comparing energy budgets for various storage pests, suggested that the unusually low number of larval instars (three) help the larger grain borer to feed and develop faster and with relatively high efficiency; they also noted the continuing high energy consumption of adult beetles.

The observation of previous authors (Bell & Watters, 1982; Shires, 1980; Subramanyam *et al.*, 1985), based on head capsule measurements, that the larger grain borêr usually has only three larval instars has been challenged by Ramírez (1990). In the course of detailed study of the biology of larger grain borer, he reports that five larval exuviae were normally observed during development. Detailed illustrations are also provided of various ultrastructural and anatomical features of all life stages of the insect, including observations of a mycetoma on the hind gut of adults. In the same publication, Ramírez reports studies of development times and mortalities on a compacted mixture of maize and wheat flour. Using a mathematical model for stage-specific survivorship, he concludes that minimal developmental mortality is obtained at 32°C and 40% relative humidity and that high humidity is a major limiting factor in the ecology of the insect. The development time (64 days) under these conditions was, however, almost twice that obtained in the author's preliminary study, with this and other substrates at 29°C and 60% r.h.

Population dynamics in rural stores

The comparatively limited geographical distribution and irregular pest incidence of larger grain borer, as compared with that of other major storage pests, has led to speculation as to the possible factors, environmental, sociological and biotic, which might determine its incidence. Since laboratory studies show that developmental optima of larger grain borer are similar to those of other storage pests, it is assumed that its incidence as a pest may be limited by competition with other pests, especially *Sitophilus* spp. or by natural enemy activity. Until recently, however, little effort has been invested in the collection of field data on larger grain borer population dynamics, in relation to different environments, storage practices and pest associations.

General studies of storage pest dynamics in Mexico have provided some information on larger grain borer, in particular at localities in the states of Guanajuato (Aguilera, 1988b), Mexico (Romero, 1986), Michoacan (Morales, 1985), Morelos (Garduño, 1988) and Oaxaca (Hernández & Rojo, 1985). In addition, studies have recently been carried out with the specific aim of providing a better understanding of larger grain borer dynamics in Costa Rica (Böye, 1988), Honduras (Novillo, 1991) and in central Mexico (Ríos, 1991). A large-scale comparative study is also currently under way in seven areas of Mexico (Dick, 1990).

In almost all the studies, maximum numbers of the three main primary pests, *Sitophilus zeamais* Motschulsky, *Sitotroga cerealella* (Olivier) and *P. truncatus*, occur at different points in the storage cycle. Although this may, to some extent, reflect differing tolerances of temperature and humidity, it is interesting to note that at a series of study sites between 1700m and 1850m altitude in Guanajuato, where seasonal influences were presumably rather uniform, a whole range of different successions were recorded (Aguilera, 1988b). Novillo (1991) explicitly provides evidence for the importance of competition between *S. zeamais* and *P. truncatus*, both in relation to the seasonal succession and the distribution of insects among cobs. Laboratory studies have provided some insight into competitive interactions between these species. For instance, Haubruge & Verstraeten (1987) observed that, on small quantities of shelled grain, *P. truncatus* tended to attack uninfested grains more than those previously infested by *S. zeamais*; however, as the authors themselves remark, it would be dangerous to extrapolate such results uncritically to real stores of maize on the cob. In view of laboratory studies indicating that loose grain usually favors the maize weevil (Cowley *et al.* 1980; Howard, 1983), it is interesting to note the common occurrence of larger grain borer in some traditional stores of shelled grain in Morelos (Garduño, 1988); however, the comparatively low humidity in this area may be a factor favoring the survival of the borer.

Secondary pests tend to be abundant in rural maize stores, especially in tropical regions. As might be expected, there is some evidence in the population dynamic studies of differing relationships to the primary pests. The incidence of *Cathartus quadricollis* (Guérin) and *Carpophilus* spp., where present, appears to be independent of that of *P. truncatus*. The dynamics of *Gnatocerus maxillosus* (Fabricius), on the other hand, in many cases correlates closely with *P. truncatus* abundance (Aguilera, 1988b; Novillo, 1991). In Africa, a close association was noted between the incidence of *Tribolium castaneum* (Herbst) and *P. truncatus* (Hodges *et al.*, 1983a) but in some of the neotropical studies *T. castaneum* appears to be displaced by *G. maxillosus* (Novillo, 1991; Ríos, 1991). The coincidence of these tenebrionids with *P. truncatus* is of interest in view of the laboratory observation that *T. castaneum* at least can affect the population increase of the primary pest, presumably by direct predation (Haubruge & Verstraeten, 1987; Rees, 1987).

The association between the histerid *Teretriosoma nigrescens* Lewis and *P. truncatus* has received considerable attention in relation to the possible use of the predator as a biological control agent in Africa. This subject is considered in more detail below, but for present purposes it may be noted that the evidence provided by population dynamics studies for the effectiveness of insect natural enemies is, at best, equivocal. Field studies in Costa Rica and laboratory studies in Germany suggested the existence of a characteristic ratio (with a mean of 6.5:1 in the field studies and approximately 10:1 in the laboratory) between the numbers of adults of *P. truncatus* and *T. nigrescens*, implying that these species may coexist in equilibrium (Böye, 1988; Leliveldt & Laborius, 1990). However, both Ríos in Mexico (1991) and Novillo in Honduras (1991) reported *P. truncatus* populations increasing exponentially in the latter part of the storage period, despite the presence of *T. nigrescens*. The parasitoid *Anisopteromalus calandrae* (Howard) has also been reported in association with *P. truncatus* (Böye, 1988; Hodges, 1986) and suggested as a possible control agent (Brower, 1990). Recent population dynamics studies in stores suggest that this parasitoid is more closely associated with *S. zeamais* (Novillo, 1991; Ríos, 1991); however, more detailed laboratory studies are currently under way in Mexico to investigate the possible existence of populations of *A. calandrae* which are adapted to, or show a preference for, *P. truncatus*.

Laboratory studies indicate that prior infestation by one species or the other can affect the outcome of competition between the maize weevil and larger grain borer (Cowley *et al.*, 1980; Howard, 1983). It is well known that both species can attack maize in the field, prior to harvest, but evidence for the occurrence and importance of field infestation is equivocal in the case of larger grain borer. Rates of field infestation ranging from 4 to 18% of cobs infested were reported at sites in Veracruz and rates of 18 and 37% in the state of Mexico (Ramírez, 1960a). *P. truncatus* was reported as the most abundant pest in field samples at an unspecified site in the northern part of the Valle de México (Quintana *et al.*, 1960a), and the second most abundant at Chapingo, also in Mexico State (Ríos, 1986). Field infestation rates of approximately 2% were recorded nearby at Montecillos (Sánchez *et al.*, 1985). However, no field infestation whatsoever by larger grain borer was encountered by Novillo (1991) in a series of field samples from the Zamorano Valley of Honduras, even though the insect was prevalent in nearby maize stores and captured in pheromone traps in the fields.