

Effects of Temperature on Six Species of Seed Beetles (Coleoptera: Bruchidae): an Ecological Perspective

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ABSTRACT

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The effects of temperature on respiration, fecundity, and developmental rates of six species of Bruchidae (Coleoptera) were examined. Species examined were *Stator generalis* Johnson and Kingsolver, *S. limbatus* (Horn), *S. pruininus* (Horn), *S. sordidus* (Horn), *Mimosestes amicus* (Horn), and *Algarobius prosopis* (LeConte). Adults and larvae both appeared to utilize two alternate, species-specific, evolutionary strategies to maximize fitness in a harsh environment and to minimize metabolic costs of survival and growth. Adult beetles may either maximize fecundity or minimize metabolic rates over all environmental temperatures. Larvae may either minimize metabolic rates over all environmental temperatures or minimize developmental time. Which strategy has been selected is correlated with the ecological feeding guild of which the species is a member. Members of the mature seed guild have higher fecundities and more rapid development, and they minimize the effects of temperature on their metabolic rates, whereas members of the scattered seed guild have lower fecundity and slower developmental rates, and their metabolic rates rise rapidly with environmental temperature. Ecological reasons for these differences are proposed and are based on competitive abilities of the adults and environmental stresses to which the larvae are subjected in the respective feeding guilds.

Southgate (1979) recently reviewed the biology of the Bruchidae (Coleoptera) and concluded that in the tropical regions of Asia, Africa, and Central and South America, where native biota is rapidly disappearing, that many of the large numbers of bruchids which are presently of little interest to humans may become pests on either present or newly developed food crops. Of greater interest here, the review also made plain that very little is known about the ecology, physiology, and hosts of the Bruchidae, even within those groups that are stored-product pests.

The impetus to examine the metabolic rate, developmental rates and thresholds, fecundity, and temperature preferences of six species of non-economic bruchids was stimulated by this paucity of information and by the publication of several papers on the ecology of species in the genus *Stator*.

Johnson and Janzen (unpublished data) proposed that *Stator generalis* Johnson and Kingsolver was limited in its distribution to an area of central Panama because of host seed distribution and availability. Their reasoning was that in areas outside of central Panama seeds are more widely scattered by horses, cattle and rodents, making them more inaccessible to the bruchids. Johnson (unpublished data) also concluded that this species, a specialist, is less well adapted to its native host, *Enterolobium cyclocarpum* (Jacquin) Grisebach, than other generalist species of the same genus are adapted to their native hosts. Johnson (1981c) proposed that *Stator pygidialis* (Schaeffer) has escaped from congeneric fellow competitors, *S. pruininus* (Horn) and *S. limbatus* (Horn), at high elevations in Arizona because these two latter species could not tolerate the temperature extremes there. Most of these assertions have little supporting physiological evidence, and some (Johnson and Janzen, unpublished data) are untestable in that they are "historical hypotheses."

A preliminary hypothesis that insect populations are limited by the environment is much more appropriate (Fujii 1967, Taylor 1980) in all these cases and is investigated here.

My purpose here is to present comparative physiological and life history data on six species of bruchids that will develop in the laboratory in continuous culture and to analyze the role of temperature in the ecological and evolutionary strategies of the bruchids. The relationships of insects and temperature in general has been well reviewed (Bursell 1964, Clarke 1967, Cloudsley-Thompson 1970) and so will not be directly dealt with, and instead stress will be placed on comparative physiological ecology of the Bruchidae.

Materials and Methods

Stator generalis, *S. limbatus*, *S. pruininus*, and *S. sordidus* (Horn), were obtained as described by Johnson (1981a,b). *Mimosestes amicus* (Horn) was reared from and maintained in the laboratory on seeds of *Cercidium floridum* Benth. *Algarobius prosopis* (LeConte) is a specialist on *Prosopis velutina* Wootton and also breeds continuously on this host in the laboratory.

Metabolic Rate

The oxygen consumption of adults of all six species and of the larvae of the four *Stator* species was measured with a 20-station Gilson differential respirometer. The methods of Wightman (1978a,b) were followed for the most part. Ten adults or between 6 and 40 larvae in their host seeds were placed in 15-ml respirometer flasks, along with five host seeds (with adults), and allowed to equilibrate for 1 h at the test temperature. A 2-cm² moist filter paper was placed in the center well of each flask. Fifteen minutes before the start of the measurements, 0.4

ml of 0.1 N NaOH was added to the side arm of the flasks to absorb the CO₂ produced. Respiration was then measured for 0.5 to 1.0 h, depending on experimental temperature, which was varied from 20°C to 50°C in 5-degree intervals. Four replicates were used for each species at each temperature, and four control flasks were used, consisting of five uninfested host seeds in each flask. After the experiment, the larvae were dissected out of the seeds and both adults and larvae were placed in a drying oven for 5 h at 75°C and were subsequently weighed. Oxygen consumption was calculated at STPD in microliters of O₂ per milligram (dry weight) per hour.

Temperature Preference

Experiments to determine preferred temperature, maximum voluntarily tolerable temperature (MVT) and upper critical temperature for most of the species by measuring activity levels of 10 bruchids were attempted by placing the 10 bruchids in a glass vial which was then placed into a water bath. The temperature of the water bath was varied from 25 to 50°C, and the activity of the bruchids was visually monitored.

Fecundity-Development

The adult fecundity and the mortality levels of the egg and larval stages were determined by placing one pair (♀ and ♂) of virgin bruchids (two repli-

cates) into a plastic petri dish with host seeds. *Enterolobium cyclocarpum* was used as a host seed for *S. generalis*, and *Acacia greggii* Gray was used as a host seed for the remaining *Stator* species in all experiments. The petri dishes were placed into environmental chambers at 25, 30 and 35°C and ca. 70% relative humidity (RH). The bruchids were provided a sugar water solution during the first 5 days of the experiment. The number of eggs laid and hatched, and the number of larvae entering the seed as 1st instars was counted. The number of adults emerging from the seeds was counted daily to determine levels of mortality at the different stages. The rates of development were determined by placing 50 or more bruchids on 50 host seeds at the various temperatures for 2 days. The emergence of adults was then monitored daily to achieve an estimate of overall rates of development.

Results

Respiration

The metabolic rate of adults of each species of bruchid increased with increasing temperature over most of the temperature range examined (Fig. 1). Such relationships are typical for many ectotherms (Kiestler and Buck 1964). All four *Stator* species showed similar increases in oxygen consumption with temperature, although the amount of oxygen

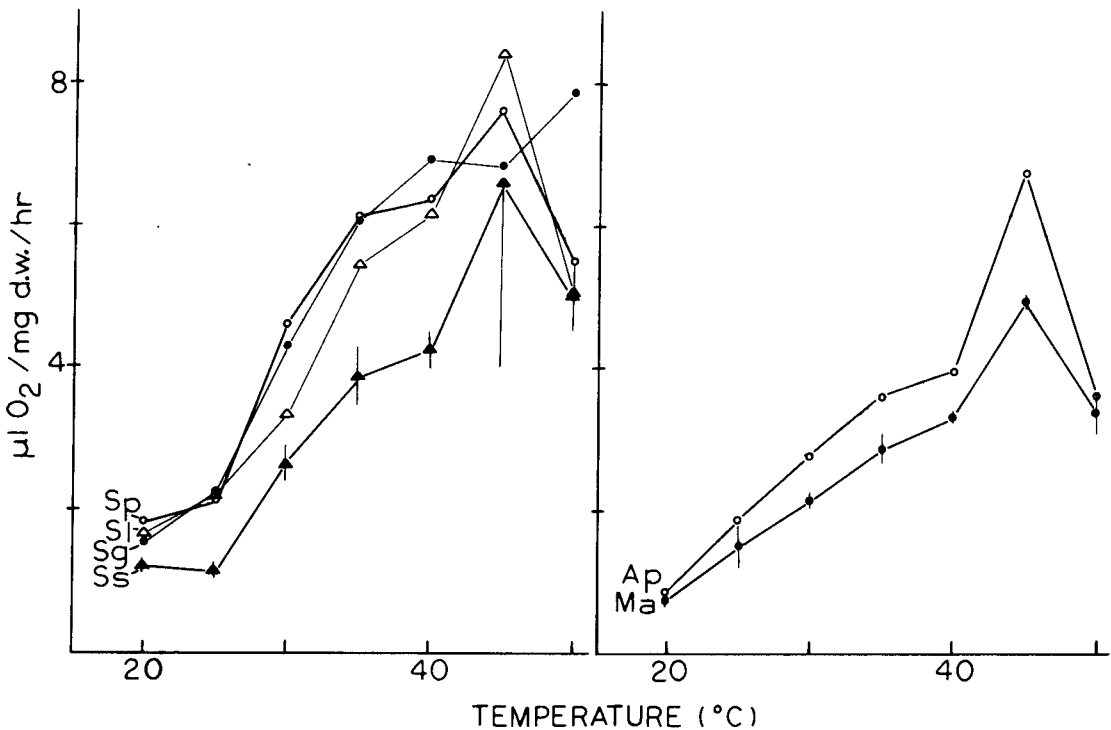


FIG. 1.—Metabolic rate-temperature relationships for six species of bruchids. The initials labeling the lines in all the figures refer to the genus-species initials: Sp, *S. pruininus*; Sl, *S. limbatus*; Ss, *S. sordidus*; Sg, *S. generalis*; Ap, *A. prosopis*; Ma, *M. amicus*. The bars on the lower lines show representative SDs.

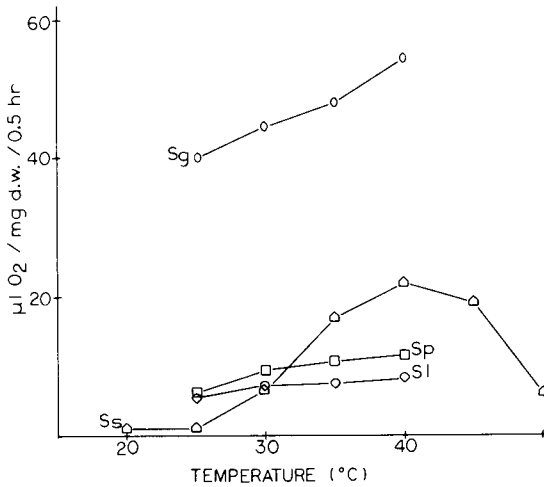


FIG. 2.—Metabolic rate-temperature relationships for the larvae of four *Stator* species. The slopes of regression lines for the data are: Sg, 0.93; Ss, 1.28; Sp, 0.36; Sl, 0.172.

consumed by *S. sordidus* per mg of body weight is significantly lower than all the other *Stator* species ($t = 3.61$, $P \geq 0.01$). *M. amicus* and *A. prosopis* also have significantly lower metabolic rates.

The larvae of the four *Stator* species also showed an increase in metabolic rate with temperature (Fig. 2). Interspecies comparisons are more difficult with larvae than with adults, because metabolism changes with development and larvae eat different species of host seeds. However, there appears to be a large difference between the larvae of *S. generalis* and the other three *Stator* species. These values for larval respiration are similar to those obtained by Wightman (1978a,b) for a species of economic bruchid, *Callosobruchus analis* (Fabr.). *Stator generalis* and *S. sordidus* larvae respond similarly to temperature increases, whereas *S. limbatus* and *S. pruininus* show only slight increases in oxygen consumption with temperature.

In the adult beetles there is a significant positive relationship of average beetle weight with metabolic rate (Fig. 3). Comparison with the regression line clearly indicates that *S. sordidus*, *M. amicus*, and *A. prosopis* have lower relative metabolic rates than the rest of the species.

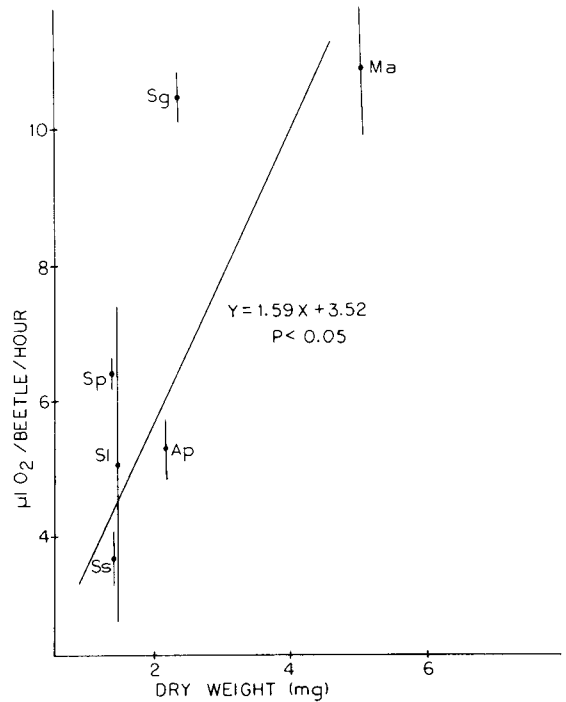


FIG. 3.—Relationship of metabolic rate at 30°C with dry weight of the bruchids examined. The regression line represents the trend for these six species and two stored product bruchids, *Zabrotes subfasciatus* (Boheman) and *Callosobruchus chinensis* L. (Kistler, unpublished data).

Activity Levels

The maximum voluntarily tolerated temperature was defined in this study as the point at which the insect actively seeks to escape from the heat (May 1979). At this point, there is a noticeable increase in the frequency of activity of the beetles. The upper stress temperature was defined as that temperature above MVT where activity levels reached a peak, after which they begin to decline. The upper critical temperature was defined as the temperature at which the beetles were no longer able to respond to changes in temperature and died after relatively short exposure to such temperatures. The values of MVT show the greatest interspecies difference, whereas the other measures are quite similar.

Table 1.—Temperature constants for four species of *Stator*

Species	Estimated developmental threshold (°C) ^a	Thermal constant (dd/50) ^b	Temp (°C)		
			Maximum voluntary	Upper stress	Upper critical
<i>S. generalis</i>	13.5	1,153	37	43	49
<i>S. limbatus</i>	13.6	946	42	45	49.5
<i>S. pruininus</i>	14.1	977	41	45	47
<i>S. sordidus</i>	11.3	1,167	40	44	49

^aCalculated by extending the lines in Fig. 5 to the abscissa.

^bCalculated from the developmental time at 30°C.

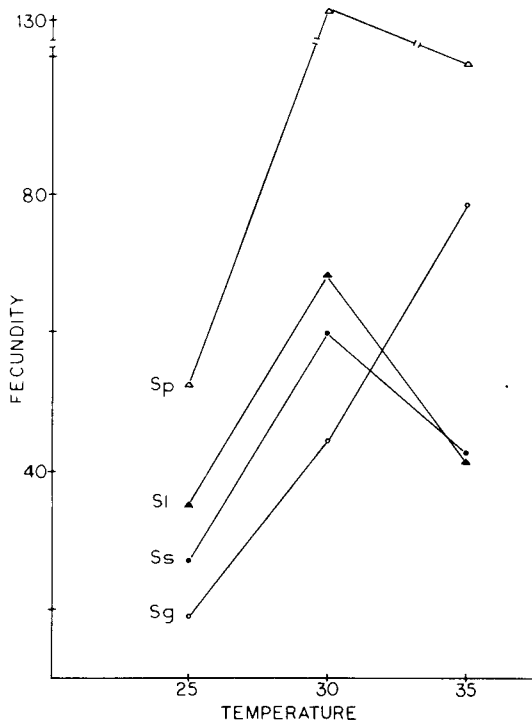


FIG. 4.—Fecundity-temperature relationships for four *Stator* species.

Fecundity and Development

A clear pattern is indicated by the consistency of the form of the fecundity curves (Fig. 4) in which all species but *S. generalis* show a maximum at ca. 30°C. These curves are similar in shape and magnitude to those described elsewhere (Howe and Currie 1964, Kistler 1979). The fecundity of *S. generalis* increases linearly over the temperatures in these experiments.

The developmental curves (Fig. 5) are typical for insects (Campbell et al. 1974). Developmental constants calculated from Fig. 5 are given in Table 1. The thermal constant is the amount of heat required over time for an insect to complete its development, whereas the developmental threshold is the temperature below which no significant development occurs. These two constants are considered by Messenger (1970) to be useful indicators of an insect's distribution and abundance. *S. sordidus* and *S. generalis* have the lowest overall developmental rates and require the greatest number of day degrees to complete their development. Mortality levels of the eggs and larvae were highly variable and appeared to be independent of temperature for all species.

Discussion

The majority of this study deals with four species of *Stator*. *S. generalis* is found only locally in central Panama on the seeds of only one host plant,

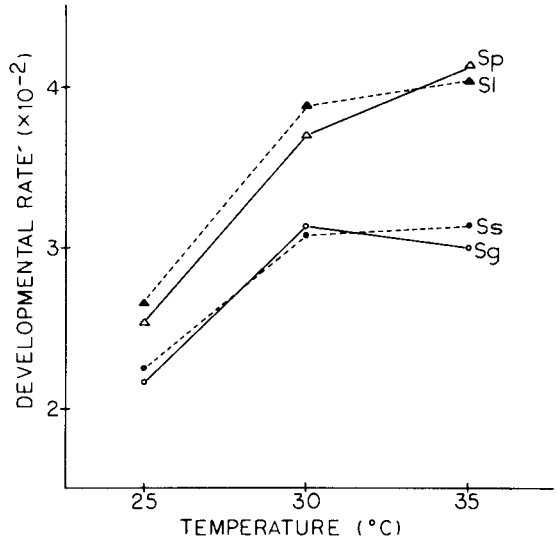


FIG. 5.—Developmental rates of four *Stator* species at three different temperatures.

Enterolobium cyclocarpum, and yet this plant is distributed throughout the tropics (C. D. Johnson, unpublished data). The closest morphological relative of *S. generalis* is *S. limbatus* (Johnson and Kingsolver 1976). The other *Stator* species are distributed throughout Arizona and the desert Southwest. *S. limbatus* and *S. pruininus* are extreme generalists, attacking 30 to 40 natural hosts, whereas *S. sordidus* is a specialist, feeding in the seeds of only three host species in nature, but remarkably, is able to develop in 20 species of nonhost seeds in the laboratory (Johnson 1981b, Center and Johnson 1976). Johnson and Kingsolver (1976) report that these three *Stator* species are not closely related. Of the remaining beetles used in this study, two are also found in the Arizona deserts, *Algarobius prosopis*, which is host specific on mesquite, *Prosopis velutina*, and *Mimosestes amicus* which may develop in the seeds of several hosts, many of which are the same hosts used by *S. limbatus* and *S. pruininus* (Johnson 1981b).

I examined several basic physiological parameters of these six species of beetles. Three of the species have maximal reproductive effort at ca. 30°C. The only exception is *S. generalis*, whose fecundity increases continually throughout the range of temperatures examined (Fig. 4). Of the three *Stator* species that are potential or actual competitors, in that they may develop in the same host seeds in the laboratory or in nature, *S. pruininus* clearly has the highest fecundity. Fecundity may be considered to be one aspect of adult fitness and competitive ability. Another aspect of adult fitness in this study is the metabolic cost of maintenance in a variable environment. The lower these metabolic costs, measured as oxygen consumption here, the more energy that should be available for other aspects of survival.

There are two groups of bruchids present (Fig. 1). One group (*A. prosopis*, *M. amicus*, and *S. sordidus*) has significantly lower metabolic costs at all environmental temperatures than all the other species. *M. amicus* and *A. prosopis* also have a slower rate of increase of metabolic rate with temperature, but this might be a function of their larger body size, could be a further adaptation to the harsh desert environment in which they must search for host seeds and food, or could be food related. All the relationships of respiration with temperature are typical to those found in other insects (Kiester and Buck 1964), in that they consist of a rapid increase in oxygen consumption to a "break" point as lethal temperatures are approached. Of course in nature these metabolic responses to temperature may be quite different, due to thermal acclimation, which in most ectotherms occurs rapidly enough to cope with changing thermal conditions on a daily and seasonal basis (Block and Young 1978, Bullock 1955, Feder 1978). These metabolic costs may also be minimized by behavioral thermoregulation at a fixed temperature, although such attempts for a very small organism may be maladaptive (May 1979). Still, thermoregulation has been found in many insect species, especially those found in desert environments (Hamilton 1971, 1975, Heath and Wilkin 1970, Henwood 1975, May 1979). Such mechanisms must undoubtedly play an important role in these desert-adapted bruchids, where environmental temperatures often reach the upper critical temperatures (Table 1).

In summary, these measures of adult fitness indicate two strategies to maximize adult fitness. The strategy of *S. pruininus* is to increase fecundity greatly compared with its potential competitors and perhaps rely more on behavioral and temporal regulation of body temperature, in effect restricting its activities to cooler periods. *S. sordidus*, *A. prosopis*, and *M. amicus* compromise fecundity and instead minimize metabolic costs due to increasing temperatures, which allows them to be active more consistently, perhaps allowing them to outcompete other species for access to host seeds or allowing for increased searching times relative to the other bruchids.

Larval Fitness

Natural selection should favor maximal developmental rates in insects that develop within the seeds of plants, since seeds are highly nutritious, and thus make excellent food for other organisms as well as for bruchids. The developmental rates of insects in general increase with increasing environmental temperature (Davidson 1944, Wellings 1981). Not all species are affected to the same extent (Spence et al. 1980), although in general there is a linear increase in rates of growth with temperature from a point where the rate is zero, the threshold temperature. At temperatures above the linear range, which is the optimal growth range, development decreases with

increasing temperature. *S. sordidus* and *S. generalis* have the slowest rates of development (Fig. 5), and thus might have difficulty competing with *S. limbatus* and *S. pruininus*, which not only develop faster but have higher fecundities. Two factors mediate the intense selection for maximal developmental rate. *S. limbatus* and *S. pruininus* are both members of the mature seed guild (Johnson 1981a), which oviposit only on mature seeds in pods on the host plant. These seeds probably are much more susceptible to predation by other seed eaters (i.e., are apparent seeds to all seed eaters) and thus developmental rate should be under strong maximizing selection. Both *S. sordidus* and *S. generalis* are members of the scattered seed guild, which oviposit only on mature seeds on the ground. These seeds should not be as subjected to predation pressure or environmental extremes (Janzen 1969). The bruchids that attack these seeds would not be subjected to extreme selection to maximize developmental rate.

The relationships of larval metabolic rates and temperature also support this hypothesis, in that both *S. generalis* and *S. sordidus* show a much greater change in oxygen consumption with increasing temperature than all the other species (Fig. 2). This is likely since seeds on the ground would not be subjected to the same environmental extremes as seeds on the tree, because shade and cover are greatly increased on the ground and soil acts as more of a thermal buffer than air. These two species would thus be under less selective pressure to regulate their metabolic rate-temperature response, because they would not be exposed to the extreme temperatures to which the mature seed guild bruchids would be exposed.

In summary, two strategies for larval development and adaptation to extreme environments were indicated. *S. sordidus* and *S. generalis*, which develop in seeds in a protected environment, lack an ability to regulate metabolic rate as temperature increases and have relatively slow rates of larval development. The strategy of *S. limbatus* and *S. pruininus*, which develop in apparent seeds, in a hostile environment, is to complete development as rapidly as possible and to try to regulate metabolic rates at a constant level over all environmental temperatures. Other members of these seed guilds may show similar strategies of adaptation (Johnson 1981a).

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