

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

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## 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

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## 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 aphyagy (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

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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 & Loeschke, 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; Amevoïn *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

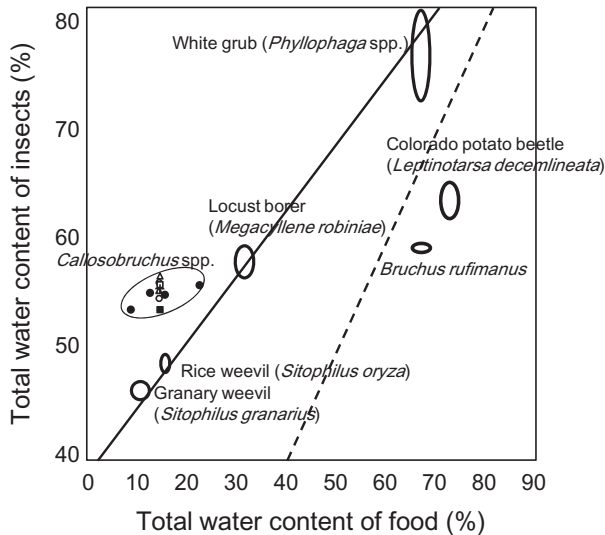


Fig. 1. Relationship between the water content of insects and their food (only Coleoptera are shown, modified from Robinson 1928, with additional data). The examples on the upper side of the broken line indicate that the water content of the insects is greater than that of the food. Granary weevil, rice 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*; △, *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 *Sator 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

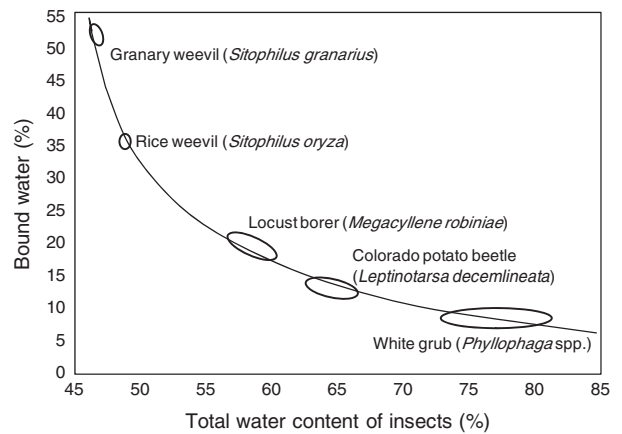


Fig. 2. Relationship between total water content and the percentage of water bound by colloids (only Coleoptera are shown, modified from Robinson, 1928). The species that live on dry food and have a small percentage of water in their own tissues retain a large percentage of water in the bound form. The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

& 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).

#### 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; Quedraogo *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<sub>2</sub> 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.

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