies that report on the thermal-mortality limits for insect

98   pests in museums are based on experience rather than on controlled experiments (Linnie,

99   1999). Furthermore, much of the literature on the temperature tolerance of dermestids is

100 difficult to access and (or) not recent (Fields, 1992; Linnie, 1999).

101 Our objectives are three-fold, we first review the literature on the tolerance of dermestid

102 beetles to extreme temperatures, discuss factors that influence this tolerance, and examine the

103 potential for extreme temperatures to control dermestids in different situations; e.g., museum

104 specimens, stored-grain products. This information will facilitate the development of standard

105 protocols to encourage adoption of extreme temperatures for use in the control of dermestid

106 pests.

107 **2. MECHANISMS OF TEMPERATURE TOLERANCE**

108 Temperature influences almost every aspect of insect biology. Temperature affects metabolic

109 rates, defines limits of physiological function, determines developmental times, impacts

110 behaviour, and ultimately influences survival of the population (Lee, 1991; Bhargava *et al.*,

111 2007). For stored-product insects, optimal temperatures maximize fitness and population

112 growth. Stored-product insects require a high minimum temperature before they can complete

113 their development. In general, temperatures above 15°C are needed for egg-laying and optimal

114 temperatures range between 25- 35°C (Fields, 1992; Strang, 1992). Suboptimal temperatures

115 (35 - 40°C and 13 - 25°C) allow completion of life cycles and reproduction, but populations

116 merely persist rather than thrive. Lethal temperatures (above 40°C and below 13°C) eventually

117 cause population extinction (Fields, 1992; Wellheiser, 1992; Bhargava *et al.*, 2007). Different

118 species can have slightly different temperature responses (Hadaway, 1955; Loschiavo, 1960;

119 Coombs, 1981; Burges, 2008; Riaz *et al.*, 2014). Cold and heat-tolerance refers to the capacity of

120 an organism to survive or tolerate exposure to temperatures and exposure times that are

121 otherwise suboptimal or lethal (Lee, 1991).

122 *2.1 Mechanisms of cold tolerance*

123   Exposure to cold can damage insect cell membranes, cause the loss of ion homeostasis, reduce

124   metabolic rates, and mechanically damage tissues (Fields, 1992; Lee, 2010). Insects enhance

125   their cold-tolerance with use of behavioural, biochemical, and physiological strategies. In

126   general, insects are classified as freeze-intolerant (die when frozen) or freeze-tolerant (capable

127   of surviving ice in their bodies) (Fields, 1992; Lee, 2010). Other systems of classification have

128   been proposed that take into consideration the different aspects of cold mortality, but these

129   have not been widely used (Nedved, 2000). All dermestids and stored-product or museum

130   collection insect pests studied to date are freeze-intolerant, and die at their supercooling point

131   (SCP), which in general range from -10 to -20°C (Evans, 1987; Strang, 1992; Fields *et al.,* 1998;

132   Linnie, 1999; Fields, 2001; Fields, *et al.,* 2012). There is significant mortality at temperatures

133   warmer than the SCP, with warmer temperatures causing less mortality (Fields, 1992; Strang

134   1992).

135   ***2.2 Mechanisms of heat tolerance***

136   Exposures to sublethal high temperatures increases metabolic rates followed by the cessation

137   of movement. Prolonged exposure can change the fluidity of cell membranes, alter ionic

138   balance, and alter the structure of macromolecules to affect cell structure and the rate of

139   metabolic reactions (Fields, 1992; Nedved, 2000; Hansen *et al*., 2011). High temperatures can

140   also increase the permeability of the cuticle wax complex causing water loss and desiccation

141   (Nedved, 2000). Heat damage is normally irreversible and, even if the insect survives heat

142   exposure, it may fail to complete development or reproduce when returned to optimal

143   temperatures (Fields, 1992; Denlinger & Yocum, 1998; Nedved, 2000; Hansen *et al*., 2011). To

144   achieve heat tolerance, heat shock or stress proteins replace the production of normal proteins,

145   which reduce the damage to susceptible proteins (Denlinger & Yocum, 1998). Previous studies

146   show that all life stages of dermestids and some other stored-product insects can survive at

147   38°C, but most of them will be killed by an exposure of 2 hours at 50°C (Michelbacher,1953;

148   Lindgren & Vincent, 1959; Evans, 1987; Fields, 1992; Phillips & Throne, 2010; Fields *et al*.,

149   2012).

150

3. FACTORS AFFECTING THERMAL TOLERANCE

Tolerance to extreme temperatures is highly variable within and among species due to multiple factors (Lee, 1991; Fields, 2001). Identifying these factors is critical when designing thermal treatments for the control of pest insects, particularly those life stages and species that are most tolerant (Beckett *et al*., 2007). Factors that affect temperature tolerance include: i) life history of the species, ii) stage of development, iii) diapause, iv) relative humidity, v) acclimation, and vi) temperature and duration of exposure (Salt, 1958; Evans, 1987; Lee, 1991; Fields, 1992; Fields, 2001; Beckett *et al*., 2007).

3.1 Life history of the species

The environmental conditions normally experienced by a species often define its thermal tolerance (Chown, 2001). For example, insects not normally found at cold temperatures usually cannot tolerate sub-zero temperatures and may die after even a brief exposure to suboptimal temperatures (Salt, 1961; Doucet, *et al.*, 2009). Most granivorous species are tropical or sub-tropical species able to breed rapidly over a fairly wide range of temperatures. In general, however, they are more susceptible to low temperatures compared to species of insects from temperate and cold zones (Burges & Burrell, 1964).

3.2 Stage of development

Thermal tolerance differs among developmental stages mainly due to their physiological differences (Salt, 1958; Fields, 1992; Danks, 1996, 2005, 2006; Beckett *et al*., 2007). Life stages of smaller size and lower water content have lower supercooling points. The digestive tract of non-feeding life stages (e.g., pupae) do not contain food particles (which can act as ice-nucleators) and, therefore, have lower SCPs than feeding stages (Denlinger, 1991; Lee, 1991). Different life stages also may be associated with different microhabitats, which can affect SCPs, freezing capacity, and loss of water (Denlinger, 1991; Fields, 1992). A lower SCP does not necessarily mean a higher cold-tolerance, for example eggs often have low SCP but are not the most cold-tolerant stage (Fields, 1992). However, within a given life stage, SCPs can often be correlated with cold tolerance (Fields, 1992; Abdelghany *et al.,* 2015).

3.3 Diapause

179   Diapause is an endocrine-mediated dormancy characterized by an arrest in development and

180   suppression of metabolism that may either be obligate or facultative (Denlinger, 1991; Bell,

181   1994). For insects with obligate diapause, each individual passes through diapause regardless of

182   the external conditions (Tauber *et al.,* 1986; Kostál, 2006). For insects with facultative diapause,

183   diapause is initiated, maintained, and terminated by external cues. Thus, depending upon

184   environmental conditions, a given generation of an insect may or may not enter diapause

185   (Tauber *et al.,* 1986; Kostál, 2006). Nair and Desai (1973a) showed that strains of *T. granarium*

186   that had a facultative diapause that was induced by crowding, prevented by isolation, and could

187   be selected so that there was no diapause under crowded conditions. In other words, they

188   produced a non-diapausing strain. Also a strain could be selected so that almost all larvae in

189   both crowded (diapausing) and isolated (non-diapausing) conditions entered into diapause. In

190   other words, they produced a strain with obligatory diapause. Their finding suggests that

191   diapause is determined by multiple genes (Burges, 1962b; Nair & Desai, 1973b). It also indicates

192   that laboratory strains could lose the ability to diapause depending upon the method of rearing

193   and generations in culture. If time is a confounding factor, tests performed over several

194   generations on the characteristics of diapause (induction, maintenance and termination) may

195   lead to erroneous conclusions if the correct controls are not present.

196   Insects entering diapause undergo physiological changes that enhance the accumulation of

197   metabolic reserves and reduce rates of energy and oxygen consumption (Tauber *et al*., 1986;

198   Denlinger, 1991). This is achieved by the activation of diapause-specific genes that encode for

199   proteins, which affect heat shock, energy metabolism and storage, hormonal regulation, and

200   clock proteins, that influence diapause induction (Kostál, 2006). Mechanisms for diapause-

201   induction and cold tolerance may interact; i.e., both are regulated by the juvenile hormone and

202   both include the production of cryoprotectants, elimination of gut contents, and dehydration of

203   body tissues (Lindgren & Vincent, 1959; Bell *et al*., 1984; Tauber *et al*., 1986; Danks, 1996, 2005,

204   2006). However, the relation between diapause and cold-tolerance is not always clear. Both are

205   dynamic processes and, even within a species, some elements of diapause and cold-tolerance

206 are linked whereas others are not (Danks, 2005, 2006). Also, depending upon the species, the

207 co-occurrence of diapause and cold-tolerance may be coincidental or reflect independent

208 responses to similar inductive cues. In addition, cold-tolerance may occur in the absence of

209 diapause (and vice versa) and may increase with acclimation (Tauber *et al*., 1986; Denlinger,

210 1991; Danks, 2005, 2006).

211 Diapause can provide higher tolerance to detrimental conditions and can improve survival to

212 extreme environments in some dermestids. The ability to undergo diapause as larvae evolved

213 to tolerate suboptimal conditions where the food supply is sporadic and unpredictable. Because

214 of this, the diapause stage allowed higher survival in their ancestral environments as scavengers

215 and in the invasion of a new niche as stored-product pests (Beck, 1973; Armes, 1988, 1990).

216 Diapause allows individuals to synchronize development within populations and to survive

217 conditions of extreme temperatures, desiccation and, increases resistance to fumigants such as

218 phosphine and methyl bromide (Burges, 1962b; Tauber *et al*., 1986; Pullin, 1996). When

219 conditions become conducive for growth and reproduction, the diapause stage terminates,

220 allowing for a rapid increase in the population. For example, adults of *T. granarium* that went

221 through diapause are larger and laid more eggs than the ones that didn't, promoting in that

222 way, a rapid increase of the population after diapause (Karnavar, 1972).

223 Most dermestids that diapause, do so as larvae. Some have obligate diapause, while others

224 have facultative diapause (Table 1). The genera *Anthrenus* and *Attagenus*, which are more

225 closely associated to the ancestral environments, have long life cycles (1-3 years) with a clear

226 stage of obligate larval diapause that enhances overwinter survival (Bell, 1994). For example,

227 *Anthrenus verbasci* can have 2 periods of diapause, first as early instar larvae and second as

228 mature larvae (Blake, 1958, 1959). *Anthrenus sarnicus* and *Anthrenus flavipes,* undergo

229 diapause as mature larvae only (Griswold & Greenwald, 1941; Armes, 1988, 1990). In these

230 three species, diapause is controlled by an "internal clock", all individuals go through diapause,

231 but the timing and duration of diapause can be affected by photoperiod and temperature

232 (Blake, 1958, 1959; Armes, 1988, 1990).

233   Facultative diapause is present mainly in *Trogoderma* spp. and is defined mainly as a density-

234   dependent phenomenon. During this stage the individual stay as mature larvae that feed and

235   moult occasionally, that can be identified by a low respiration rate (Beck 1971a) and a longer

236   larval stage (Burges, 1959, 1960, 1962a, 1962b; Nair & Desai, 1972, 1973a, 1973b). This stage is

237   induced by factors that can act alone or in combination, such as exposure to low temperatures,

238   inadequate food, rearing at low or high densities (Burges 1962b; Nair & Desai, 1972, Table 1).

239   The diapause induced by larval crowding has been widely studied in *T. granarium*, but a similar

240   facultative diapause has been described in *Attagenus elongatulus* (Barak & Burkholder, 1977),

241   *Attagenus unicolor* (Baker, 1977), and *Dermestes maculatus* (Osuji, 1975). This type of diapause

242   is terminated by a rapid increase in temperature after exposure to low temperatures. When

243   larvae undergo diapause as a result of crowded conditions, the renewal of food has little effect

244   on termination and is effective only when accompanied by isolation (Burges, 1962a; Nair &

245   Desai, 1973a). In contrast, larvae of *T. glabrum* and *T.variabile* have a facultative diapause

246   defined as density-independent. The density-independent diapause is triggered by short

247   photoperiods, low temperatures, small food volumes, isolation (not by crowding) or

248   disturbance of the larvae (Loschiavo, 1960; Burges, 1961, Wright & Cartledge, 1994;

249   Abdelghany *et al*, 2015). The termination of the density-independent diapause can be

250   spontaneous or follow changes in density of larvae, a rapid increase in temperature,

251   photoperiod, or the presence of pupae (Loschiavo, 1960; Burges, 1961; Beck 1971a, 1971b;

252   Wright & Cartledge, 1994).

253   The type of dormancy seen in dermestids has generated disagreement, because it is different

254   than most insects (Tauber et al., 1986; Bell, 1994). For example, larvae of *Trogoderma* spp.

255   occasionally move, feed and moult during dormancy (Burges, 1959, 1960; Nair & Desai, 1972;

256   Barak & Burkholder, 1977; Bell, 1994). Beck (1971a) suggested that these larvae should not be

257   considered in diapause. Burges (1959) questioned whether *T.* granarium is in quiescence or in

258   diapause when dormant. Future studies should, in particular, identify triggers for induction and

259   termination of diapause, and develop methods to better identify diapausing individuals.

260   ***3.4 Relative humidity***

261 Dermestid beetles are xerophilous (thrive in dry environments) and are able to survive feeding

262 on food with water content below 10% (Zhantiev, 2009). This likely reflects the use of water

263 obtained from metabolism, the absorption of water from the air, and (or) other strategies

264 (Hinton, 1953 cited in Zhantiev, 2009; Edney, 1971; Zhantiev, 2009).

265 Lack of water can also enhance insect mortality at extreme temperatures (Convey, 2000;

266 Everatt *et al.,* 2014). The mechanisms of injury caused by extreme temperatures and

267 desiccation are similar in terms of osmotic stress and elicit similar responses for survival

268 (Convey, 2000). Low relative humidity can reduce cold tolerance in other stored-product insects

269 such as *Cryptolestes ferrugineus, Oryzaephilus surinamensis, Rhyzopertha dominica, Sitophilus*

270 *granarius, S. oryzae and Tribolium castaneum* (Evans, 1983; Fields, 1991). Similarly, at

271 temperatures between 40- 55°C, low humidity (< 50% RH) greatly reduces survival (Fields, 1992;

272 Beckett *et al*., 2007), but humidity has less effect on mortality at higher temperatures.

273 **3.5 Acclimation**

274 Acclimation is a phenomenon whereby insect survival at extreme temperatures is enhanced by

275 a brief exposure to less severe cold or high temperatures (rapid cold/heat hardening)

276 (Denlinger *et al.,* 1991). It is associated with the expression of heat shock proteins or stress

277 proteins (hsp), which protect organisms from heat/cold shock by stabilizing and preventing the

278 aggregation, and improper folding of proteins (Denlinger *et al.,* 1991; Fields *et al*., 1998; Beckett

279 *et al*., 2007). In pest-control applications, there is little evidence suggesting that heat-

280 acclimation has any practical significance at temperatures used for control, 50-60°C (Evans,

281 1987). At low temperatures, rapid rates of cooling prevent acclimation, which otherwise can

282 increase survival by 2- to 10-fold (Evans, 1987; Fields, 1992; Beckett *et al*., 2007). For *T.*

283 *variabile*, cold-acclimated diapausing larvae are much more cold-tolerant than non-acclimated

284 diapausing larvae (Abdelghany *et al*., 2015).

285 **3.6 Temperature and duration of exposure**

286 The level of mortality experienced by insects at a given temperature is a function of the

287 duration of exposure (Salt, 1958; Fields, 1992; Strang, 1992; Linnie, 1999). The relationship is

288 normally determined experimentally to calculate the combination of temperature and duration

289 needed to kill a given percentage of the population (Fields, 1992; Fields & White, 2002;

290 Eliopoulos *et al*., 2011). In *T. variabile,* 100% of non-diapausing larvae are killed after 17 days of

291 exposure to -5°C compared to 1 day at -20°C (Table 2) (Abdelghany *et al.,* 2015).

292 **Table 2.** Time necessary to reach mortality at sub-zero temperatures for different species of
293 economically important dermestid beetles.
294

Species	Reference	Life stage	Accli-mation	Tempe-rature (°C)	Duration	Mor-tality (%)
Trogoderma granarium	Lindgren & Vincent (1959)	Starved larvae	-	-10 to -7	36 d	40
		Fed larvae	-	-10 to -7	36 d	100
	Mathlein (1961)	Larvae	Yes	-2	180 d	45
				-5	90 d	23
				-10	30 d	97
				-19	15 d	100
					10 d	100
	Solomon & Adamson (1955)	Larvae	-	-3 to -8	10 mo	<4
	Voelkel (1924) cited in Hinton, 1945	Larvae	Yes	-10	72 h	11
		Larvae	No	-10	25 h	73
		Larvae	No	-16	24 h	98
		Adults	No	-16	16 h	100
	Eliopoulos *et al.,* (2011)	Young larvae	-	-16	4 h	100

Species	Reference	Life stage	Acclimation	Temperature (°C)	Duration	Mortality (%)
		Old larvae		-16	24 h	95
		Young adult		-16	12 h	92
		old adult		-16	12 h	97
	Zacher (1938) cited in Strang (1992)	Larvae 4th instar	-	-10	25 h	50
	Reynolds & Rundle (1967)	Larvae	No	-10	0 - 3.5 h	3
					7.5 - 41 h	76
					48 - 72 h	91
	Wilches *et al*., (2014)	Eggs, Pupae, Adults	No	-10	20 d	100
		Larvae	No	-10	7 d	45
		Diapausing larvae	No	-10	7 d	25
Trogoderma variabile	Abdelghany *et al.,* (2015)	Eggs	No	0	4 d	95
		Larvae	No	0	32 d	95
		Larvae	Yes	0	240 d	95
		Diapausing larvae	No	0	53 d	95
		Diapausing larvae	Yes	0	>275 d	50
		Larvae	No	-5	17 d	100
				-10	10 d	100
				-15	6 d	100

Species	Reference	Life stage	Accli-mation	Tempe-rature (°C)	Duration	Mor-tality (%)
		Diapausing larvae	Yes	-20	1 d	100
				-5	175 d	100
				-10	100 d	100
				-15	49 d	100
				-20	25 d	100
		Pupae	No	0	25 d	95
		Adults	No	0	15 d	95
Trogoderma inclusum	Reguzzi *et al.,* (2011)	All life stages	No	-22	3 h	100
		Larvae	Yes	-22	3 h	90
		Adults	No	-10	5 h	95
		Eggs, larvae, pupae	No	-10	6 h	100
Trogoderma angustum	Bergh *et al.,* (2006)	Larvae	No	-20	3 d	95
Attagenus fasciatus	Ali *et al.,* (1997)	Pupae	-	-5	7 h	100
		Pupae		0	6 d	100
Attagenus pellio	Florian (1986)	Eggs	-	-18	4 h	100
Attagenus smirnovi	Bergh *et al.,* (2006)	Larvae	No	-20	1 d	100

Species	Reference	Life stage	Accli- mation	Tempe- rature (°C)	Duration	Mor- tality (%)
				-14	1 d	100
				-12	1 d	98
Attagenus unicolor	Back & Cotton (1926) cited in Strang (1992)	Larvae	-	-4	198 d	100
	Salt (1936)	Larvae	-	-22	several min	100
		Pupae/adults		-24	several min	100
Attagenus woodroffei	Bergh *et al.,* (2006)	Larvae	No	-20	1 d	100
Anthrenus verbasci	Linnie (1999)	All life stages	-	-20	3 h	100
		Eggs, adults		-10	3 h	100
		Larvae		-10	24 h	10
		Pupae		-10	24 h	80
	Arevad (1979)	Eggs/pupae/adults	-	-20	2 h	100
	Bergh *et al.,* (2006)	Larvae	No	-20	1 d	93
Anthrenus museorum	Arevad (1974) cited in Strang (1992)	Larvae	-	-20	2h	<100
	Arevad (1979)	Adults	-	-20	1 h	100
		Eggs		-20	6 h	100

Species	Reference	Life stage	Accli-mation	Tempe-rature (°C)	Duration	Mor-tality (%)
	Bergh *et al.,* (2006)	Larvae	No	-20	3 d	70
Anthrenus flavipes	Back & Cotton (1926) cited in Strang (1992)	All life stages	-	-18	1 d	100
Dermestes vorax	Dawson (1984) cited in Strang (1992)	Larvae	-	-15	6 d	100
Dermestes maculatus	Strang (1992)	All life stages	-	-23	6 h	100
	Linnie (1999)	Eggs	-	-10	6 h	100
		Larvae, Pupae		-10	24 h	< 35
		Adults		-10	9 h	100
		All life stages		-20	3 h	100
	Zhang (2012)	Adults	No	-20	6 h	100
Reesa vespulae	Bergh *et al.,* (2006)	Larvae	No	-20	3 d	100
		Larvae		-20	1 d	80
	Mehl (1975) cited in Strang (1992)	Larvae	-	-20	2 d	>90
		Larvae		-10	14 d	>90
	Arevad (1974) cited in Strang (1992)	Larvae	-	-20	1 h	>90

295 *Blank cells represent unavailable information

296 **4. CONTROL OF DERMESTIDS WITH EXTREME TEMPERATURES**

297   Extreme high and low temperatures are becoming more widely used to eradicate infestations

298   of dermestids in storage facilities and museum collections (Bergh *et al*., 2006). However, most

299   dermestid species can enter diapause (Table 1), which may increase their tolerance to extreme

300   temperatures (Fields, 1992; Bell, 1994). Thus, successful application of extreme temperatures

301   requires information on the mortality of given species under different combinations of

302   temperatures and durations, and consideration of how factors such as diapause or acclimation

303   affect thermal tolerance (Burges & Burrell, 1964; Strang, 1992; Fields, 2001).

304   In the following sections, we briefly report on the literature pertaining to the thermal tolerance

305   of dermestids. Relevant papers initially were identified with key word searches in the databases

306   SCOPUS, Google Scholar, Research Gate, and Science Direct. The key words used for these

307   searches were low temperatures/ high temperatures, control, Dermestidae (or each of the

308   genera of economic interest). Additional papers, mainly published prior to 1960, were identified

309   by examining references cited in more recently published papers. Papers not published in

310   English were not considered.

311   **4.*1 Low temperature***

312   We identified 23 papers pertaining to the survival of economically-important dermestid beetles

313   at low temperatures (Table 2). Seven of these were published since 2005; the remainder were

314   either published prior to 1980. The greatest quantity of information was found for *T. granarium*

315   larvae held at -10°C. Depending upon the study, mortality of > 95% is achieved after 30 d of

316   exposure (Lindgreen & Vincent 1959; Mathlein 1961), of 91% after 72 h (Reynolds & Rundle,

317   1967), of 73% (Voelkel,1924 cited in Hinton, 1945) and 50% (Zacher,1938 cited in Strang, 1992)

318   after 25 h. This variation may be due to use of different methods (Fields, 1992; Zhang, 2012).

319   Many studies provide little or no information on whether larvae were acclimated or in

320   diapause, how the data were analysed, or on confidence limits to assess the variation in

321   responses among individuals.

322   Only six studies have assessed the effect of acclimation and diapause on cold-tolerance.

323   Lindgreen & Vincent (1959) showed that starvation reduced the mortality of *T. granarium*

324   larvae held for 36 days at -10 ^{o}C (Table 2). These starving larvae were likely in diapause (Burges,

325   1960). Three studies report an acclimation protocol before exposing the larvae of *T. granarium*

326   (Voelkel, 1924 cited in Hinton, 1945), *T. inclusum* (Reguzzi *et al*., 2011) and *T. variabile*

327   (Abdelghany *et al*., 2015) to sub-zero temperatures. Results of these studies indicate that

328   acclimation enhances survival at low temperatures (Table 2). Only one study reported on how

329   the combined effect of diapause and acclimation affected temperature tolerance. In a study on

330   *T. variable*, Abdelghany *et al.,* (2015) showed that the two factors were synergistic, with

331   acclimation being the main factor that increases cold-tolerance in this insect.

332   Variation among studies confounds the detection of general patterns (Table 2). The larval

333   stages appear to be the most cold-tolerant in the majority of dermestid species, particularly for

334   *T. granarium* (Mansbridge, 1936; Solomon & Adamson, 1955). To achieve > 90% mortality for

335   larvae held at -10°C, 30 days is required for *T. granarium* (Mathlein 1961), compared to 6 h for

336   *T. inclusum* (Reguzzi *et al*., 2011).

337   Low temperatures are more likely than high temperatures to be used in thermal treatments for

338   pest control because, although longer exposure is needed to reach mortality, they are less likely

339   to damage the treated product (Evans, 1987; Linnie, 1999). On products with low moisture

340   content, temperatures as low as -29°C have little effect on product quality but, in most

341   products, too-high temperatures can lead to deleterious chemical and biochemical changes and

342   most of these depend on the way the heat is delivered (Evans, 1987). Avoiding damage to the

343   product requires studies specific to the product to determine the combination of temperature

344   and duration exposure needed to achieve control, followed by post-treatment studies to assess

345   product quality (e.g., for processed foods, preserved specimens, textiles) or viability (e.g., for

346   bulk seeds) (Burges & Burrell, 1964; Evans, 1987; Fields, 1992; Fields *et al.,* 2012).

347   ***4.2 High temperature***

348   We identified 24 papers reporting on the control of dermestids with high temperatures (Table

349   3). The most recent of these was published in 2002 (Wright *et al.*, 2002), only two of the studies

350   considered the effect of diapause, and no studies assessed the effect of acclimation on heat-

351   tolerance. The rarity of such studies is likely because diapause does not typically increase

352   survival at temperatures used for heat treatments (50-60°C) (Evans, 1981). Wright *et al.* (2002)

353 reported that diapause does not increase heat tolerance in larvae of *T. variabile* held for 4

354 minutes at 56°C. However, Battu *et al.,* (1975) reported the need of a longer exposure time at

355 50°C to reach 95% mortality in *T. granarium* larvae in diapause (20 h) compared to non-

356 diapausing larvae (5.3 h).

357 **Table 3.** Time necessary to reach >90% mortality at high temperatures for different species of
358 economically important dermestid beetles, no beetles in these studies were acclimated.
359

Species	Reference	Life stage	R.H. (%)	Tempe-rature (°C)	Duration	Mortality (%)
Attagenus scalaris	Abdel-Rahman *et al.,* (1981)	Larvae	-	50	35 min	100
Attagenus fasciatus	Ali (1997)	Pupae	-	45	18 h	100
				50	30 min	100
	Ali (1992)	Larvae	-	50	20 min	100
Attagenus pellio	Zacher (1927) cited in Strang (1992)	Eggs/larvae	-	52	20 min	100
Anthrenus verbasci	Linnie (1999)	All life stages	-	50	6 h	100
Anthrenus flavipes	Ayappa *et al.,* (1957)	Pupae	30	41	2 h	100
			90	41	1 h	100
Anthrenus coloratus	Ali (1997)	Larvae	-	50	12 min	100
Anthrenus sarnicus	Armes (1985) cited in Linnie (1999)	All life stages	-	40	2 h	>90

Species	Reference	Life stage	R.H. (%)	Temperature (°C)	Duration	Mortality (%)
Dermestes maculatus	Nakayama *et al.,* (1983)	All life stages	-	50	30-60 min	>90
	Linnie (1999)	All life stages	-	50	3 h	100
Dermestes coarctatus	Yokoyama (1927) cited in Strang (1992)	Larvae/pupae/adults	-	50	1 h	100
				55	15 min	100
Trogoderma granarium	Battu, *et al.,* (1975)	Diapausing larvae	70	42	16 d	95
				45	6 d	95
				50	20 h	95
		Larvae	70	42	13 d	95
				45	4.2 d	95
				50	5.3 h	95
		Pupae	70	50	16 h	100
			70	55	2 h	100
	Husain & Bhasin (1921)	Larvae	-	50	5 h	>90
		Larvae		54	20 min	>90
				60	4 min	>90
	Lindgren & Vincent (1959)	Eggs	-	57	3 min	95
	Lindgren *et al.,* (1955)	All life stages	75	55	8 min	95

Species	Reference	Life stage	R.H. (%)	Tempe-rature (°C)	Duration	Mortality (%)
			95	55	15min	95
	Fleurat-Lessard (1985)	larvae	-	70	16 sec	100
	Ismail *et al.,* (1988)	All life stages	-	60	30 min	100
	Taheri (1988)	All life stages	-	45	4 d	100
	Mookherjee *et al.,* (1968)	Pupae	-	50	16 h	100
	Saxena, *et al.,* (1992)	Pupae	-	45	48 h	84
				55	2 h	100
	Shoab (2009)	Larvae	-	60	2 min	100
		Larvae		57	5 min	100
		Larvae		54	12 h	100
		Larvae		51	48 h	100
	Zacher (1927) cited in Strang (1992)	Larvae	-	50	5.6 h	>90
				52	1.5 h	>90
				53	0.5 h	>90
				54	20 min	>90
				55	10 min	>90
				58	5 min	>90
				71	1 min	>90
				82	0.5 min	>90

Species	Reference	Life stage	R.H. (%)	Tempe-rature (°C)	Duration	Mortality (%)
	Wilches *et al.,* (2014)	Eggs, Pupae, Adults	-	45	7 d	>90
Trogoderma variabile	Wright *et al.,* (2002)	Egg	0	56	4 min	98.6
		Small larvae			2 min	91
		Large larvae			4 min	100
		Diapause larvae			4 min	93.3
		Pupae			4 min	100
		Adult female			4 min	96.4
	Kirkpatrick & Tilton (1972)	Adults	-	40	>24 h	>90
				45	12 h	>90
				50	5 min	>90
				55	1 min	>90

360
361 *Blank cells represent unavailable information
362
363 The mechanisms of mortality are similar between extreme temperatures and desiccation,

364 adaptations to dehydration may enhance temperature tolerance (Danks, 1996, 2000). Insects

365 adapted to tolerate dry environments will likely able to better tolerate extreme temperatures

366 (Danks, 1996, 2000). *Trogoderma granarium* and *A. verbasci* appear to be the most heat-

367 tolerant of the dermestids (Table 3). When held at 50°C, exposure for more than 5 h is required

368 to achieve >90% mortality for these species; whereas a similar level of mortality can be

369 achieved within minutes for other dermestid species. The result of *T. granarium* being more

370 heat-tolerant is not unexpected, given that it is endemic to hot and dry environments (Hinton,

371 1945; Banks, 1977; Eliopoulos, 2013). In contrast, *T. variable*, which has a Neartic origin (Table

372 1), seems to be less heat-tolerant, reaching >90% mortality in less than 5 minutes at 50°C

373 (Kirkpatrick & Tilton, 1972; Wright *et al.,* 2002). Studies on *A. flavipes* and *T. granarium* also

374 suggest that relative humidity (rh) plays an important role in heat tolerance and when

375 increased, it might increase heat tolerance (Lindgren *et al*., 1955; Ayappa *et al*., 1957)

376 Within the dermestids, *T. granarium* is among those that have greatest thermal tolerance such

377 that temperature treatments sufficient for its control would likely suffice for other species

378 (Howe, 1965; Fields, 1992). In general, the published literature indicates that dermestid species

379 cannot survive exposures of more than 3 days at temperatures below -20°C or more than 2

380 hours above 50-60°C (Table 3). Future studies to control dermestids at high and low

381 temperatures must include different life stages of the insect, a wide range of temperatures and

382 exposure times, and standardization of the analytical methods to determine the lethal time for

383 the 50 and 95% of the population (LT$_{50}$ and LT$_{95}$). The most widely used regression nowadays is

384 the probit regression, which must be used only when the mortality vs time data follows a

385 sigmoidal shape and should be reported with its variance estimates (fiducial limits) in order to

386 be comparable (Fields, 1992).

387 **4.3 Models**

388 Mathematical models can be used to design effective thermal treatments for pest control. Such

389 models require data on the survival of a species at different combinations of temperature and

390 duration of exposure. Such data are normally obtained in laboratory studies for the most cold-

391 /heat-tolerant life stage, including stages in diapause (Fields, 1992; Abdelghany *et al*., 2015).

392 Mortality of insects under constant temperatures can be modeled using kinetic or empirical

393 models; e.g., modified fundamental kinetic and modified complementary log-log

394 transformation models (Jian *et al.,* 2010). Mortality can be modelled as a function of time

395 required for the facility to reach the lethal temperature, the duration required for exposure to

396 that lethal temperature, and the maximum/minimum temperature required for mortality

397 (Subramanyam *et al*., 2011). Mathematical models also have been developed for the use of

398   non-constant temperatures to control stored product pests; e.g., heat accumulation model and

399   heat treatment zones model (Jian *et al.,* 2013). Application of existing models may be condition

400   dependent. Hence, models may require validation for a given combination of species,

401   temperature range, and site (e.g., building, container, and product) of application (Jian *et al.,*

402   2010).

403   Models also can be developed to predict the risk of future global spread and establishment for

404   a given insect pest (Paini & Yemshanov, 2012). This can be done with species occupancy

405   models, by identifying the optimal temperature and humidity for the pest development,

406   reproduction and survival, and then matching this information to geographic regions where the

407   pest does not yet occur (Banks, 1977). Such models have been developed for *T. granarium,*

408   which is a major pest of stored grains and a quarantine pest in Canada, USA, and Australia

409   because, if introduced and (or) established into these countries it would cause high economic

410   losses. Paini & Yemshanov (2012) assessed the risk of *T. granarium* arriving in Australia using a

411   first-order Markov chain model. This model used information on *T. granarium*'s current

412   distribution and the probability of its presence in countries where it has not yet been reported,

413   to determine the most likely source countries and ports of entry into Australia. Previous studies

414   indicate that *T. granarium* requires conditions of > 20°C average temperature for at least four

415   months in a year to establish and reach pest status (Hadaway, 1955; Howe & Lindgren, 1957).

416   Based on this information, mathematical models predict that *T. granarium* is unable to

417   establish anywhere in Canada, except possibly in heated storage facilities (Ameen, 2012).

418   However, these models may need to be reassessed, given new information on the thermal

419   tolerance of cold-acclimated insects or insects in diapause, plus a general warming of

420   temperatures in recent decades due to climate change (Estay *et al.,* 2009).

421   **5. Conclusions**

422   The development of protocols using extreme temperatures to control dermestids is hindered

423   by a general lack of information on the thermal tolerance of acclimated individuals, and on

424   individuals in diapause. Diapause research on dermestids can be difficult, because of the high

425   degree of ecological plasticity among species and the diverse physiological and environmental

426   cues that trigger diapause induction (Table 1) (Bell, 1994; Zhantiev, 2009). Species exhibiting

427   density-dependent diapause may be particularly good models to study the effects of diapause

428   on thermal tolerance, because diapause induction is independent of temperature and,

429   therefore, is not confounded by temperature acclimation (Nair & Desai, 1972; Abdelghany,

430   2015).

431   The diapause stage in dermestids makes their control difficult and enhances the pest status of

432   some species. Diapause allows these insects to use an intermittent food supply and survive

433   adverse conditions such as low temperature or the application of insecticides. The factors and

434   their magnitude necessary to induce and terminate diapause must be clearly identified in order

435   to manipulate diapause and develop more effective methods of pest control for dermestids.

436   Although it has not been greatly assessed, diapause together with acclimation can increase

437   significantly the temperature tolerance of dermestids (Fields, 1992; Abdelghany *et al*., 2015).

438   Studies on the development of strategies and models to control dermestid species should

439   include the study of diapause and acclimated larvae of each species. Larvae under these

440   conditions are likely the most resistant to the method of control (Burges, 1962b; Wright &

441   Cartledge, 1994; Denlinger, 2008).

442   This review shows that from the practical point of view our knowledge about heat/ cold-

443   tolerance on dermestid beetles is fragmentary and the methods used are not very rigorous or

444   standardized. Future studies should, in particular, identify triggers for induction and

445   termination of diapause, and develop methods to better identify diapausing individuals. The

446   clear identification of other factors inducing and terminating diapause may lead to the

447   manipulation of environmental conditions to prevent induction of the tolerant diapausing stage

448   and the success of control methods such as the use of extreme temperatures (Nair & Desai,

449   1972; Wright & Cartledge, 1994; Kostál, 2006). Studies on extreme temperatures needed for

450   control of dermestid pests should consider factors such as species and life stages to be

451   exposed, rates of cooling and heating, well specified environmental conditions used in the

452   experiment besides details of mathematical analyses used and the consideration of the

453   mortality at various temperatures to be used in mathematical modelling of the control method.

454   **6. Acknowledgements**

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