Evolutionary diversification of bruchine beetles : Climate-dependent traits and development associated with pest status

Tuda, Midori
Institute of Biological Control, Faculty of Agriculture, Kyushu University

https://hdl.handle.net/2324/25731

出版情報：Bulletin of Entomological Research. 101 (4), pp.415-422, 2011-08. Cambridge University Press
バージョン：

Bulletin of Entomological Research (2011) **101**, 415–422 doi:10.1017/S0007485310000660

Evolutionary diversification of bruchine beetles: climate-dependent traits and development associated with pest status

M. Tuda*

Institute of Biological Control, Faculty of Agriculture, Kyushu University,
Fukuoka 812-8581, Japan

Abstract

A number of insect species infest human households and stored foods and products, leading to their designation as pests. Until recently, little was known about the factors driving the evolution of pests that feed on stored dry foods. Here, I review the effects of changes in climate and species interactions on the evolution and ecology of beetles that feed on dried seeds/grains. My review focuses on evidence that the host utilization by part of the species in the subfamily Bruchinae (Chrysomelidae) is a preadaptation for utilizing stored dry seeds and grains, thus leading to their status as a pest. These and other stored product pest beetles retain a higher percentage of water in their body, relative to the water content of their diet, than beetles that feed on fresh crops. I review the studies that have documented adaptation, acclimation and polyphenetic response to high temperatures and desiccation and/or made direct comparisons between these traits between developmental stages, populations and among higher taxonomic groups. Finally, I review evidence for the effects of environmental change on insect host-parasitoid and competitor assemblages.

Keywords: Bruchidae, preadaptation, heat, stored crop pest, arid season, phytophagous insects

(Accepted 30 September 2010)

Introduction

A number of insect species infest human households and stored foods and products, leading to their designation as pests (Marlatt, 1896; Alfieri, 1931). These animals share a number of distinct biological characteristics which have brought about their widespread distribution. One of the most important characteristics is their tolerance to a wide range of physical environments. For example, some species are able to utilize foods that have a wide range of moisture content (Linsley, 1944). Other characteristics include polyphagy and aphagy (Linsley, 1944; Tuda *et al*., 2005). Despite the economic and social impact of these pests (up to 9% loss in developed countries and up to 20%, or more, loss in developing countries: Phillips & Throne, 2010), little is known about the factors that drive their evolution. Here, I review the effects of species interactions and climate on the evolution and ecology of beetles (bruchine seed beetles, in particular; see also Labeyrie, 1981; Fujii *et al*., 1990; Yoshida, 1990). I also review the studies of adaptation, acclimation and polyphenetic response to high temperatures and desiccation and the evidence for the effects of environmental change on host-parasitoid and competitor assemblages.

Evolution of dry food use as a preadaptation to becoming a stored food pest

It has been hypothesized that the human cultivation of grains in tropical/subtropical climates promoted the evolution of pests that rely on stored grains/legumes for some part of their life cycle (Cotton, 1956). However, recent studies suggest that changes in climate and in host plant assemblages associated with different climates were a prerequisite for the evolution of host utilization in insects that are now considered

---

*Fax: +81-92-642-3040
E-mail: tuda@grt.kyushu-u.ac.jp

to be stored grain pests (Tuda *et al.*, 2006b). Furthermore, there is evidence that the species split between stored bean pests and that the non-pest sister species occurred long before the human cultivation of beans (Alvarez *et al.*, 2005).

The majority of seed beetles from the subfamily Bruchinae (Coleoptera: Chrysomelidae) utilize the seeds of the bean family (Fabaceae) as larval hosts (Johnson, 1981). After hatching from eggs deposited on or near seeds by their mothers, the larvae feed and pupate inside the seeds. Partly because of this life cycle, some members of the subfamily are considered to be serious pests of leguminous plants. Utilization of dry beans for larval hosts is most likely, an ancestral trait in bruchine seed beetles (Tuda *et al.*, 2006b). Interestingly though, some bruchines utilize only immature, soft seeds (Southgate, 1979; Decelle, 1981; Alvarez *et al.*, 2005; Tuda *et al.*, 2006b; M. Tuda, unpublished). It is unlikely that the evolution of the use of dry seeds was driven by the use of cultivated legumes. Instead, this trait is likely a preadaptation for becoming a pest of stored beans (Watanabe, 1985; Tuda *et al.*, 2006b). We hypothesize that this unique feeding trait may be explained by climate (long, arid seasons) and the associated plant taxa, not their cultivation status. The long period of time in which seeds are available may also allow multivoltinism (Southgate, 1981; Ishihara, 1998; Alvarez *et al.*, 2005). Our recent study is the first to test competing hypotheses about the evolution of dried food pests (Tuda *et al.*, 2006b). Our data suggested that the length of the dry period contributed more to the evolution of a life cycle that incorporated the use of dry food than temperature *per se*. This is probably due to the long period of food availability associated with dry season (Tuda *et al.*, 2006b). Although this host-utilization phenotype may be ancestral, it is not strictly phylogenetically constrained as it is observed sporadically throughout the bruchine subfamily (M. Tuda, unpublished). Recently, several closely related species of bruchine beetles that feed on either dry seeds or fresh seeds were identified (Tuda, 2003; Tuda & Morimoto, 2004). A comparison of these species affords an opportunity to test the factor(s) driving the evolution of host-utilization traits that are associated with stored bean pests (Tuda, 2007).

Many pest insects of stored products were already preadapted to exploit the small quantities of naturally stored dry or rotten plant and animal materials, including dry seeds, fruits, pollen, dead insects, and hairs or feathers in the nests and webs of birds, mammals, spiders and insects (Linsley, 1944). Most of these insects are scavengers or predaceous, unlike bruchines. Therefore, the climate effect on the preadaptation suggested for bruchine beetles may not be applied to these insects. Furthermore, besides these natural causes, humans have likely had a considerable influence on the evolutionary processes. For example, the storage of large amounts of grain for long periods of time, particularly during World War I and II, may have promoted the adaptation of potential pests to storage conditions.

Adaptation to arid climates

The tolerance for changes in temperature and humidity varies among the developmental stages of insects, such as *Drosophila* (Krebs & Loeschcke, 1995; Gilchrist *et al.*, 1997), the kelp fly (Klok & Chown, 2001) and *Tribolium*, a pest of stored, dried foods (Oosthuizen, 1935; Mahroof *et al.*, 2003). As such, holometabolous insects and amphibians experience different habitat climates at each life-history stage. The egg and adult stages tend to be exposed to the ambient environment and may be tolerant of severe climate extremes (Howe & Currie, 1964; Bale & Hayward, 2010). A number of behavioral and physiological adaptations to aridity have been noted in these life stages. For example, some bruchines lay their eggs in layers or cover them with fecal material. This prevents the eggs from desiccation, as well as from egg parasitoids (Teran, 1962; Prevett, 1966; Janzen, 1971; Mitchell, 1977; Delobel *et al.*, 1995; Tuda, 2007). The eggs are also tolerant to a wide range of both humidity and temperature (Howe & Currie, 1964). Adults and larvae have a greater proportion of water in the bound form than the pupae (Kagoshima, Ishibashi, Tuda, & Iwaya-Inoue, unpublished). Most bruchine beetles enter diapause (reproductive quiescence) as adults (Utida, 1954; Sano, 1967; Ouedraogo *et al.*, 1991; Amevoin *et al.*, 2005; Appleby & Credland, 2007; review by Bell, 1994), larvae (Donahaye *et al.*, 1966; Shimada & Ishihara, 1991) or both (Kurota, 2004). This phenomenon has also been reported in other beetle species that feed on dry, stored foods (review by Bell, 1994). The absence of diapause during the pupal stage is common among beetles, but not in other orders (Leather *et al.*, 1993). This suggests that the physiological tolerance of beetles to extreme temperatures differs among the developmental stages (Mahroof *et al.*, 2003). This difference may, in part, be a by-product of morphological reorganization, with little or no evolutionary significance (Bowler & Terblanche, 2008). However, there is evidence that the expression of at least one of the genes encoding heat-shock proteins is down-regulated during the pupal (and late larval) stages in the stored pest beetle, *Tribolium castaneum* (Mahroof *et al.*, 2005).

A classic physiological study by Robinson (1928) revealed that stored grain pest beetles retain disproportionately high levels of water in their body relative to the dried grains they feed on (fig. 1). The same is true for bruchine beetles. For example, larvae of *Callosobruchus* beetles feed on dry beans, whereas those of *Bruchus rufimanus* feed only on immature beans. Despite the difference in water content of the food source, both species have a similar proportion of body water (fig. 1). Furthermore, in these and other stored-product pests, the majority of body water is conserved in the bound form to minimize its loss (fig. 2) (Robinson, 1928). The cells of all living tissues contain millions of minute colloidal particles, which attract and bind water as a film on their surfaces. The water, thus bound, is held by the colloidal bodies with a powerful force (Robinson, 1928). By conserving water in this less mobile form, the insects gain resistance against both dry and cold environments (Robinson, 1927; Block, 1996). Similarly, heat-resistant individuals of *C. chinensis* are characterized by longer adult life duration in very dry air (Kiyoku, 1962). This ‘side effect’ of adaptation to arid environments is seen in *Callosobruchus* beetles. In some species, the use of dry beans appears to have promoted a habitat shift (or expansion) from subtropical to temperate regions (Tuda *et al.*, 2006b). Furthermore, the mechanisms proposed for insect mortality at high temperatures are the same as those for low temperatures (Tauber & Tauber, 1986; Fields, 1992). These include changes in membrane lipid property (Gibbs, 1998; Patel *et al.*, 2001), rate imbalances (Hochachka & Somero, 1984; Fields, 1992), perturbation of ionic activities (Cloudsley-Thompson, 1962; Mullins, 1985) and desiccation (Cloudsley-Thompson, 1962; Fields, 1992).

Behavioral adaptation to aridity is observed in *C. maculatus*. Females mate more frequently under water deficiency, presumably because they can obtain a water source from male

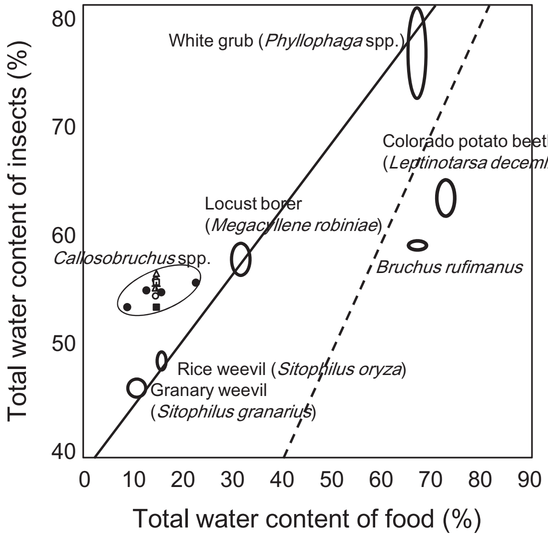

Fig. 1. Relationship between the water content of insects and their food (only Coleoptera are shown, modified from Robinson 1928, with additional data). The examples on the upper side of the broken line indicate that the water content of the insects is greater than that of the food. Granary weevil, rice weevil (Curculionidae) and *Callosobruchus* beetles (Chrysomelidae: Bruchinae) are stored seed/grain pests, whereas the Colorado potato beetle (Chrysomelidae), locust borer (Cerambycidae), white grub (Scarabaeidae) (Robinson, 1928) and broad bean beetle, *Bruchus rufimanus* (Chrysomelidae: Bruchinae) (Kagoshima & Tuda, unpublished data) are pests of fresh vegetables and trees, at one or more life stages. ●, *Callosobruchus chinensis* (Ishii, 1952); ○, *C. chinensis*; Δ, *C. maculatus*; □, *C. analis*; ■, *C. phaseoli*; +, *Zabrotes subfasciatus* (Utida, 1966). The data were collected from the adults of all species except for the white grub (larvae) (Robinson, 1928).

ejaculates (Edvardsson, 2007). They also prefer drier beans for oviposition (Hudaib *et al.*, 2010).

Acclimation and adaptation to high temperatures

Mellanby (1954) may have been the first author to demonstrate thermal acclimation at high temperatures in insects. Mealworm, *Tenebrio molitor*, larvae that were acclimated to temperatures of 37 and 30°C died at 44 and 42°C, respectively, supporting the 'beneficial acclimation' hypothesis (Leroi *et al.*, 1994). Using *C. chinensis*, Kiyoku (1960) observed acclimation and adaptation to high temperature (35°C) in support of this hypothesis. However, the 'beneficial acclimation' hypothesis has been challenged in the latest decade. For example, thermal adaptation (or acclimatization) to a habitat was examined by exposing the bruchine beetle *Stator limbatus* to a range of temperatures (Stillwell & Fox, 2005). Exposure to (and acclimation to) high temperatures during the immature stages of several species of bruchines leads to a general reduction in fecundity, irrespective of the tested oviposition temperature (Ishikura, 1939; El-Sawaf, 1956; Stillwell & Fox, 2005). This reduction in fecundity seemingly supports 'colder is better' hypothesis (Huey *et al.*, 1999), which is induced by a reduction in body size as is typical in ectothermic organisms (Atkinson, 1994). Overall, either 'colder is better' hypothesis or 'optimal developmental temperature' hypothesis (Cohet & David, 1978; Huey *et al.*, 1999 or 'deleterious acclimation' hypothesis (Loeschcke & Hoffmann, 2002; Wilson & Franklin, 2002) seems to be supported both in *S. limbatus* (Stillwell & Fox, 2005) and *Zabrotes subfasciatus* (Howe & Currie, 1964). Acclimation of other insects that feed on stored products depends on the range of the highest temperatures, and this is ascribed to thermal effect on biochemical process (Fields, 1992). Survival at very high, sublethal temperatures (40–50°C) may be improved by acclimation at high temperatures. However, survival at extremely high, lethal temperatures (55–80°C) is not affected by acclimation. Within this temperature range (56–60°C), denaturation and inactivation of pyruvate kinase, a key enzyme in glycolysis, is induced and is likely responsible for mortality (Hochachka & Somero, 1984).

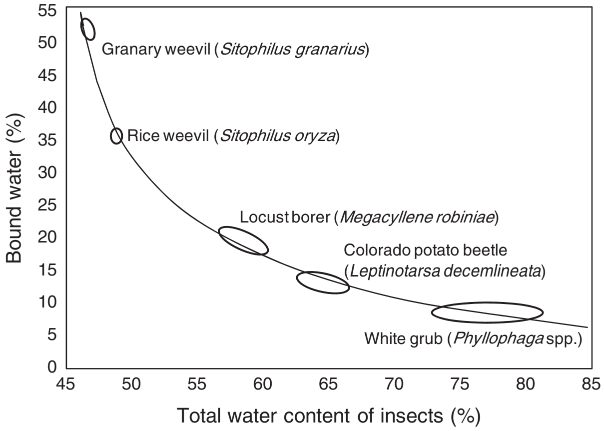

Fig. 2. Relationship between total water content and the percentage of water bound by colloids (only Coleoptera are shown, modified from Robinson, 1928). The species that live on dry food and have a small percentage of water in their own tissues retain a large percentage of water in the bound form. The data were collected from the same developmental stages as in fig. 1 for each species.

Effect of climate and the host plants on polyphenism, population density and competitive/predatory interactions

Climate does not act alone on phytophagous insects. The host plants also alter the fitness of insect herbivores in a predictable manner. By selecting different host plants, *C. maculatus* is able to survive over a wider range of temperatures and humidity than is optimal in a limited range of climate (Howe & Currie, 1964). Stillwell *et al.* (2007b) noted an increase in fitness at high temperatures for traits associated with body size (i.e. growth rate, fecundity and body size itself) but not for larval survival or development time. Temperature has a significant effect on the success of small males during intraspecific competition for mates (Moya-Larano *et al.*, 2007). Both temperature and the host plant type affect the size of the nuptial gift, as seminal fluids (ejaculates), offered by the males (Fox *et al.*, 2006). Furthermore, it appears that there is an interaction effect between these two variables. Variation in the body size of *S. limbatus* throughout its range was attributed to differences in host plant seed size, moisture (humidity) and seasonality (variation in humidity, precipitation and temperature), but not to mean temperature (Stillwell *et al.*, 2007a). Moisture also partially explains the geographic variation in sexual dimorphism (Stillwell *et al.*, 2007a). Conversely, in

C. maculatus, experiments at a constant temperature suggest that higher temperatures induce greater sexual dimorphism in body size (Stillwell & Fox, 2007). This is probably caused by sexual conflicts related to fitness optimization strategies, which may increase population fitness (Rankin & Arnqvist, 2008; Arnqvist & Tuda, 2010). Early-emerging (smaller) males are more likely to find mates, particularly if the females are ready to mate soon after emergence (Rönn *et al*., 2008) and are reluctant, or refuse, to mate more than once (Edvardsson & Tregenza, 2005; Sakurai & Kasuya, 2008). However, larger females tend to take longer to develop and are more fecund and, thus, fitter (Yanagi & Miyatake, 2002; Vamosi, 2005; Vamosi & Lesack, 2007), especially when resource replacement cycle is long (Sibly *et al*., 1991).

The optimal temperature for rapid development in insects tends to be higher than the optimal temperature for survival and reproduction (Howe & Currie, 1964; Braby & Jones, 1994). The optimal humidity is typically high for development, survival and reproduction. However, very high humidity levels enhance fungus development and increase mortality in immature beetles. The effects of temperature/humidity on populations and/or species should, therefore, be compared on lifetime fitness (Deutsch *et al*., 2008; Yanagi & Tuda, 2010).

There are two adult morphs, the flight form (or active form in reproductive diapause) and non-flight form, in some bruchine seed beetles. High or increased temperature, long thermoperiods, extreme day-lengths, high seed water content and high larval density induce the flight form of *C. maculatus* (Utida, 1954, 1965, 1969; Sano, 1967; Sano-Fujii, 1984; Ouedraogo *et al*., 1991). The flight form is partially heritable (Caswell, 1960; Sano-Fujii, 1986). These environmental factors also have a similar effect on induction of the active morph in other species congeneric to *C. maculatus* (temperature effect in *C. subinnotatus* (Appleby & Credland, 2007); density effect in *C. subinnotatus* and *C. rhodesianus* (Amevoin *et al*., 2005; Appleby & Credland, 2007); and seed water content in *C. chinensis* (Nahdy *et al*., 1999)).

Most phytophagous arthropods engage in predator-prey or parasitoid-host interactions in nature. Predictions regarding how climate change will alter these interactions are crucial for conservation of biological diversity and for biological control practices. An understanding of the effects of climate change on these interactions in wild populations relies on direct observation and analysis of field populations with the associated climate data (Tuda & Shima, 2002; Tuda *et al*., 2006a). Alternatively, demographic experiments that use model species provide a useful tool for understanding the general rules governing the effects of climate on whole ecosystems.

Studies have shown that just a 2°C increase in the temperature reduces the population size of seed beetles via a decrease in density-dependent rates of egg hatching and larval survival (Tuda, 1993; Tuda & Shimada, 1993). Furthermore, such an increase in temperature also affects the coexistence of the seed beetle and its parasitoid populations (Tuda & Shimada, 1995, 2005). However, the effect is highly species specific. Both the host and the parasitoid will coexist if the functional response of the parasitoid stabilizes the host-parasitoid population dynamics following an increase in temperature (M. Tuda, unpublished data).

Phytophagous insects also participate in competitive interactions, although competition may occur less frequently than predation (Jermy & Szentesi, 2003). Changes in climate (e.g. a 2°C rise and humidity change) alter the interspecific competitive success of two *Callosobruchus* beetle species, which may be ascribed by different environmental effects on development time and fecundity between the two species (Fujii, 1967). Furthermore, Davis *et al*. (1998) showed that allowing dispersal along temperature clines altered the outcome of competition and species distribution in laboratory-reared *Drosophila* metapopulations.

Genetics of thermal adaptation

Development time and metabolic rate of *C. maculatus* are affected by temperature and by the interaction between mitochondrial haplotype and nuclear genotype (or mitonuclear interaction) (Dowling *et al*., 2007; Arnqvist *et al*., 2010). Such mitonuclear interactions (Ballard & Rand, 2005) may be ubiquitous in insect thermal response. There is evidence that mtDNA transmission rates of *Drosophila* is temperature dependent (Nagata & Matsuura, 1991) and that nuclear genome is involved in the temperature dependency (Doi *et al*., 1999). Although these studies using a model beetle shed light on the genetic background of the thermal response in beetles, our understanding of the genetic mechanisms controlling thermal adaptation is poor. Thus, this area of research offers considerable promise in the future.

Future directions

This review focused on climate effects on the evolution, developmental stages, variation within and among taxonomic groups, species interactions and coexistence in holometabolous insects, particularly beetles. Genetic effects on physiological plasticity and adaptation tend to be underestimated in previous studies, except for some that have used model organisms such as *Drosophila* (Hoffmann *et al*., 2003) and *Arabidopsis* (Siomos, 2009). For well-studied laboratory model insects, however, extra caution must be paid to eliminate bottleneck events and artificial selection due to laboratory conditions and rearing. Populations that were reared in a large batch for a small number of generations (<<20) (for timescale of selection, see Tuda (1998) and Tuda & Iwasa (1998)) or several smaller populations with a moderate gene flow may be used.

Recent advances in molecular methods will improve our understanding of adaptation and acclimation to climate. On one hand, studies on molecular mechanisms of adaptation/acclimation to climate changes in beetles might benefit from DNA sequence data of a stored pest beetle, *T. castaneum* (*Tribolium* Genome Sequencing Consortium, 2008). For example, an evolutionary process may be uncovered for the close correlation between enzyme genotypes and the expression of a heat shock protein in a leaf beetle, *Chrysomela aeneicollis* (Dahlhoff & Rank, 2000). In addition, approaches using phylogeny-based inference may improve the ability to distinguish between ecological plasticity and phylogenetic signals in climate-dependent traits. Comparative methods, such as have been used to describe the distribution of the variation in thermal tolerance at different levels of taxonomic hierarchy (Chown, 2001), may employ the molecular-phylogeny-based hypothesis testing.

Quantification of the effects of global climate changes will be needed to predict future changes in phenology (Doi *et al*., 2010; Musolin *et al*., 2010), dispersal (Berg *et al*., 2010; Srygley *et al*., 2010), their synchronization with interacting species (Yukawa & Akimoto, 2006; Hance *et al*., 2007; van Asch & Visser, 2007; Klapwijk *et al*., 2010) and their population-dynamic consequences (Gilg *et al.*, 2009) at local and regional scales (Kiritani, 2006; Tabachnick, 2010). A number of climate models predict that several regions of the world will experience more or more severe droughts as a result of rises in atmospheric CO_2 and global temperature (Solomon *et al.*, 2009; Xie *et al.*, 2010). In these regions, particular attention should be paid to monitor any increase in the density and diversity of herbivorous insects, including stored crop pests.

Acknowledgements

This work was supported by Grants-in-Aid for Scientific Research from JSPS.

References

Alfieri, A. (1931) Les insects de la tombe de Toutankhamon. *Bulletin de la Société Royale Entomologique d'Égypte* **3–4**, 188–189.

Alvarez, N., McKey, D., Hossaert-McKey, M., Born, C., Mercier, L. & Benrey, B. (2005) Ancient and recent evolutionary history of the bruchid beetle, *Acanthoscelides obtectus* Say, a cosmopolitan pest of beans. *Molecular Ecology* **14**, 1015–1024.

Amevoin, K., Glitho, I.A., Monge, J.P. & Huignard, J. (2005) Why *Callosobruchus rhodesianus* causes limited damage during storage of cowpea seeds in a tropical humid zone in Togo. *Entomologia Experimentalis et Applicata* **116**, 175–182.

Appleby, J.H. & Credland, P.F. (2007) The role of temperature and larval crowding in morph determination in a tropical beetle, *Callosobruchus subinnotatus*. *Journal of Insect Physiology* **53**, 983–993.

Arnqvist, G. & Tuda, M. (2010) Sexual conflict and the gender load: correlated evolution between population fitness and sexual dimorphism in seed beetles. *Proceedings of the Royal Society, Series B* **277**, 1345–1352.

Arnqvist, G., Dowling, D.K., Eady, P., Gay, L., Tregenza, T., Tuda, M. & Hosken, D.J. (2010) The genetic architecture of metabolic rate: environment specific epistasis between mitochondrial and nuclear genes in an insect. *Evolution* **64**, 3354–3363.

Atkinson, D. (1994) Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* **25**, 1–58.

Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology* **213**, 980–994.

Ballard, J.W.O. & Rand, D.M. (2005) The population biology of mitochondrial DNA and its phylogenetic implications. *Annual Review of Ecology, Evolution and Systematics* **36**, 621–642.

Bell, C.H. (1994) A review of diapause in stored-product insects. *Journal of Stored Products Research* **30**, 99–120.

Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A. & Ellers, J. (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* **16**, 587–598.

Block, W. (1996) Cold or drought: the lesser of two evils for terrestrial arthropods? *European Journal of Entomology* **93**, 325–339.

Bowler, K. & Terblanche, J.S. (2008) Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Reviews* **83**, 339–355.

Braby, M.F. & Jones, R.E. (1994) Effects of temperature and hostplants on survival, development and body size in three tropical satyrine butterflies from north-eastern Australia. *Australian Journal of Zoology* **42**, 195–213.

Caswell, G.H. (1960) Observations on an abnormal form of *Callosobruchus maculatus* (F.). *Bulletin of Entomological Research* **50**, 671–680.

Chown, S.L. (2001) Physiological variation in insects: hierarchical levels and implications. *Journal of Insect Physiology* **47**, 649–660.

Cloudsley-Thompson, J.L. (1962) Lethal temperatures of some desert arthropods and the mechanism of heat death. *Entomologia Experimentalis et Applicata* **5**, 270–280.

Cohet, Y. & David, J. (1978) Control of adult reproductive potential by pre-imaginal thermal conditions; a study in *Drosophila melanogaster*. *Oecologia* **36**, 295–306.

Cotton, R.T. (1956) *Insects Pests of Stored Grain and Grain Products*. Minneapolis, MN, USA, Burgess.

Dahlhoff, E.P. & Rank, N.E. (2000) Functional and physiological consequences of genetic variation at phosphoglucose isomerase: Heat shock protein expression is related to enzyme genotype in a montane beetle. *Proceedings of the National Academy of Sciences USA* **97**, 10056–10061.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* **67**, 600–612.

Decelle, J. (1981) Bruchidae related to grain legumes in the Afro-tropical area. pp. 193–197 *in* Labeyrie, V. (*Ed.*) *The Ecology of Bruchids Attacking Legumes (Pulses)*. The Hague, The Netherlands, Dr W. Junk Publishers.

Delobel, A., Couturier, G., Kahn, F. & Nilsson, J.A. (1995) Trophic relationships between palms and bruchids (Coleoptera, Bruchidae, Pachymerini) in Peruvian Amazonia. *Amazoniana* **13**, 209–219.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA* **105**, 6668–6672.

Doi, A., Suzuki, H. & Matsuura, E.T. (1999) Genetic analysis of temperature-dependent transmission of mitochondrial DNA in *Drosophila*. *Heredity* **82**, 555–560.

Doi, H., Takahashi, M. & Katano, I. (2010) Genetic diversity increases regional variation in phenological dates in response to climate change. *Global Change Biology* **16**, 373–379.

Donahaye, E., Navarro, S. & Calderon, M. (1966) Observations on the life cycle of *Caryedon gonagra* (F.) on its natural host in Israel, *Acacia spirocarpa* and *A. tortilis*. *Tropical Science* **8**, 85–89.

Dowling, D.K., Abiega, K.C. & Arnqvist, G. (2007) Temperature-specific outcomes of cytoplasmic-nuclear interactions on egg-to-adult development time in seed beetles. *Evolution* **61**, 194–201.

Edvardsson, M. (2007) Female *Callosobruchus maculatus* mate when they are thirsty: resource-rich ejaculates as mating effort in a beetle. *Animal Behaviour* **74**, 183–188.

Edvardsson, M. & Tregenza, T. (2005) Why do male *Callosobruchus maculatus* harm their mates? *Behavioral Ecology* **16**, 788–793.

El-Sawaf, S.K. (1956) Some factors affecting the longevity, oviposition and rate of development in the southern cowpea weevil, *Callosobruchus maculatus* F. (Coleoptera: Bruchidae). *Bulletin de la. Societe Entomologique d'Egypte* **40**, 29–95.

Fields, P.G. (1992) The control of stored-product insects and mites with extreme temperatures. *Journal of Stored Products Research* **28**, 89–118.

Fox, C.W., Stillwell, R.C., Wallin, W.G. & Hitchcock, L.J. (2006) Temperature and host species affect nuptial gift size in a seed-feeding beetle. *Functional Ecology* **20**, 1003–1011.

Fujii, K. (1967) Studies on interspecies competition between the azuki bean weevil, *Callosobruchus chinensis*, and the southern cowpea weevil, *C. maculatus*. II. Competition under different environmental conditions. *Researches on Population Ecology* **9**, 192–200.

Fujii, K., Gatehouse, A.M.R., Mitchell, R., Johnson, C.D. & Yoshida, Y. (1990) *Bruchids and Legumes: Economics, Ecology and Coevolution*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Gibbs, A.G. (1998) The role of lipid physical properties in lipid barriers. *American Zoologist* **38**, 268–279.

Gilchrist, G.W., Huey, R.B. & Partridge, L. (1997) Thermal sensitivity of *Drosophila melanogaster*: Evolutionary responses of adults and eggs to laboratory natural selection at different temperatures. *Physiological Zoology* **70**, 403–414.

Gilg, O., Sittler, B. & Hanski, I. (2009) Climate change and cyclic predator-prey population dynamics in the high Arctic. *Global Change Biology* **15**, 2634–2652.

Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology* **52**, 107–126.

Hochachka, P.W. & Somero, G.N. (1984) *Biochemical Adaptation*. Princeton, NJ, USA, Princeton University Press.

Hoffmann, A.A., Sorensen, J.G. & Loeschcke, V. (2003) Adaptation of *Drosophila* to temperature extremes: bringing together quantitative and molecular approaches. *Journal of Thermal Biology* **28**, 175–216.

Howe, R.W. & Currie, J.E. (1964) Some laboratory observations on the rates of development, mortality and oviposition of several species of Bruchidae breeding in stored pulses. *Bulletin of Entomology Research* **55**, 437–477.

Hudaib, T., Hayes, W., Brown, S. & Eady, P.E. (2010) Effect of seed moisture content and d-limonene on oviposition decisions of the seed beetle *Callosobruchus maculatus*. *Entomologia Experimentalis et Applicata* **137**, 120–125.

Huey, R.B., Berrigan, D., Gilchrist, G.W. & Herron, J.C. (1999) Testing the adaptive significance of acclimation: a strong inference approach. *American Zoologist* **39**, 323–336.

Ishihara, M. (1998) Geographical variation in insect developmental period: effect of host plant phenology on the life cycle of the bruchid seed feeder *Kytorhinus sharpianus*. *Entomologia Experimentalis et Applicata* **87**, 311–319.

Ishii, S. (1952) Studies on the host preference of the cowpea weevil (*Callosobruchus chinensis*. L.). *Bulletin of National Institute of Agricultural Science, Series C* **1**, 185–256 (in Japanese with English summary).

Ishikura, S. (1939) Influence of temperature and humidity at the developmental period upon the oviposition of *Bruchus chinensis* L. *Oyo Dobutsu Zasshi* **11**, 41–52 (in Japanese).

Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics* **2**, 465–492.

Jermy, T. & Szentesi, A. (2003) Evolutionary aspects of host plant specialisation – a study on bruchids (Coleoptera: Bruchidae). *Oikos* **101**, 196–204.

Johnson, C.D. (1981) Seed beetle host specificity and the systematics of the Leguminosae. pp. 995–1027 *in* Polhill, R.M. & Raven, P.H. (*Eds*) *Advances in Legume Systematics, Part 2*. Kew, UK, Royal Botanical Gardens.

Kiritani, K. (2006) Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Population Ecology* **48**, 5–12.

Kiyoku, M. (1960) Experimental studies on the influence of an abnormally high temperature upon some biological characters in insects survived the heat-treatment and those in their offsprings. *Scientific Reports of the Faculty of Agriculture Okayama University* **16**, 25–32.

Kiyoku, M. (1962) Studies on the lethal action of abnormally high temperature on insects, XVIII. general consideration and conclusions on the results of the serial studies published hitherto. *Scientific Reports of the Faculty of Agriculture Okayama University* **19**, 17–28.

Klapwijk, M.J., Groebler, B.C., Ward, K., Wheeler, D. & Lewis, O.T. (2010) Influence of experimental warming and shading on host-parasitoid synchrony. *Global Change Biology* **16**, 102–112.

Klok, C.J. & Chown, S.L. (2001) Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic kelp fly, *Paractora druexi* (Diptera: Helcomyzidae). *Journal of Insect Physiology* **47**, 95–109.

Krebs, R.A. & Loeschcke, V. (1995) Resistance to thermal stress in preadult *Drosophila buzzattii*: Variation among populations and changes in relative resistance across life stages. *Biological Journal of the Linnean Society* **56**, 517–531.

Kurota, H. (2004) Overwintering strategies depending on high cold hardiness in nondiapause stages in *Bruchidius dorsalis* (Coleoptera: Bruchidae). *Environmental Entomology* **33**, 1163–1168.

Labeyrie, V. (1981) The ecology of bruchids attacking legumes (pulses). The Hague, Dr W Junk Publishers.

Leather, S.R., Walters, K.F.A. & Bale, J.S. (1993) *The Ecology of Insect Overwintering*. Cambridge, UK, Cambridge University Press.

Leroi, A.M., Bennett, A.F. & Lenski, R.E. (1994) Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proceedings of the National Academy of Sciences USA* **91**, 1917–1921.

Linsley, E.G. (1944) Natural sources, habitats and reservoirs of insects associated with stored food products. *Hilgardia* **16**, 187–224.

Loeschcke, V. & Hoffmann, A.A. (2002) The detrimental acclimation hypothesis. *Trends in Ecology & Evolution* **17**, 407–408.

Mahroof, R., Subramanyam, B., Throne, J.E. & Menon, A. (2003) Time-mortality relationships for *Tribolium castaneum* (Coleoptera: Tenebrionidae) life stages exposed to elevated temperatures. *Journal of Economic Entomology* **96**, 1345–1351.

Mahroof, R., Zhu, K.Y., Neven, L., Subramanyam, B. & Bai, J. (2005) Expression patterns of three heat shock protein 70 genes among developmental stages of the red flour beetle *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Comparative Biochemistry and Physiology A* **141**, 247–256.

Marlatt, C.L. (1896) The clothes moths. *United States Department of Agriculture Division of Entomology Bulletin* **4**(n.s.), 63–69.

Mellanby, K. (1954) Acclimatization and the thermal death point in insects. *Nature* **173**, 582–583.

Mitchell, R. (1977) Bruchid beetles and seed packaging by Palo Verde. *Ecology* **58**, 644–651.

Moya-Larano, J., El-Sayyid, M.E.T. & Fox, C.W. (2007) Smaller beetles are better scramble competitors at cooler temperatures. *Biology Letters* **3**, 475–478.

Mullins, D.E. (1985) Chemistry and physiology of the haemolymph. pp. 355–400 *in* Kerkut, G.A. & Gilbert, L.I. (*Eds*) *Comprehensive Insects Physiology*. Oxford, UK, Pergamon Press.

Musolin, D.L., Tougou, D. & Fujisaki, K. (2010) Too hot to handle? Phenological and life-history responses to simulated climate change of the southern green stink bug *Nezara viridula* (Heteroptera: Pentatomidae). *Global Change Biology* **16**, 73–87.

Nagata, Y. & Matsuura, E.T. (1991) Temperature dependency of electron-transport activity in mitochondria with exogenous mitochondrial DNA in *Drosophila*. *Japanese Journal of Genetics* **66**, 255–261.

Nahdy, M.S., Silim, S.N. & Ellis, R.H. (1999) Effect of field infestations of immature pigeonpea (*Cajanus cajan* (L.) Millsp.) pods on production of active (flight) and sedentary (flightless) morphs of *Callosobruchus chinensis* (L.). *Journal of Stored Products Research* **35**, 339–354.

Oosthuizen, M.J. (1935) The effect of high temperature on the confused flour beetle. *Minnesota Technological Bulletin* **107**, 1–45.

Ouedraogo, P.A., Monge, J.P. & Huignard, J. (1991) Importance of temperature and seed water content on the induction of imaginal polymorphism in *Callosobruchus maculatus*. *Entomologia Experimentalis et Applicata* **59**, 59–66.

Patel, S., Nelson, D.R. & Gibbs, A.G. (2001) Chemical and physical analyses of wax ester properties. *Journal of Insect Science* **1**(4), 7pp.

Phillips, T.W. & Throne, J.E. (2010) Biorational approaches to managing stored-product insects. *Annual Review of Entomology* **55**, 375–397.

Prevett, P.F. (1966) Observations on biology in the genus *Caryedon* Schoenherr (Coleoptera: Bruchidae) in Northern Nigeria with a list of associated parasitic Hymenoptera. *Proceedings of the Royal Entomological Society of London, Series A* **41**, 9–16.

Rankin, D.J. & Arnqvist, G. (2008) Sexual dimorphism is associated with population fitness in the seed beetle *Callosobruchus maculatus*. *Evolution* **62**, 622–630.

Robinson, W.M. (1927) Water binding capacity of colloids a definite factor in winter hardiness of insects. *Journal of Economic Entomology* **20**, 80–88.

Robinson, W.M. (1928) Water conservation in insects. *Journal of Economic Entomology* **21**, 898–902.

Rönn, J.L., Katvala, M. & Arnqvist, G. (2008) Interspecific variation in ejaculate allocation and associated effects on female fitness in seed beetles. *Journal of Evolutionary Biology* **21**, 461–470.

Sakurai, G. & Kasuya, E. (2008) Different female mating rates in different populations do not reflect the benefits the females gain from polyandry in the adzuki bean beetle. *Journal of Ethology* **26**, 93–98.

Sano, I. (1967) Density effect and environmental temperature as the factors producing the active form of *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). *Journal of Stored Products Research* **2**, 187–195.

Sano-Fujii, I. (1984) Effect of bean water content on the production of the active form of *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). *Journal of Stored Products Research* **20**, 153–161.

Sano-Fujii, I. (1986) The genetic basis of the production of the active form of *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). *Journal of Stored Products Research* **22**, 115–123.

Shimada, M. & Ishihara, M. (1991) Two types of overwintering larvae in a wild multivoltine bruchid, *Kytorhinus sharpianus* Bridwell (Coleoptera, Bruchidae). *Applied Entomology and Zoology* **26**, 289–297.

Sibly, R.M., Smith, R.H. & Moller, H. (1991) Evolutionary demography of a bruchid beetle. 4. genetic trade-off, stabilizing selection and a model of optimal body size. *Functional Ecology* **5**, 594–601.

Siomos, M.F. (2009) Shaped by the environment – adaptation in plants. *FEBS Journal* **276**, 4705–4714.

Solomon, S., Plattner, G.K., Knutti, R. & Friedlingstein, P. (2009) Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences USA* **106**, 1704–1709.

Southgate, B.J. (1979) Biology of the Bruchidae. *Annual Review of Entomology* **24**, 449–473.

Southgate, B.J. (1981) Univoltine and multivoltine cycles: their significance. pp. 17–22 *in* Labeyrie, V. (*Ed.*) *The Ecology of Bruchids Attacking Legumes (Pulses)*. The Hague, The Netherlands, Dr W. Junk Publishers.

Srygley, R.B., Dudley, R., Oliveira, E.G., Aizprua, R., Pelaez, N. Z. & Riveros, A.J. (2010) El Nino and dry season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical wet to dry forests. *Global Change Biology* **16**, 936–945.

Stillwell, R.C. & Fox, C.W. (2005) Complex patterns of phenotypic plasticity: Interactive effects of temperature during rearing and oviposition. *Ecology* **86**, 924–934.

Stillwell, R.C. & Fox, C.W. (2007) Environmental effects on sexual size dimorphism of a seed-feeding beetle. *Oecologia* **153**, 273–280.

Stillwell, R.C., Morse, G.E. & Fox, C.W. (2007a) Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. *American Naturalist* **170**, 358–369.

Stillwell, R.C., Wallin, W.G. & Fox, C.W. (2007b) Phenotypic plasticity in a complex world: interactive effects of food and temperature on fitness components of a seed beetle. *Oecologia* **153**, 309–321.

Tabachnick, W.J. (2010) Challenges in predicting climate and environmental effects on vector-borne disease episystems in a changing world. *Journal of Experimental Biology* **213**, 946–954.

Tauber, M.J. & Tauber, C.A. (1986) *Seasonal Adaptation of Insects*. Oxford, UK, Oxford University Press.

Teran, A.L. (1962) Observaciones sobre Bruchidae del Noroeste Argentino. *Acta Zoologica Lilloana* **18**, 211–242.

***Tribolium* Genome Sequencing Consortium** (2008) The genome of the model beetle and pest. *Tribolium castaneum*. *Nature* **452**, 949–955.

Tuda, M. (1993) Density dependence depends on scale; at larval resource patch and at whole population. *Researches on Population Ecology* **35**, 261–271.

Tuda, M. (1998) Evolutionary character changes and population responses in an insect host-parasitoid experimental system. *Researches on Population Ecology* **40**, 293–299.

Tuda, M. (2003) A new species of *Callosobruchus* (Coleoptera: Bruchidae) feeding on seeds of *Dunbaria* (Fabaceae), a closely related species to a stored-bean pest, *C. chinensis*. *Applied Entomology and Zoology* **38**, 197–201.

Tuda, M. (2007) Applied evolutionary ecology of insects of the subfamily Bruchinae (Coleoptera: Chrysomelidae). *Applied Entomology and Zoology* **42**, 337–346.

Tuda, M. & Iwasa, Y. (1998) Evolution of contest competition and its effect on host-parasitoid dynamics. *Evolutionary Ecology* **12**, 855–870.

Tuda, M. & Morimoto, K. (2004) A new species *Megabruchidius sophorae* (Coleoptera, Bruchidae), feeding on seeds of *Styphnolobium* (Fabaceae) new to Bruchidae. *Zoological Science* **21**, 105–110.

Tuda, M. & Shima, K. (2002) Relative importance of weather and density dependence on the dispersal and on-plant activity of the predator *Orius minutus*. *Population Ecology* **44**, 251–257.

Tuda, M. & Shimada, M. (1993) Population-level analysis on reduction in equilibrium population size of the azuki bean beetle. *Researches on Population Ecology* **35**, 231–239.

Tuda, M. & Shimada, M. (1995) Developmental schedules and persistence of experimental host-parasitoid systems at two different temperatures. *Oecologia* **103**, 283–291.

Tuda, M. & Shimada, M. (2005) Complexity, evolution and persistence in host-parasitoid experimental systems, with *Callosobruchus* beetles as the host. *Advances in Ecological Research* **37**, 37–75.

Tuda, M., Chou, L.-Y., Niyomdham, C., Buranapanichpan, S. & Tateishi, Y. (2005) Ecological factors associated with pest status in *Callosobruchus* (Coleoptera: Bruchidae): high host specificity of non-pests to Cajaninae (Fabaceae). *Journal of Stored Products Research* **41**, 31–45.

Tuda, M., Matsumoto, T., Itioka, T., Ishida, N., Takanashi, M., Ashihara, W., Kohyama, M. & Takagi, M. (2006a) Climatic and inter-trophic effects detected in 10-year population dynamics of biological control of the arrowhead scale by two parasitoids in southwestern Japan. *Population Ecology* **48**, 59–70.

Tuda, M., Ronn, J., Buranapanichpan, S., Wasano, N. & Arnqvist, G. (2006b) Evolutionary diversification of the bean beetle genus *Callosobruchus* (Coleoptera: Bruchidae): traits associated with stored-product pest status. *Molecular Ecology* **15**, 3541–3551.

Utida, S. (1954) 'Phase' dimorphism observed in the laboratory population of the cowpea weevil, *Callosobruchus quadrimaculatus*. *Oyo Dobutsu Zasshi* **18**, 161–168. (in Japanese with English summary).

Utida, S. (1965) 'Phase' dimorphism observed in the laboratory population of the cowpea weevil, *Callosobruchus maculatus*. IV. The mechanism of induction of the flight form. *Japanese Journal of Ecology* **15**, 193–199. (in Japanese with English summary).

Utida, S. (1966) Water content of body in several kinds of the bean weevil. *Japanese Journal of Applied Entomology and Zoology* **10**, 39–43. (in Japanese with English summary).

Utida, S. (1969) Photoperiod as a factor inducing the flight form in the population of the southern cowpea weevil, *Callosobruchus maculatus*. *Japanese Journal of Applied Entomology and Zoology* **13**, 129–134. (in Japanese with English summary).

Vamosi, S.M. (2005) Interactive effects of larval host and competition on adult fitness: an experimental test with seed beetles (Coleoptera: Bruchidae). *Functional Ecology* **19**, 859–864.

Vamosi, S.M. & Lesack, T.L. (2007) Direct effects of larval competition on development time and fecundity in seed beetles. *Evolutionary Ecology Research* **9**, 1131–1143.

van Asch, M. & Visser, M.E. (2007) Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology* **52**, 37–55.

Watanabe, N. (1985) Oviposition habit of *Sulcobruchus sauteri* (Pic) and its significance in speculation on the pre-agricultural life of seed beetles attacking stored pulses (Coleoptera: Bruchidae). *Kontyu* **53**, 391–397.

Wilson, R.S. & Franklin, C.R. (2002) The detrimental acclimation hypothesis: response. *Trends in Ecology & Evolution* **17**, 408.

Xie, S.-P., Deser, C., Vecchi, G.A., Ma, J., Teng, H. & Wittenberg, A.T. (2010) Global warming pattern formation: Sea surface temperature and rainfall. *Journal of Climate* **23**, 966–986.

Yanagi, S. & Miyatake, T. (2002) Effects of maternal age on reproductive traits and fitness components of the offspring in the bruchid beetle, *Callosobruchus chinensis* (Coleoptera: Bruchidae). *Physiological Entomology* **27**, 261–266.

Yanagi, S. & Tuda, M. (2010) Interaction effect among maternal environment, maternal investment and progeny genotype on life history traits in *Callosobruchus chinensis*. *Functional Ecology* **24**, 383–391.

Yoshida, T. (1990) Historical review of bruchid studies in Japan. pp. 1–24 *in* Fujii, K., Gatehouse, A.M.R., Mitchell, R., Johnson, C.D. & Yoshida, Y. (*Eds*) *Bruchids and Legumes: Economics, Ecology and Coevolution*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Yukawa, J. & Akimoto, K. (2006) Influence of synchronization between adult emergence and host plant phenology on the population density of *Pseudasphondylia neolitseae* (Diptera: Cecidomyiidae) inducing leaf galls on *Neolitsea sericea* (Lauraceae). *Population Ecology* **48**, 13–21.