Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates
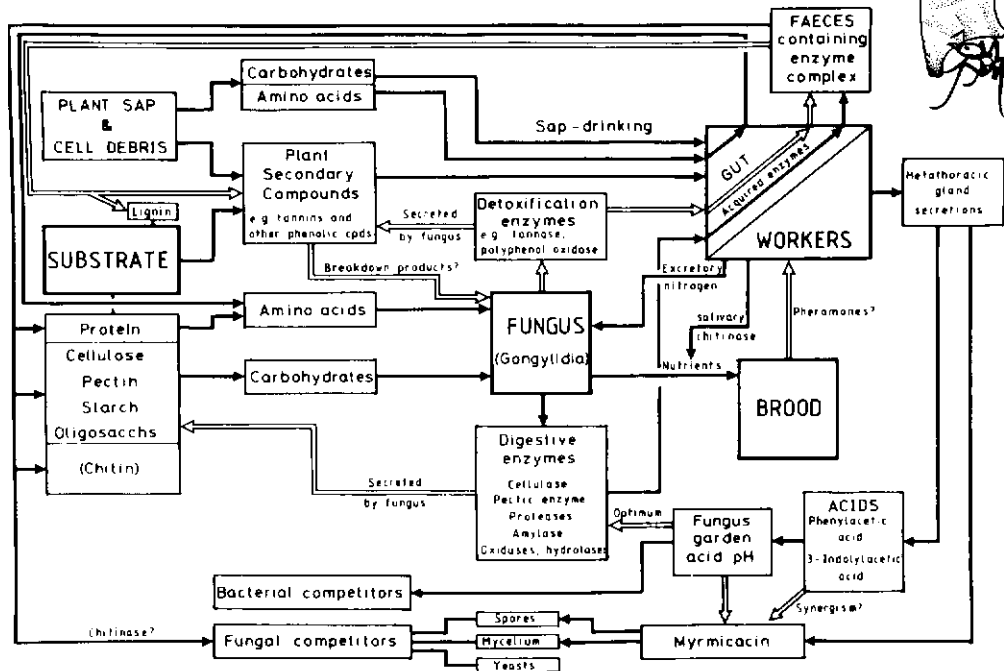

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Nutritional Ecology of Bruchid Beetles

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8.1   INTRODUCTION

There are about 1300 described species of seed beetles (Bruchidae) in the world and about as many again to be described. Bruchid larvae are only known to feed in seeds; 33 families of plants have been reported as hosts (Kingsolver, 1979; Johnson, 1981a). However, most species are host-specific, feeding in one plant family; according to Johnson (1970) approximately 84% of the known hosts of bruchids are in the Leguminosae. The remainder are in the Palmae (4.5%), Convolvulaceae (4.5%), and Malvaceae (2%). The other 5% of the host records are from 29 other families. Of the 5%, the Combretaceae, Rhamnaceae, Sterculiaceae, and Tiliaceae are fed upon most by bruchids.

Bruchids are distributed throughout the world, but more have been found from some regions than others. Pic (1913) recorded about as many Old World species (403) as New World species (423). There are not great differences in numbers between temperate (356) and tropical (448) bruchid faunas recorded by Pic; however, more study in the tropics will probably increase this difference. There is a great difference between South American species (193) and African species (80) (Johnson, 1981a).

In this chapter we summarize and discuss available data on the nutrition of bruchids. These data are correlated with the relatively large amount of published data on the ecology, evolution, and systematics of bruchids.

8.2   BRUCHID UTILIZATION OF SEEDS

8.2.1   Life Cycle

Seed beetles attack seeds in a variety of ways. Usually the adult female oviposits on a seed or pod and the larva chews through the egg chorion, pod wall, and/or seed coat into a seed. The first-instar larva is highly modified to enter seeds and has many spines and hairs for this purpose; it molts into a legless grub shortly after entering the seed. It then feeds inside one seed or, in some bruchids, inside two to several seeds, and it molts usually three more times as it continues to feed and increase in size. It usually then pupates inside a single seed, although some species leave the seed and pupate outside in a cocoon while others may glue several seeds together as a pupal chamber. After pupation, the adult completes a round exit hole that was prepared by the larva and emerges from the seed. Adult bruchids feed on pollen and probably nectar and are not known to feed on or in seeds, except incidentally, when emerging or when a female chews a hole in a pod for oviposition. Some species of bruchids survive for many generations in containers of seeds in the laboratory or in storage without the adults feeding (Johnson, 1981a).

A host plant of Bruchidae has long been considered by bruchid specialists

to be the plant whose seeds provide nourishment for the development of the larvae. The most recent compilation of the hosts of bruchids of the world was by Johnson (1981a). Additional host records have been published by Johnson (1983a–c, 1984a,b) and Kingsolver (1982, 1983).

8.2.2 Economic Importance

Some 20 species in several bruchid genera feed on economically important plants and have thus become cosmopolitan through commerce. Species in the Old World genera *Bruchus*, *Bruchidius*, *Callosobruchus*, and *Caryedon* and in the New World genera *Acanthoscelides* and *Zabrotes* are economic pests, breeding successfully in stored seeds. The ability of the bruchids of stored products to pass through many generations on the same seeds until the food reserves are exhausted has been well documented, as has the amount of damage caused to harvested crops. Preharvest infestation is very serious, because bruchids gain entry to products prior to storage (Southgate, 1979). For additional information on stored-product arthropods, see Baker and Loschiavo (Chapter 10) and Rodriguez and Rodriguez (Chapter 11).

8.2.3 Seeds As a Resource

According to Hopkins (1983), the typical pattern is that one bruchid species attacks only a few host species and that most host species are attacked by only one bruchid species, or in some cases very few. However, the bruchids attacking *Parkia* in Amazonian Brazil do not conform to this pattern. Hopkins found that the bruchid diversity of *Parkia* was higher than on any other legume genus studied.

Janzen (1978) discussed several reasons why seeds are a desirable food source for animals and how plants have evolved devices to protect their seeds.

1. Seeds are nutrient-rich. This seems indisputable, because the more reserves the seedling has available, the greater are its chances of survival. The seed is generally dormant and contains little water. It is not gathering resources and can therefore minimize inert internal construction materials.

2. Seed availability is not constant. As food begins to become more erratic in abundance, animals may evolve various mechanisms for waiting between food items and maximizing their return when the food is present. It appears that the bruchids that feed on trees in tropical deciduous forests deal with the extreme within- and between-year variation in seed abundance for a given species by waiting and being mobile rather than by being able to move between different host species (Janzen, 1975).

3. Great interspecific variation in secondary seed chemistry. The more dissimilar the secondary compounds in seeds of different species, the more host-specific the animals that feed on seeds are likely to be. Circumstantial evidence suggests that seeds of given species are chemically unique. First, it

is probable that most seeds have several classes of defensive compounds (e.g., protease inhibitors and/or lectins, alkaloids or uncommon amino acids, other glycosides, a polyphenol, etc.). Second, there are strong selective pressures for divergence in seed chemistry among sympatric species, because any two species with the same defense would present a larger food source to seed predators. Thus any change that causes sympatric species to diverge in seed chemistry would probably be favored (Janzen, 1973; Cates and Rhoades, 1977). Third, surveys of seeds for single classes of secondary compounds among a taxonomic group show great diversity in their nature and concentration.

4. Seed secondary compounds are detrimental to seed predators. If seed secondary compounds were not significant to seed predators, seed specificity would be much reduced. Janzen (1978) suggested that the toxicity of secondary compounds to seed predators selects for host specificity for two reasons. First, the more toxic the food, the more physiologically and biochemically specialized the animal may have to be to use it. Second, the more a population feeds on a seed species over evolutionary time, the more likely it is to evolve to where it is dependent on the secondary compounds in the seed.

8.3   ADULT NUTRITIONAL ECOLOGY

Adult bruchids have adapted to seed "feeding" via host selection mechanisms and physiological responses. The selection of a host involves the ability to find, recognize, and accept a plant, and at a finer level to choose a specific fruit, pod, or seed for oviposition. Physiological responses are mainly concerned with the allocation of limited adult energy resources to adult maintenance, longevity, and reproduction.

8.3.1   Host Specificity

In many years of collecting seeds and rearing bruchids from them, it was evident to the senior author that in the majority of cases only one or a few species of host plants were utilized by one bruchid species. It was also noted that most host plant species had only one or a few bruchids in their seeds.

Janzen (1974) reported that in Costa Rica over 80% of the bruchid species he studied had only one known host plant. He later published similar results, also from Costa Rica (Janzen, 1980). Over the total range of the beetles, Johnson and Slobodchikoff (1979) obtained similar results: 82.5% of the bruchid species had three or fewer recorded *Cassia* hosts and 16.5% had 5–10 recorded hosts. Most species of *Cassia* (90.5%) support three or fewer bruchid species, while the remaining species support from five to seven species of bruchids. Thus, most *Cassia* bruchids are very host-specific, and most host plants support only a few species of bruchids in their seeds.

Johnson (1981b) obtained similar results when he analyzed host preferences of several species of *Acanthoscelides*. Johnson and Slobodchikoff (1979) hypothesized that species of *Cassia* that harbor 5–7 bruchid species in their seeds have few or no toxins whereas the other species of *Cassia* with fewer bruchid species in their seeds are very toxic. Also, each seed produced as a result of cross pollination is potentially different from every other seed in the same fruit. Thus, every new seed, as a new individual, potentially has different protective mechanisms against seed predators than its parents.

In most bruchid–host relationships we do not know why bruchids feed or do not feed in a given legume taxon. Further research is required to determine whether the reason for a bruchid feeding in specific seeds is due to seed chemistry, seed or pod morphology, or other factors. Recent studies have shown that congeneric species of bruchids feed in seeds of plants that are in the same taxonomic group. Johnson and Kingsolver (1976) showed that species of *Stator* attack seeds of species of plants in the Mimosoideae (Leguminosae) much more often than those of other plants. Kingsolver and Johnson (1978) showed that species of *Mimosestes* also prefer seeds in the Mimosoideae. Johnson (1970, 1977a,b) showed that species of *Acanthoscelides* prefer seeds of species in the Papilionoideae (Leguminosae) and that some species of *Acanthoscelides* are restricted to individual genera and species. However, Johnson and Kingsolver (1971) and Forister and Johnson (1971) showed that some *Acanthoscelides* feed only in nonleguminous seeds (e.g., Rhamnaceae and Sterculiaceae). Interesting evolutionary problems are suggested by the studies on *Acanthoscelides prosopoides*, which feeds in the seeds of a rhamnaceous species (Johnson and Kingsolver, 1971); *Amblycerus vitis*, which feeds in Arizona wild grape seeds (Vitaceae) (Johnson and Kingsolver, 1975); and *Neltumius texanus*, which feeds in seeds of the rhamnaceous *Condalia* (Johnson, 1978).

Johnson and Janzen (1982) noted that the ranges of most bruchids are usually contiguous with their known hosts. However, this is not true in all cases. *Stator generalis* is restricted to an area in central Panama, but its only host, the guanacaste tree *Enterolobium cyclocarpum*, has a widespread distribution in the Neotropics. They suggested that the restricted distribution of *S. generalis* is due to ecological factors, primarily because guanacaste seeds are not available in amounts or in a pattern appropriate for *S. generalis* to survive. Kistler (1982) alternately proposed that physiological limitations might also restrict *S. generalis*.

8.3.2 Host Selection

Host selection in the Bruchidae may be divided into at least two processes: selection of host plants and selection of oviposition sites. Our knowledge of these processes comes from studies on oviposition preferences of stored-product species and inferences from combined field-laboratory experiments. Bruchid host plants must have appropriate chemicals and nutrients in the

seeds (Johnson and Slobodchikoff, 1979; Janzen, 1980), and seeds must be a certain size (Janzen, 1969). Bruchids may also limit host selection (or be limited by hosts) via physiological, behavioral, or ecological mechanisms (Johnson, 1981c, d; Kistler, 1982). Extreme specialists such as *S. generalis* (Johnson and Janzen, 1982) or *Caryedes brasiliensis* (Rosenthal, 1983) may have restricted themselves to the highly toxic seeds of one host plant by developing expensive physiological detoxification mechanisms. Thus, host choice may be evolutionarily limited (i.e., specialism and generalism are evolutionary strategies). Behavior, ecology, or host plant induction (Hopkins' host selection principle) may limit or determine host preference. In the laboratory, *Stator sordidus* is physiologically capable of feeding on 20 hosts, but in nature it feeds on only three. It has digestive and detoxifying mechanisms in the larval stage, but is either behaviorally or ecologically limited from its potential hosts in nature (Johnson, 1981d).

Host choice may also be limited by behavioral patterns of the pods of potential host plants. Johnson (1981c) recognized three feeding guilds for the Bruchidae: "mature-pod" bruchids oviposit only on the surfaces of seed pods; "mature-seed" bruchids oviposit only on mature seeds still in the pods on the plant; and "scattered-seed" bruchids oviposit mainly on seeds after they have fallen to the ground (Johnson, 1981c). The bruchids in these guilds have adapted their life history and physiological strategies (energy allocation) to attacking seeds at different times (Kistler, 1982). Many mechanisms seem to influence host selection, but preliminary data indicate a large role of behavior, ecology, and physiology as well as genetics in host plant selection.

Most work has been done in trying to delimit host preference and selection in laboratory experiments with stored-product and other generalist species of bruchids, and in the field with choice of host plants by bruchids. Pollen, ripe pods, and/or mature seeds may stimulate ovaries and testes to produce gametes and may also stimulate mating. Oogenesis and mating in *Zabrotes subfasciatus* are stimulated to a limited extent by both ripe and immature pods (*Z. subfasciatus* oviposits only on mature seeds). Ripe seeds further stimulate ovarian production and initiate oviposition (Pierre, 1980; Pimbert and Pierre, 1983). The number of eggs laid on different hosts is variable, and some females will not oviposit on some host seeds (Seddigi, 1972; Janzen, 1977; Johnson, 1981d). Females can locate host seeds long distances from the parent plant and often prefer to search over long distances for unattacked pristine seeds instead of ovipositing on seeds or fruits that already contain eggs laid by other females (Wilson and Janzen, 1972; Wright, 1983). Wasserman and Futuyma (1981) showed through a series of selection experiments that host choice mechanisms and ovipositional behavior were susceptible to artificial selection. Seed coat texture (Nwanze et al., 1975; Nwanze and Horber, 1976), seed curvature (Avidov et al., 1965), pubescence (Green and Palmblad, 1975), seed or fruit size (Janzen, 1969; Hare and Futuyma, 1978; Hare, 1980), and induction have all been shown to affect host choice for oviposition. Bruchids may also affect oviposition by

other bruchids through the use of oviposition markers (Oshima et al., 1973). Generalist species of bruchids may also prefer different hosts at different times throughout the year, thus acting as sequential specialists. Host choice in this case may be largely determined by host seed abundance, induction, or search image changes (Kistler and Hetz, unpublished data). Thus, bruchids are probably using a suite of physical, chemical, and behavioral cues to select specific oviposition sites on specific host seeds.

8.3.3 Physiological Responses

Extensive work has shown that when energy and nutrients are limited in adult bruchids, there is a strict trade-off between longevity and reproductive output that is mediated to some extent by energy content and intake. Energy content is influenced by the seeds fed upon. Female *C. maculatus* are less fecund when reared from Azuki beans (*Vigna angularis*) than from pigeon peas (*Cajanus cajan*) (Wasserman, 1981; Wasserman and Futuyma, 1981). That this difference in fecundity might be based on total energy content of the adult is supported by work in our laboratory. The metabolic rate of adult *Mimosestes amicus* is different when they are reared on seeds of *Prosopis velutina* and *Cercidium floridum* (Fig. 8.1) (Kistler, 1982, 1985). Secondly,
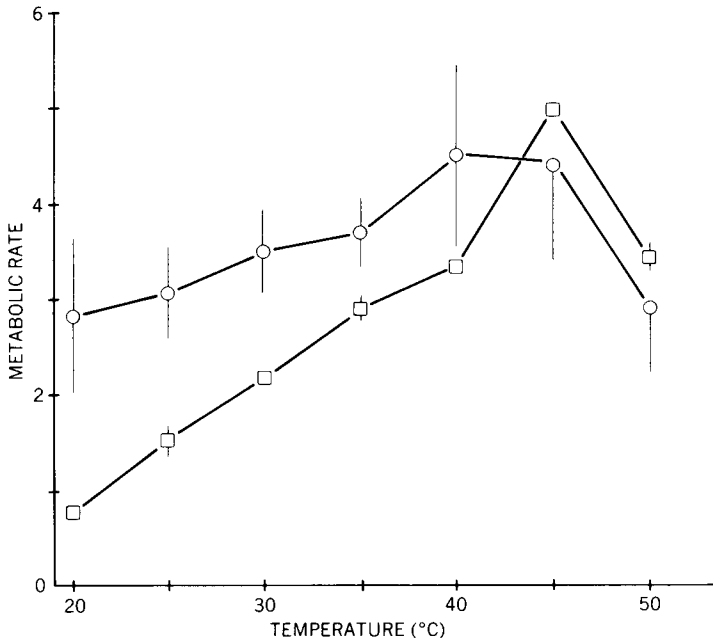

Fig. 8.1.   Metabolic rate (μl O_2/mg dw/h) of adult *Mimosestes amicus* as a function of temperature on two different resource seeds: *Cercidium floridum* (squares) and *Prosopis velutina* (circles). (After Kistler, 1982, 1985). Reprinted by permission of the Entomological Society of America.

energy allocation is highly dependent on adult energy intake. According to Janzen (1980), adult bruchids feed on pollen and nectar. This feeding influences ovarian and testicular production, oogenesis, and longevity (Pajni and Sood, 1975; Leroi, 1978; Pesho and Van Houten, 1982). Pollen is necessary for survival of the pea weevil (*Bruchus pisorum*) for the 8–10 months of the year that hosts of this univoltine species are absent. Only pollen of the host plant stimulates ovarian growth; other pollens merely sustain life for long periods. Ingested pollen promotes growth of oocytes and increases the probability and frequency of copulation (Pesho and Van Houten, 1982), and its absence may totally inhibit male copulation and female ovarian production (Pajni and Sood, 1975). Laboratory studies with *Acanthoscelides obtectus* show that food type influences longevity, ovarian production, and fecundity. Solutions of sucrose, glucose, and fructose or a pollen–honey–water mixture result in maximal longevity and fecundity (Leroi, 1978, 1981).

Another source of nutrition for females is the male secretions injected during copulation. These contain high-molecular-weight proteins or mucopolysaccharides. One mating may provide enough sperm to fertilize eggs of nonfed females, but multiple copulations are common in bruchids (Pesho and Van Houten, 1982; Kistler, personal observation). Two fractions of the male secretions are responsible for stimulating ovaries to produce eggs, and some (especially amino acids) may be broken down and incorporated into the yolk. However, the importance of this trophic role for the male secretions seems to be minor in *A. obtectus* (Huignard, 1983). The intake of nutrients by the larvae, the adults, or by copulation can free bruchids of the necessity of longevity–fecundity trade-offs. When a nutrient solution is provided to adults, fecundity and longevity are independent of each other (Leroi, 1978; Kistler, 1985).

When no food is available to adults (e.g., in most stored-product species), food stored from larval stages is important. Unfed *C. analis* expend 10% of their dry body weight in egg production (dry weight) (Wightman, 1978b). Three species fed on a sucrose solution expended up to 68% of their dry body weight in egg production (Kistler, 1985). There is an increase in longevity in individuals that are not allowed to oviposit (Bushnell and Boughton, 1940; Sandner and Pankanin, 1973; Leroi, 1980). The major energy drain appears to be reproduction, but the cost of maintenance may limit reproductive output. For example, a longer preovipositional period lowers the fecundity of female *A. obtectus* (Bushnell and Boughton, 1940; Leroi, 1980). If, however, the preovipositional period is short, individuals of *C. maculatus* still lay their normal number of eggs (Gokhale and Srivastava, 1975). This apparent behavioral plasticity in relation to energy limitation also has a genetic component. Huignard and Biemont (1978) studied four strains of *A. obtectus*. Strains A and B live at high altitudes, where host predictability is low and the host plant is available for only a brief period. These strains live 3–4 times longer and mate and oviposit only after host seeds have been present for an extended period of time, and the number of eggs produced and

laid is less than that of strains from lower altitudes. These latter strains, C and D, live where host availability and predictability are high, have a greatly decreased longevity, and reproduce very early in life. Females are receptive upon emergence, and egg production begins in the absence of host seed stimuli.

Most of the limited data available on chemical changes with age in the Bruchidae indicate a close correlation with ovarian production and egg laying. Protein content decreases with age in female *Zabrotes subfasciatus* and *C. maculatus* and more or less corresponds with the initiation of new vitellogenesis on day 3 of life (Sharma and Sharma, 1979a). Lipids and glycogen show similar decreases with age until nutrients fall below some "lethal" level. Again, the most rapid decreases are during the reproductive phase of life (Sharma and Sharma, 1979b, 1980). The high initial lipid content of these species (30–50% fresh weight vs. less than 10% for many other insects) may also represent a nutritional strategy for these nonfeeding species or may be a general feature of all Bruchidae resulting from very seasonal and unpredictable resources (Wightman, 1978b; Sharma and Sharma, 1979b). Acid and alkaline phosphatases, which play important roles in development, nutrition, and egg maturation of *C. analis*, increase to day 3 of life and then decrease until increasing just prior to death. Maximal egg production also occurs on day 3. These substances are thus most abundant during this intensive period of egg maturation and laying in females and sperm and secretion production in males. The increases just prior to death are likely to be due to tissue breakdown and catabolism after all or most of the stored energy compounds have been utilized in an effort to prolong survival (Dhand and Rastogi, 1975).

8.3.4 Predator Satiation

Janzen (1969) suggested that some plants have evolved a strategy termed "predator satiation": they produce a large number of small seeds, often with seed set tightly synchronized so that seeds are available only during a limited time. Also, the small seeds tend to be dispersed rapidly. These traits allow seed predators to consume many seeds, and yet some seeds escape before total infestation can occur. The trade-off for these plants is that seed mortality is very high and the small seeds (with little reserves of energy) have a reduced chance of survival even if they do escape predation.

The problem for the bruchids, then, is to counter this increase in seed number, reduction in seed size, and rapidity of dispersal with an evolutionary strategy of their own. Bruchids feeding in seeds of plants that evolve this strategy must either feed on more seeds, become smaller themselves, move to a different host with seeds having suitable food quality and quantity, or become extinct. For example, Center and Johnson (1974) observed that *Acanthoscelides aureolus* in *Astragalus* seeds is usually much larger than when in smaller seeds of *Lotus scoparius*. They also observed that very

small adults of *Sennius morosus* emerged from single seeds; normally the larva feeds on a seed cluster and an adult of normal size emerges. Johnson (1981c) also observed many species of *Stator* to feed on seeds on the ground after the seeds had been dispersed. Other examples of bruchids feeding on more seeds but inside the pod prior to dispersal are two species each of *Acanthoscelides* and *Sennius.*

Janzen (1969) listed 31 "traits of the Leguminosae that may be functional in eliminating or lowering bruchid destruction of seeds." Included are such traits as seed toxicity, seeds so thin that bruchids cannot mature in them, flaking of seed pod surface, which may remove eggs laid there, and dehiscence, fragmentation, or "explosion" of pods, scattering the seeds to escape from ovipositing females. According to Center and Johnson (1974), countermechanisms that bruchids have apparently evolved to these traits include feeding in seeds that are toxic by many species of *Acanthoscelides*, each larvae consuming several small seeds in *Acanthoscelides* and *Sennius*, ovipositing beneath the flaking seed pod surface by at least one species of *Acanthoscelides*, feeding on immature seeds before flaking can occur, and ovipositing by several species only on seeds after they have fallen to the ground from rapidly dehiscing pods.

8.4 LARVAL NUTRITIONAL ECOLOGY

Once adult bruchids have oviposited, further development depends on the adaptations of larvae to the host chosen by the parent. Such adaptations must include mechanisms to avoid predators or parasitoids until the larvae enter the seeds, mechanisms to enter the host seeds, and mechanisms to deal physiologically with the seed contents. The larvae must be able to eat, assimilate, and avoid or detoxify toxins. In this section we deal briefly with morphological and behavioral strategies of larvae and develop in greater detail the successful physiological adaptations of bruchid larvae to their host seeds.

Developing within a protected, nutrient-packed resource such as a seed should provide physiological and energetic advantages and should allow use of energy for purposes other than those found in exposed surface feeders (e.g., defense, mobility, etc.). The energetics of larval *Callosobruchus analis* indicate that this may be the case for the Bruchidae (Wightman, 1978a). These larvae have a production : respiration ratio (P : R) ranging from 54 to 142% in different instars. These relatively high P : R ratios indicate that *C. analis* expends a relatively small proportion of its energy for maintenance, similar to other sedentary species. Their high assimilation efficiency (assimilation/consumption = 85%) indicates that a seed is a concentrated resource with little unutilizable components (e.g., cellulose and lignin). The net (production/assimilation = 59%) and gross (production/consumption = 50%) growth efficiencies are also relatively high and indicate efficient use of as-

similated food. Newly emerged *C. analis* have a caloric value (7.17 cal/mg) that is higher than most Coleoptera (range 5.2–6.2 cal/mg). A high adult respiratory quotient (RQ = 0.72) and a very high lipid content (49.1% dw) indicate that most metabolic energy demands are supplied by lipid metabolism. Wightman's data clearly demonstrate that *C. analis* and probably other seed feeders more efficiently utilize a nutritious, limited resource and convert a larger proportion of their diet into nutritious compounds such as lipids than is typical for many insects feeding in unprotected habitats or on less nutritious resources.

Feeding in a seed also has limitations in that all resources are contained in the seed. Seeds usually have a water content of less than 10%. Newly emerged bruchids have a water content of around 50% (*C. analis*, 48%; *C. maculatus*, 35–59%; *Mimosestes amicus*, 39%; *Algarobius prosopis*, 43%; *Neltumius arizonensis*, 43%) (Wightman, 1978b; Kistler, 1985). The larvae apparently live on metabolic water during development and efficiently convert the seed into lipids and other water storage compounds (1.0g lipid releases 1.07g water when catabolized). Water content of adults is maintained by lipid breakdown until death, even in the absence of water intake (Wightman, 1978b).

8.4.1 Morphological Adaptations

The morphological adaptations that enable bruchid larvae to enter seeds have been detailed by Pfaffenberger and Johnson (1976). Some first-instar larvae possess well-developed legs, while others are apodous. Larval legs may be used for walking, providing mobility which allows the young larva some degree of host choice and frees the parent to place eggs in less exposed sites. *Algarobius prosopis* and *Acanthoscelides obtectus* eggs are not laid on the seed or pod surface but in cracks, crevices, exit holes of other bruchids, or areas damaged by herbivores (Kunhikannan, 1923; Swier, 1974; Kistler, 1985). Such egg placement in *A. prosopis* significantly decreases parasitism of eggs by trichogrammatid wasps and may decrease all types of egg predation (Kistler, 1985). The highly mobile first-instar larva then chooses an appropriate host seed, providing a greater flexibility in host seed choice than when such decisions are made solely by the parent. The second function of larval legs is as an aid in entering very dense seeds or those with very hard seed coats. *Caryobruchus gleditsiae* larvae utilize their legs, which terminate in a very sharp, heavy claw, to aid in boring into extremely hard seeds (Pfaffenberger and Johnson, 1976). Also associated with these well-developed legs are increased sclerotized surface areas and musculature (Pfaffenberger, 1982). In contrast, species that infest soft seeds or attack immature pods or seeds are usually apodous and exhibit specialized characteristics to aid in entering soft hosts. *Mimosestes protractus* lacks legs but has short, decurved spines, which apparently aid in "swimming" through the sappy pulp of an immature pod (Pfaffenberger and Johnson, 1976), where longer or

straighter appendages might impede larval movement. Each resource thus dictates specific morphological traits that are required for successful resource use, which may in turn limit the potential number of hosts for each species in nature.

8.4.2   Physiological Adaptations

The metabolic cost of feeding and associated rate of development in a resource are dependent on the adaptations of larvae to host seeds as a resource as well as to the strategy of the species (Janzen, 1977; Kistler, 1982, 1985). Both cost and rate of development may be influenced by the nutrients (or ratios of nutrients) and toxins (which must be avoided or detoxified) present in seeds and by predator avoidance.

Metabolic and developmental rates of larvae of bruchids are discussed by Kistler (1982, 1985). These data indicate that both the metabolic cost of feeding on a seed (as assessed by metabolic rate) and the developmental rate (time required for development in that species of host seed) vary between bruchid species in the same species of host and within the same bruchid species reared on different species of hosts (Fig. 8.1). This variation indicates that development in a given host resource entails differential costs. *Stator generalis*, an extreme specialist, is the only bruchid that is able to develop in the very hard, toxic seeds of *Enterolobium cyclocarpum* (Janzen and Higgins, 1979; Johnson and Janzen, 1982) and has a high metabolic cost of development. This species also has a significantly lower developmental survival on its host seeds (48%) than all other *Stator* species on their major hosts (range 75–81%) (Johnson, 1982). *Mimosestes amicus* also has a high cost of development, but it is an extreme generalist. Thus, extreme specialists and extreme generalists may find it metabolically expensive to develop in some hosts. Such high costs of successful resource utilization may limit the success (in terms of survival and relative abundance) of generalists on many host plants (e.g., *M. amicus* is not very successful on *Prosopis velutina*, although it is more successful on *Cercidium floridum;* Kingsolver and Johnson, 1978; Kistler, 1985), thereby limiting even generalists to a few specific host plants (e.g., equal to specialists; Cates, 1981).

Researchers have begun to examine the biochemical adaptations of bruchids to their host seeds and to pinpoint some of the costs involved in feeding in seeds with different nutrients and toxins. The nutrients and toxins of a seed may be differentially located in seeds of different species or even in seeds of the same plant. This may be due to the combined parent–offspring makeup (seed coat and endosperm vs. embryonic tissues) of the seed (Gunn, 1981) or to different defense strategies of different species of plants. Janzen (1977) allowed *Callosobruchus maculatus* to oviposit on 63 different species of seeds. Volatile seed coat toxins killed eggs on 17% of the seeds. Seed coat hardness, thickness, or toxicity prevented larvae from entering 59% of the seeds, and seed contents killed larvae in 92% of the 63 species of seeds.

These results demonstrate that *C. maculatus* is unable to deal with the multitude of seed defenses, and yet species of bruchids exist that can and do feed in most or all of these 63 seed species.

8.4.2.1 Trypsin Inhibitors. The apparent lack of gut proteases in bruchids led Applebaum (1964) to suggest that this single factor might have allowed the radiation of bruchids onto legumes. Seeds of the Leguminosae often contain many short chain peptides or seed proteases but also contain unusually high levels of enzymes that inhibit peptidases (e.g., trypsin and chymotrypsin). Applebaum based his hypothesis on experiments in which he found low protease activity in homogenates of bruchid midguts, and he also found that developmental rates and survival were unaffected by the incorporation of trypsin inhibitors into bruchid diets. Alternatively, many bruchids may use free amino acids as a source of nitrogen (Rosenthal and Janzen, 1983), thus circumventing the action of protease inhibitors. The success of *Callosobruchus chinesis* increased with trypsin inhibitor content in ten varieties of seeds (Roy and Bhat, 1975). This indicates that trypsin inhibitors in seeds may serve mainly as storage proteins and not as a defense as indicated by Applebaum (1964). Thus, not only have bruchids avoided the negative effects of protease inhibitors, but they may actually use these compounds, which may make up to 10% of total seed protein (Weder, 1981), as a major source of dietary protein.

Not all legume seeds possess trypsin inhibitors, and there is a wide diversity of trypsin inhibitor-like enzymes (Weder, 1981). Gatehouse and Boulter (1983) found that only one out of 5000 varieties of cowpeas was significantly resistant to *C. maculatus*. Through studies using artificial diets, they found that resistance was due to a specific "cowpea trypsin inhibitor" and that other trypsin inhibitors had much less or no antimetabolic effect. This specific trypsin inhibitor affected the bruchids by decreasing the availability of required sulfur amino acids by inhibiting gut proteases and sequestering these amino acids in an indigestible form as a part of the trypsin inhibitor molecule. Thus, bruchids are not totally insensitive to protease inhibitors, and trypsin–like enzymes are present in the digestive systems of at least some bruchids. Nonprotein amino acids (e.g., L-dopa and L-homoarginine) may decrease or prevent bruchid survival in seeds. Similarly, 32% of the protein amino acids are lethal to *C. maculatus* at a concentration of 5%. Many of these amino acids are found in only low levels in the natural host, cowpeas. Thus, ratios of protein amino acids in the diet may influence the rates of amino acid uptake and use (Janzen et al., 1977).

8.4.2.2 Starches and Sugars. Starches and sugars, along with proteins, are major constituents of seeds fed upon by bruchids. Alpha-amylases are important enzymes for starch digestion in insects (Podoler and Applebaum, 1971a). Podoler and Applebaum (1971b) found that the alpha-amylase of *Callosobruchus chinensis* had a K_m value (Michaelis constant is the concen-

tration of substrate at which the reaction velocity is half of its maximal value or at which half of the enzyme active sites are filled) that was 10-fold greater than the K_m value of the alpha-amylase contained in the seeds from which the beetles were reared. The bruchid amylase also had an activation energy that was much lower than amylases of most other animals. Thus, this alpha-amylase is a very effective enzyme for starch breakdown and is more highly adapted than alpha-amylases of many other organisms. However, the complex granular structures of starches in seeds often inhibit the action of bruchid amylases (Podoler and Applebaum, 1971b). The beetles apparently increase starch digestion two- to threefold by utilizing seed amylases to supplement their own alpha-amylase to aid in initial digestion of these complex starch granules (Podoler and Applebaum, 1971c,d). These studies also indicate that, to grow adequately, bruchids require a high carbohydrate/ protein ratio, a high simple sugar content (mono- and disaccharides), a low amylose/amylopectin ratio, and an unidentified methanol-soluble factor (the last was required for bruchid survival; Podoler and Applebaum, 1971d).

Some legume seeds contain soluble heteropolysaccharides, which may also affect digestion in some bruchids but not in others, depending on their ability to degrade a large part of the integral basic core structure of the heteropolysaccharide where most of the toxicity resides (Applebaum et al., 1970; Applebaum and Guez, 1972).

8.4.2.3 Other Toxins. In contrast to those compounds that serve not only as defenses for the seed but also as nutritional sources for seed-feeding insects, other compounds serve mainly for defensive purposes. Saponins are contained in many legume seeds (Applebaum and Birk, 1972). These act as feeding deterrents in aphids and as surfactants altering membrane permeability "of the insect gut"; in *C. chinensis* they cause a hormonal imbalance that prevents pupation. Seeds of *Phaseolus vulgaris* contain a phytohemagglutinin that apparently prevents the more than 75 species of bruchids in Costa Rica from feeding in these seeds (Janzen et al., 1976). When Janzen incorporated this phytohemagglutinin into artificial seeds, the survival of *C. maculatus* sharply decreased. Alkaloids also have a substantial effect on survival of *C. maculatus* (Janzen et al., 1977). Janzen (1969) found that of the 36 species of plants he studied, those that were free from bruchid infestation had toxic deterrents in their seeds.

Several species of toxic seeds are attacked by bruchids. Trelease and Trelease (1937) and Johnson (1970) cite collectively numerous examples of species of *Astragalus* that have poisonous seeds and are fed upon quite commonly by several species of *Acanthoscelides*. Seeds of species of *Erythrina*, *Abrus*, *Dioclea*, and *Sarothamnus* are known to contain toxins and are also eaten by bruchids (Janzen, 1971). Rotenone in the seeds of *Cracca virginiana* has no ill effect on the larvae of *Acanthoscelides obsoletus* (Bridwell, 1938). Brett (1946) reported that the toxin "amorpha," which occurs in pods of *Amorpha fruticosa*, acted as both a stomach and contact

insecticide. He determined this substance to be much more abundant in glands scattered over the surface of the fruit than in seeds, which apparently contain few or no toxins. We interpret all of these examples as a specific bruchid having evolved resistance to a specific toxin; that is, each bruchid would probably be susceptible to toxins found in seeds of plants other than its hosts.

The most complete study of resource use in larvae of bruchid beetles is being carried out by Gerald Rosenthal and his colleagues using *Caryedes brasiliensis*, which feeds in the toxic, canavanine-containing seeds of *Dioclea megacarpa,* a leguminous neotropical vine. Canavanine, like many other nonprotein amino acids, acts as a toxin to most bruchids as well as to larvae of other insect species (Rosenthal and Janzen, 1983) but has no negative effect on *C. brasiliensis*. Canavanine in seeds of *D. megacarpa* comprises 13% of dry seed weight and 55% of all seed nitrogen. Canavanine is toxic because it is a structural analogue of arginine that is incorporated into proteins, thus altering their physiochemical properties (Rosenthal, 1983). Larvae of *C. brasiliensis*, in contrast to other insects (Janzen et al., 1977; Rosenthal, 1977), avoid significant incorporation of L-canavanine into protein structure because of a highly discriminatory protein-synthesizing system that discriminates between L-arginine and L-canavanine (Rosenthal and Janzen, 1983). Further, *C. brasiliensis* degrades L-canavanine for use as its major dietary source of nitrogen. L-canavanine is broken into L-canaline and urea by the action of arginase. The resulting highly toxic L-canaline is broken down to homoserine and ammonia, and the urea is largely broken down by urease, which is rare in insects (Cochran, 1975) but common in bruchid larvae. Some of the ammonia is reincorporated in the formation of glutamine from glutamic acid (Rosenthal, 1983; Rosenthal et al., 1982). Thus, a suite of mechanisms allows *C. brasiliensis* to feed in toxic seeds and to use the toxin as a major dietary source of nitrogen. If much of this detoxification results from a symbiotic gut flora (Rosenthal, 1983; Rosenthal et al., 1982), then much of the specificity and evolution of the Bruchidae may be the result of such symbiotic–mutualistic relationships.

The high nitrogen content of seeds may require unique "noninsect" methods of nitrogen excretion in seed-consuming phytophagous insects such as the Bruchidae. The mechanism of canavanine and canaline breakdown in *C. brasiliensis* may be typical of metabolism by bruchids in other seeds, many of which possess an abundance of nonprotein amino acids as storage or defense compounds (Bell, 1978). Thus, both urea and ammonia may be common by-products in seed-feeding insects, unlike many other terrestrial insects in which uric acid predominates. Fecal material of *C. brasiliensis* contains only 11% uric acid; 47.1% is urea, and 41.9% is ammonia (Rosenthal and Janzen, 1981). This strategy allows nitrogen excretion without increasing metabolic costs that would be incurred in the conversion to uric acid of the large amounts of urea and ammonia produced in canavanine detoxification and utilization.

8.4.3 Pupal Resources

Use and reallocation of resources gained during larval feeding occur during the pupal stage. Free amino acids and glycogen in pupae of *C. maculatus* decrease rapidly, whereas total lipid increases from 20% to 25% of total fresh body weight at day 3 and thereafter decreases (Sidhu and Kang, 1979). Glycogen appears to be the major energy source for the first 3 days in the pharate pupa, and it also supplies materials for chitin synthesis; lipids apparently provide the energy for the later pupal and adult stages. Thus, the success of the pupal stage is dependent on the storage of nutrients during the larval stage.

8.5   ABIOTIC FACTORS AFFECTING FEEDING PERFORMANCE AND STRATEGIES OF BRUCHIDS

Bruchids, as largely ectothermic organisms, are greatly affected by temperature, which may limit their populations through its impact on their ecological and evolutionary feeding strategies. Many temperate species of bruchids appear to be limited to a univoltine life cycle because of temperature (Johnson, 1981d). The success of *C. maculatus* as a stored product pest may be due to its extremely high temperature resistance. *Callosobruchus rhodesianus*, which is a pest at high altitudes in southern Africa, is able to withstand low temperatures (Southgate, 1978). Temperature affects fecundity and longevity (Utida, 1971; Sharma et al., 1979; Kistler, 1982, 1985); also, even brief periods of exposure to moderately high temperatures (36°C) may affect both fecundity and fertility of both males and females of some species (Huignard and Biemont, 1974; Hamed, 1981). Much of the resistance to cold or heat is due to the physiological state of the bruchids. In *Bruchus pisorum* the ratios of water and fat are important factors in cold tolerance (Burov and Karpunina, 1967).

Different species of bruchids may have different ecological and evolutionary responses to changes or extremes in temperature. Kistler (1982, 1985) examined the physiological and developmental responses of eight desert species of bruchids to temperature. These species segregated into two groups based on the responses by adults to temperature. One group minimized the effects of temperature change, such as might occur diurnally in desert ecosystems, by increasing its metabolic rate at a much slower rate than the second group, whose metabolic rate increased very rapidly and consistently with increasing temperature. Larvae of *Stator pruininus* and *S. limbatus* showed a capability to regulate their metabolic rate as temperature increased and had a very rapid developmental period. These two species are members of the mature seed guild (Johnson, 1981c), which oviposit directly on and develop in mature seeds on the host plant. These host seeds are probably more exposed to temperature extremes and more susceptible to

seed predators and parasitoids. Thus the developmental strategies of these two species may be a result of selection pressures for rapid development to avoid being eaten by a seed predator and for resistance to temperature fluctuations, which would also allow for a further increase in developmental rate.

Resource type, especially in generalist species, may affect individual performance of seed feeders (Fig. 8.1) as well as their population stability. Fujii (1983) examined long-term (approximately 30 generations) population dynamics of *Zabrotes subfasciatus* on three different resource seeds. On red kidney beans (*Phaseolus vulgaris*), the population levels were lower and the dynamics were distinctly different from populations in the other two resource types. In no case were there significant evolutionary changes in the populations during the experiment, and in all cases the population dynamics were relatively stable. Resource type alone may thus regulate population levels, dynamics, and stability. The lack of an evolutionary change seems to indicate that genetic inertia (resistance to genetic change) may be limiting the ability to increase adaptedness.

8.6 CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Because of their importance in feeding in seeds of cultivated legumes and their unique habit of feeding only in seeds, the nutritional ecology of bruchids is of interest in both applied and basic contexts. Seeds are of significance because of their reproductive importance to plants and because they provide nutrient-rich sources of food for animals. Bruchids expend a relatively small proportion of their energy intake for maintenance and are relatively efficient in utilizing seed contents. The performance of adult bruchids is limited by a trade-off between longevity and reproductive output. Many species of bruchids do not need to feed as adults but the quality of food of the larvae may profoundly affect adult behavior and fecundity. Larval adaptations include behaviors allowing escape from parasites and predators, morphological structures facilitating entering host seeds, and physiological mechanisms to deal with the nutritional and allelochemical composition of seed coats and contents. Although bruchids feed in a variety of toxic seeds, each species is probably susceptible to toxins found in seeds of plants other than its hosts. Various means of countering or utilizing toxins are discussed. Temperature may have a profound effect on short-term development of bruchids and on their evolution, and food resource type may regulate population levels, dynamics, and stability.

Among the research that needs to be done on the nutritional ecology of bruchid beetles are determining (1) the basic nutritional requirements for stored-product bruchids as well as those that are of current interest because of their ecological and evolutionary uniqueness, (2) the detoxication of toxic compounds in seeds, (3) the role of gut symbionts in digestion and detoxica-

tion, (4) the chemistry of seeds that are fed upon by few bruchids and those that are fed upon by many bruchids, (5) the comparative digestive abilities of generalist and specialist bruchids, (6) the allocation of energy by non-stored-product bruchids and especially by generalists versus specialists, and (7) the effects of seed chemistry and bruchid chemistry on parasitoids and predators.

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