Crowding, Maternal Age, Age at Pupation, and Life History of *Zophobas atratus* (Coleoptera: Tenebrionidae)

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ABSTRACT In *Zophobas atratus* (F.), crowding of larvae inhibits pupation, whereas isolation of crowded larvae triggers pupation, allowing duration of the larval stage to be manipulated experimentally. Effects of larval and adult crowding, birth order (maternal age), and duration of larval stage (larval age at pupation) on larval growth, adult reproduction, and adult longevity were determined in a factorial experiment spanning 2 1/2 generations. Larval growth decreased with density and increased with birth order. As larvae grew, they became repelled by other larvae and dispersed for pupation: the proportion pupating successfully first rose with age, then fell as death at metamorphosis became more frequent. Experimental isolation of larvae produced cohorts of adults that had spent 4, 7, and 10 mo as larvae. Body weight of these adults increased with larval age, decreased with larval density, and was higher for males. These F_1 adults were allowed to breed at high and low density until they died. Lifetime egg and larval production generally decreased with birth order and larval age and increased with adult density. Male (but not female) longevity was strongly reduced by adult crowding. Both male and female longevity declined with birth order and larval age. The experimental factors acted on lifetime reproduction largely through their effects on longevity, but there remained a direct negative effect of birth order and larval age. Body weight and reproduction were uncorrelated because females of early birth order and early pupation were lowest in body weight but had the highest reproductive output. Females produced their highest-quality offspring early in life, but the effect was delayed until their offspring reproduced. These effects are discussed in light of their possible importance in this beetle's life history and population dynamics.

KEY WORDS population dynamics, birth order, reproduction

THE LIFE HISTORY of animals is shaped by the age-specific schedule of mortality and fecundity imposed on them by the environment and by the variability of that environment. These factors are thought to determine when the animal will first breed, how many and what size offspring it will have, and how much effort it will put into reproduction as opposed to other functions (Stearns 1976). They will also shape the timing of reproductive effort within generations and the norms of reaction to environmental variables. Among insects exploiting highly localized resources, crowding may be an especially important variable, affecting both larvae and adults, with consequences for either or both stages. Many individual or population-level effects have been reported. Crowding can affect growth rates, adult size, developmental period, and adult fecundity (for examples, see review by Klomp [1964], bibliography by Barbosa & Peters [1975]).

Crowding during the adult stage generally has negative effects on fecundity, fertility, and longevity (Watt 1960, Lloyd & Park 1962, Klomp 1964, Sinclair 1989). Crowding in the larval stage may either increase or decrease longevity, and the effect may be tempered by feeding (Terzian & Stahler 1949, Miller & Thomas 1958, Haupt & Busvine 1968). Reduction of adult body size often results from larval crowding and may lead to reduced fecundity (Calder 1984). Crowding may also stimulate development rate (Ellis 1959, Hodjat 1969) and may affect morphology in insects such as locusts and aphids (Dixon 1977, Harrison 1980).

In most cases, then, crowding reduces the capacity of individuals for reproduction and may act through one or more life-history parameters to reduce population growth rate (Stiling 1988, Hassell et al. 1989).

Dispersal is a common response to high population densities in many insects and is usually thought to serve the purpose of "escape" or "colonization" (Stinner et al. 1983, Stiling 1988). Crowding causes the production of specialized dispersing individuals in a number of species (Harrison 1980). Among tenebrionid beetles, adult *Tribolium confusum* Jacquelin Du Val and *T. castaneum* (Herbst) show increased dispersal as density increases (Naylor 1959, 1961, 1965; Ghent 1963, 1966; Ogden 1970), which, depend-

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ing on species, can be interpreted as either escape or colonization. Insects also move to seek appropriate habitat for each life stage, such as pupation sites, but this movement is not often included under dispersal.

In some animals, an environmental condition may have an effect not on the mother but on her offspring (Rossiter 1991), giving rise to a delayed effect. Most obvious of such delayed effects is that of maternal age. In some cases, the "quality" of offspring, as measured by longevity, growth rates, weight, diapause, or resistance to stress, changes as females age (review: Mousseau 1991, Mousseau & Dingle 1991, Phelan & Frumhoff 1991). Preliminary experiments have shown a maternal effect on the growth rate of offspring of *Zophobas atratus* (F.) (unpublished data), similar to that found in *Tenebrio molitor* L. (Ludwig & Fiore 1960, 1961).

Biology of *Zophobas atratus*. *Z. atratus* (= *Z. rugipes;* [Tschinkel 1984]) is a large, black tenebrionid beetle often found in the guano deposits of a variety of bats (Tschinkel 1981). Its range extends from southern Arizona and the West Indies to northern South America. Mature larvae weigh 0.8 to 1.2 g and can occur in densities of dozens of large larvae per liter of guano. Large guano deposits can host populations of many thousand larvae. The association with guano is probably not obligate, and *Z. atratus* has been collected from compost and may be capable of exploiting other accumulations of organic debris. In the laboratory, it grows well on bran or other grain products.

Adults live on the surface of the medium and deposit their eggs in it; larvae spend their feeding lives within the medium, dispersing from it to seek pupation sites away from active larvae (Tschinkel 1981). Reproduction seems to lack strong seasonality, and populations seem to lack discrete age cohorts (personal observations).

The response of *Z. atratus* and several other tenebrionid beetle species to crowding is quite different from the "normal" effects of crowding. In these species, crowding, through tactile stimulation, directly inhibits metamorphosis (Tschinkel & Willson 1971). In the laboratory, if larvae are kept crowded throughout their lives, they continue to grow but never pupate, finally losing fat body and vitality and dying as senescent larvae. On the other hand, after they reach a minimal weight and age (or both), isolating larvae will cause them to pupate. Most tenebrionids surveyed by Tschinkel & Willson (1971) showed this inhibition to varying degrees, and it is probably an important phenomenon throughout the Tenebrionidae, possibly including such much-studied species as *Tenebrio molitor, Tribolium* spp. (Botella & Ménsua 1986), and several *Eleodes* species.

The inhibition of metamorphosis by crowding probably evolved in response to cannibalism. Cannibalism is common among the tenebrionid beetles and dominates population dynamics in species of *Tribolium* (King & Dawson 1972). In *Z. atratus,* the pharate pupal and pupal stages are most vulnerable (Tschinkel 1978), and most of these placed among active larvae in a natural population were cannibalized (Tschinkel 1978, 1981).

Pupation-ready but crowded *Z. atratus* larvae leave the crowded food mass and seek the isolation needed to undergo metamorphosis. In the laboratory, Tschinkel & van Belle (1976) and Tschinkel (1978) demonstrated that, as larvae grow, they change from aggregation or random dispersion to a dramatic overdispersion (i.e., mutual repulsion). In natural populations, this change in behavior brings about the departure of a larva from the feeding aggregations, followed by pupation in an undisturbed site (Tschinkel 1981). Naylor (1965), Ghent (1966), and King & Dawson (1973) found a perhaps related density-dependent tendency for *Tribolium* larvae to disperse from densely populated flour and to pupate in less-dense regions.

The research in this article grew out of my work on the inhibition of metamorphosis by crowding in *Z. atratus* and several other tenebrionid beetles. I reasoned that larval dispersal for pupation represents a "choice" that affects the larva's adult body weight and age at first reproduction, two important life-history tactics. Natural selection of the timing of this larval choice could therefore act on several life-history characteristics indirectly. This study tested the effects of experimentally varying the larval "choice" of age at pupation and of larval and adult crowding and maternal age on the subsequent reproductive output and longevity of these beetles. The results represent a case study of the intra- and intergenerational reaction norms to these life-history factors.

Materials and Methods

Collection and Maintenance. The beetles were collected as several hundred larvae from a man-made cave near Heredia, Costa Rica, in 1965. A large population (many thousands) of them was thriving on the droppings of fruit bats and other bats. In the laboratory, they were maintained in metal boxes on wheat bran and water, having passed through about 15 to 20 generations in the laboratory at the time the experiment was begun. Although it is possible that unintended laboratory selection may have resulted in changes of life history, strains freshly collected from other localities after the experiment was half completed had similar life histories and showed only minor quantitative differences in the characters important to this study. Such differences could also have been geographic strain differences.

Mature larvae confined in escape-proof crowded cultures failed to pupate, but did so if isolated (Tschinkel & Willson 1971). Stock cultures were kept going by isolation of larvae for pupation every 4 to 5 mo and placement of 100 to 300 of the resulting adults in a culture box on fresh bran. As the larvae grew, they converted the bran into frass, which was sifted out at intervals and replaced with fresh bran. Shortly before these experiments were begun, the diet was changed to a 1:1 mixture of bran and cricket feed (a mixture of grains, animal protein, and minerals), a diet on which the larvae grew faster. All rearing and experimentation was at 28°C under constant light.

Experimental Cohorts (Fig. 1). (1) Parental cohort: Many larvae were isolated from stock cultures, resulting in an even-aged cohort of adults (P cohort) (Fig. 1). About 500 pairs of these were placed in a metal culture box (35 by 35 by 10 cm) containing culture medium 3 to 4 cm deep covered with toweling (to receive water).

(2) F_1 larval cohorts: Females of the P cohort laid their eggs in the bran, and 1-wk samples of eggs were collected early in the cohort's life (fourth week, approximately the first eggs laid), in the middle (fifteenth week), and late (twenty-first week). At those collection times, 95, 45, and 15% of the P cohort were still alive. These egg samples were allowed to hatch, and the larvae were placed in metal culture boxes to grow at either high (3,500 larvae initially) or low (1,200 larvae initially) larval density (Fig. 1). The number of larvae was estimated or counted monthly. At that time, 52 larvae were selected randomly from each of these larval cultures, and 25 of these larvae were weighed. The tendency to disperse was tested monthly by placement of all 52 weighed larvae in a dispersarium (Tschinkel & van Belle 1976) for 2 d. The dispersarium is a circular, 31-cm, Plexiglas arena opening on its perimeter into 26 identical 14-cm chambers. Larvae prefer the chambers over the arena and are free to assort themselves among the chambers. Dispersion of larvae among the chambers was estimated from chamber and arena occupancy. Overdispersion resulted in more single-occupant chambers, fewer multiple-occupant chambers and empty chambers, and more larvae in the arena than expected by chance alone. Such mutual repulsion by larvae is associated with dispersal behavior preparatory to pupation (Tschinkel 1978, 1981). In this study, chamber-occupancy data from the second day were used to compute an index of dispersion based on the difference between the expected and observed number of chambers with zero, one, and two or more occupants. The expected numbers were estimated from the Poisson distribution (see Tschinkel & Van Belle [1976] for details). When the observed distribution was not significantly different from the expected (random), each estimate was between -1 and 1. The three estimates were not completely dependent because some larvae usually failed to enter chambers and remained in the arena. Significant overdispersal caused the differences for single-occupant chambers to exceed 1 and those for empty chambers and chambers with more than one occupant to be less than -1. The sum of their absolute values thus exceeded 3. Significance of deviations from random dispersion among the chambers of the dispersarium was tested against a Poisson distribution with a chi-square test. At the same time, a sample of 100 weighed larvae was isolated individually in the chambers of a pupatorium in a test of their ability to pupate upon isolation. After 12–14 d, those pupating or dying were counted and weighed. Those remaining active larvae were returned to their culture. Thus, as each larval culture grew, information on weight gain, tendency to disperse, and ability to pupate was collected at monthly intervals.

(3) F_1 adult cohorts: At three times (4, 7, and 10 mo of age) during the growth of these F_1 larval cultures, 200 to 400 larvae were isolated, causing them to pupate (Tschinkel & Willson 1971). Shortly after eclosion, the F_1 adults were weighed, sexes were identified, and they were placed in screen-lidded plastic boxes (10.5 by 10.5 by 3 cm) at either low density (one pair per box, 25 boxes) or high density (five pairs per box, five boxes). All beetles were individually numbered with black numerals on white paint spots on the pronotum. Mortality was recorded once per week. As beetles died, I kept density as nearly constant as possible by combining low-density boxes, replacing dead high-density females with radiation-sterilized females, or combining high-density boxes. No data were taken on replacement male or sterilized replacement female beetles. They provided density only. The females laid their eggs through a metal screen into a layer of 150 ml of flour (Wondra) from which the eggs were sifted weekly and counted (fecundity). Adults fed on a coarse, baked mixture of bran and flour, which could not pass through the screen. The eggs were then allowed to hatch on a fabric screen 1 cm above a moist paper towel in another plastic box so that newly hatched larvae would drop through the screen before cannibalizing other eggs. Hatched F_2 larvae were counted weekly (fertility). Three times during the lives of the F_1 adults (fourth, tenth, and twentieth weeks of age), these F_2 larvae were set up for growth in plastic boxes at either high (75 larvae) or low (35 larvae) density (Fig. 1). I estimated growth of these F_2 larvae by counting and weighing them at 8 and 14 wk of age. One group was also surveyed at 20 wk.

Experimental Design and Analysis. There were four independent variables: (1) birth order (= maternal age at the time the F_1 egg was laid; three levels: early, middle, late); (2) density of F_1

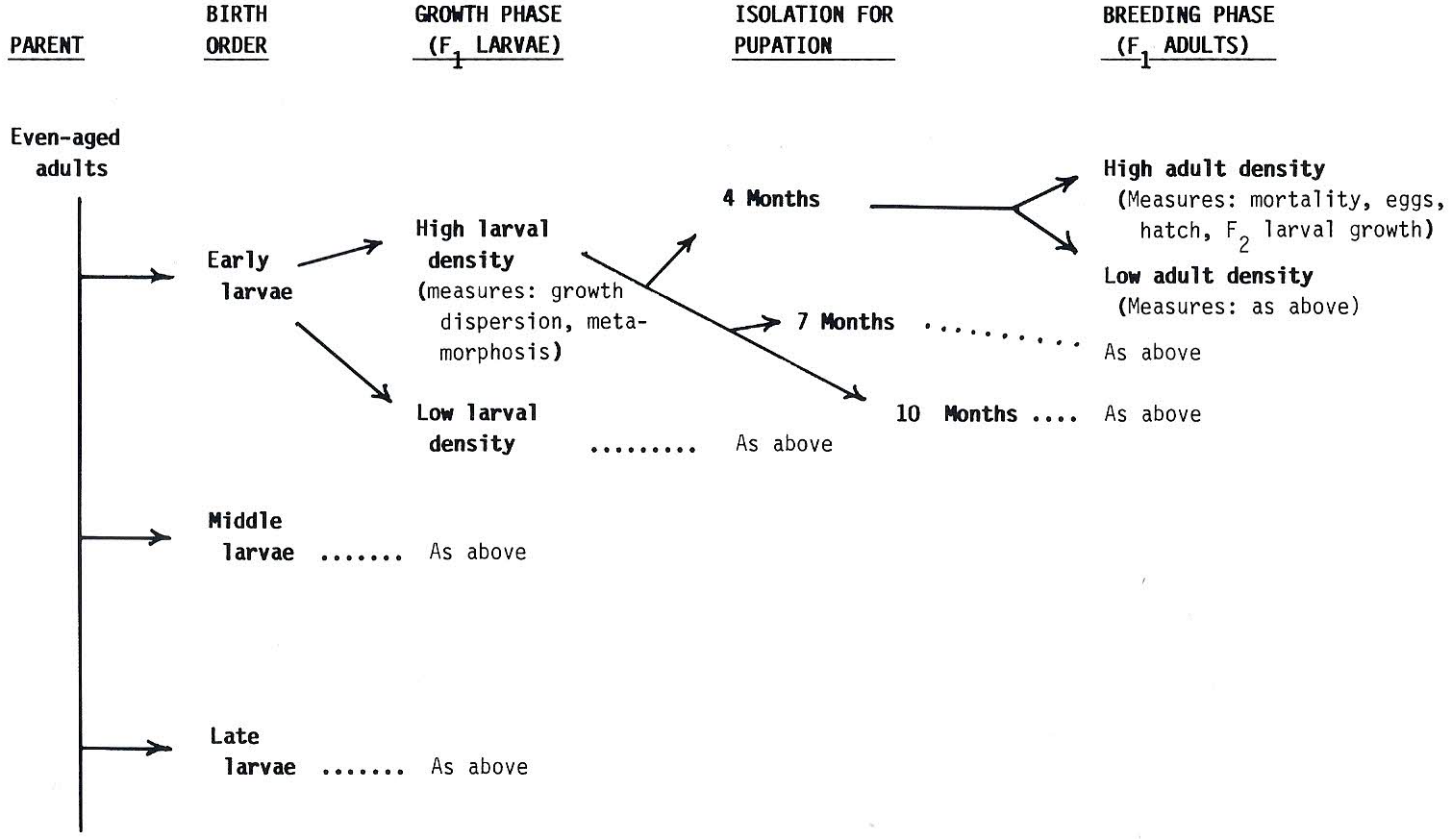

Fig. 1. Flow chart of the factorial experiment, showing sequence of actions and measures.

larval cultures during growth (two levels: high, low); (3) age of F_1 larvae at metamorphosis (three levels: 4, 7, and 10 mo); and (4) density at which F_1 adults bred (two levels: one and five pairs per box). To balance the cells for analysis of variance (ANOVA), data from groups of five one-pair boxes were randomly combined (into "pseudo boxes") for analysis. Each datum was thus based on a "pseudo box" or a five-pair box. This design resulted in a total of 36 treatment groups ($3 \times 2 \times 3 \times 2$) in the F_1 portion of the experiment. Because F_2 larval birth order was tested at three levels, there were 108 F_2 larval treatment groups (3×36). The experimental design was a split-split plot (larval and adult densities), with each F_1 adult treatment nested within one of three birth orders.

For F_1 larvae, the dependent variables for each monthly growth check were weight, dispersal index, percentage pupating, percentage dying at metamorphosis, weight, and sex of pupae. For the F_1 adults, dependent variables were weekly mortality, eggs laid, and eggs hatched.

Most data were analyzed by three-, four-, or five-way ANOVA and covariance (or both) with the programs of SPSS (Hull & Nie 1981) and BMDP, as appropriate. Larval growth was analyzed as a repeated-measure ANOVA by BMDP (Dixon et al. 1988). The proportion of variance explained was calculated as the ratios of the sums of squares.

Results

F_1 Larval Growth. The mean weight of the larvae in the F_1 cohorts increased from 30 to 75 mg at 50 d to 620–960 mg at 230 d (Fig. 2). Larvae in low-density cultures grew significantly faster than those at high densities ($F = 343$; df = 1, 864; $P < 0.0001$). Larvae later in the birth order also grew significantly faster than early larvae ($F = 66.6$; df = 2, 864; $P < 0.0001$). Larval age accounted for 72% of the explained variation in larval weight (a repeated measure) ($F = 380$; df = 5, 864; $P < 0.0001$), larval density for 13%, and birth order and its interaction with larval age for 10%. Other interactions explained an additional 4%. The low-density cultures were terminated at 230 d, but the high-density cultures continued for another 2 mo, by which time they achieved weight similar to the final weights of larvae from low-density cultures. The last 2 mo of data, however, are not presented in Fig. 2.

As the F_1 larvae grew, their tendency to repel one another, and thus to over disperse, increased. This behavior, estimated in the dispersarium apparatus, was correlated with an increasing tendency to leave crowded situations, seek isolation, prepare a pupal chamber, and begin metamorphosis (Tschinkel 1978, 1981). In Fig. 3, the tendency to overdisperse is shown as the sum of the absolute values of the differences between the observed and expected number of chambers with zero, one, and more than one larvae. Significant overdispersal appeared in some groups at 110 d and in all by 140 d (Fig. 3). Overdispersal increased gradually with larval age, and age accounted for 74% of the explained variation ($F = 31.8$; df = 4, 7; $P < 0.001$), but this effect of time was significantly different for the different birth orders (BO × Time interaction, $F = 4.16$; df = 7, 7; $P < 0.05$; 17% of explained variation). Larval density interacted significantly with birth order (LD × BO interaction, $F = 5.69$; df = 2, 7; $P < 0.05$; 7% of variation). Overall, 96% of the variation was explained by the factors time, birth order, and larval density. The main effects of birth order and larval density were small and showed little regular pattern, except that overdispersion leveled off earlier in the faster-growing middle- and late-birth-order treatments. Overall, age (time) by itself was by far the most important determinant of the tendency to over disperse.

Another aspect of overdispersion with age was that the number of larvae unable to compete successfully for chambers increased. These larvae were found in the arena. At 4 mo of age, less than a quarter of the larvae were found in the arena, but by 7 mo, this number had increased to 35 to 40%, suggesting keener competition. Larval age accounted for >70% of the explained variation in the number of larvae in the arena ($F = 127$; df = 2, 2; $P < 0.008$). A higher proportion of high-density larvae remained in the arena ($F = 36.6$; df = 1, 2; $P < 0.05$).

These changes in weight and behavior paralleled the ability of larvae to undergo successful metamorphosis upon isolation. Fig. 4 shows the percentage of samples of isolated larvae that underwent successful molt to adulthood in relation to age, birth order, and larval density. These factors explained 85% of the variation in percentage successful adult molt. For most larval treatment groups, successful metamorphosis increased with age up to about 170 d, then declined again ($F = 3.59$; df = 4, 7; $P = 0.067$; Fig. 4). The early increase in successful metamorphosis paralleled the increase in larval body weight (Fig. 2) and was slower for larvae in high-density cultures, suggesting that larval weight may drive capacity for metamorphosis. Larval density accounted for 16% of the explained variation ($F = 6.01$; df = 1, 7; $P < 0.05$), and age accounted for 38%. Birth order did not have a significant effect.

Lack of successful metamorphosis took two forms. Either the isolated larva remained active throughout the 2-wk test period, or it died in the process of metamorphosis. Much of the mortality was associated with ecdysis, but some occurred during the pharate pupal or pupal stage. Death during metamorphosis largely accounted for the decline in successful metamorphosis in larvae older than 170 d (Fig. 4). In the high-density

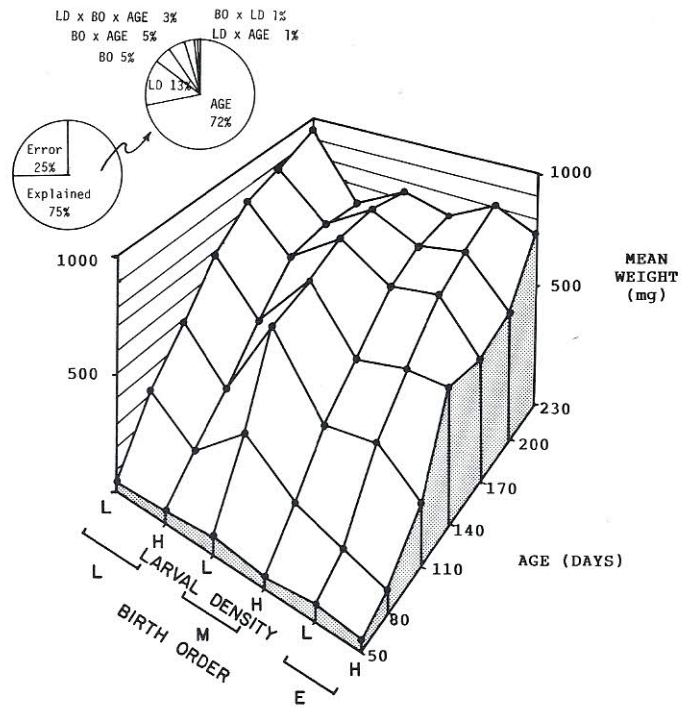

Fig. 2. Relationship between birth order, density of larval cultures, and weight of larvae. Pie charts show the percentage of the total variation that is explained by the factors and the percentage of the explained variation accounted for by each factor and interaction. $n = 750$.

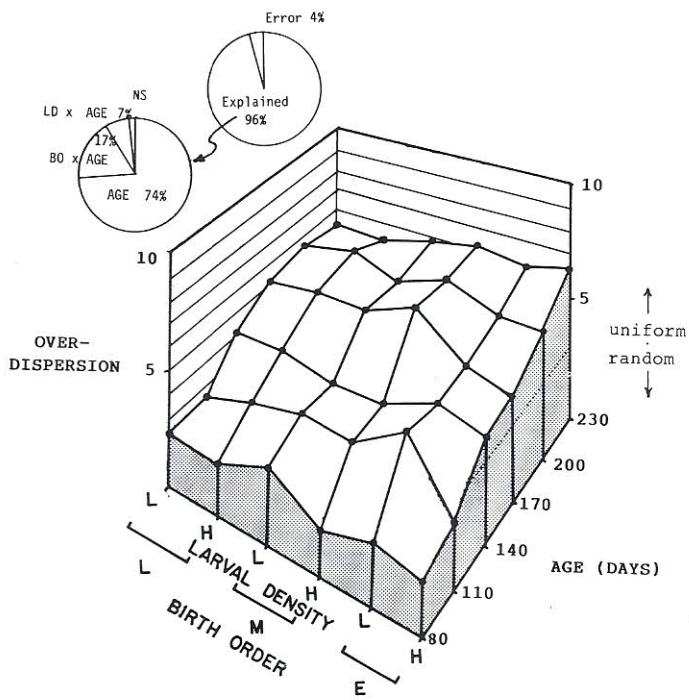

Fig. 3. Increase of the overdispersal response of larvae in relation to their age, the density of their culture, and their birth order. Overdispersion was estimated as the sum of the absolute values of the excess singly occupied chambers and the deficit of multiply occupied and unoccupied chambers (see text for details). Dotted horizontal line shows value above which disperion is significantly uniform. $n = 30$.

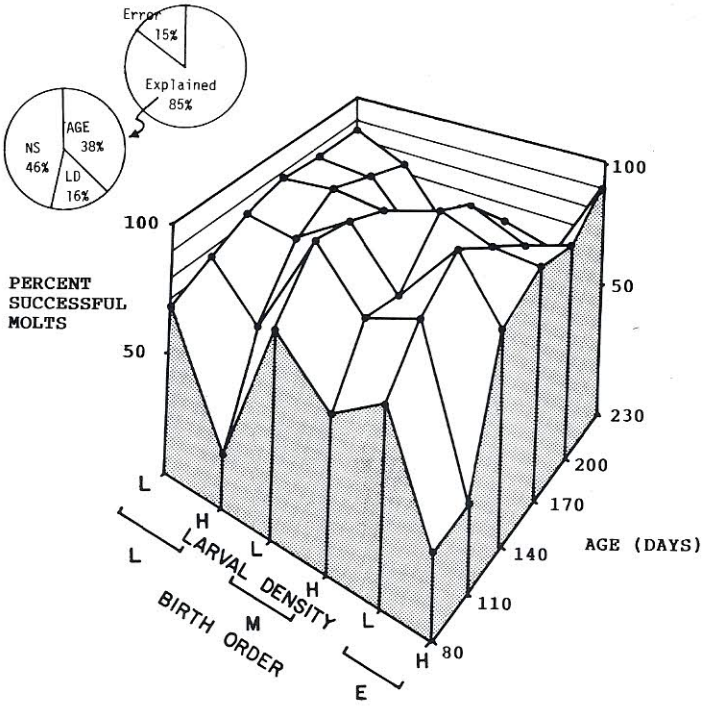

Fig. 4. Percentage of larvae successfully completing metamorphosis as a function of age, birth order, and larval density. As larvae age, an increasing proportion complete metamorphosis, but eventually the proportion declines again as a result of increasing mortality during metamorphosis. Other than larval age, only larval density has an effect. $n = 30$.

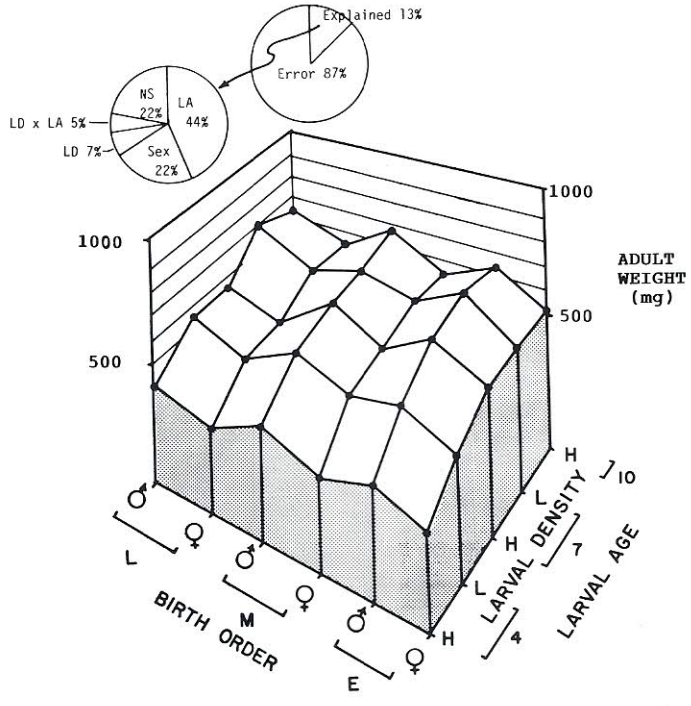

Fig. 5. Adult body weight as a function of sex, birth order, larval density, and larval age at pupation. Larval age and sex explain most of the variance, but larval density and its interaction with age also contribute. Males are always heavier than their female counterparts. Weight increases with age and decreases with larval density. $n = 750$ adults.

cultures, the proportion dying during metamorphosis increased to 10 to 35% during the two additional months of growth not shown in Fig. 4. Overall, larval age accounted for 68% of the explained variation ($F = 25.4$; df = 4, 7; $P < 0.001$), and its interaction with larval density ($F = 7.56$; df= 4, 7; $P < 0.01$) accounted for 20%. By itself, larval density accounted for only 3% ($F = 5.21$; df = 1, 7; $P = 0.05$).

On the other hand, early failure to pupate (Fig. 4) resulted when larvae remained active upon isolation, but later failure resulted from death during the process of pupation. This result suggested that larvae must attain some threshold weight to pupate and that they must do so before some age-related phenomenon interferes with their capacity to survive pupation. Oddly, the tendency to disperse (Fig. 3) was only weakly related to larval density, suggesting that it depends only on age and may not be strongly dependent on body weight. This result in turn suggests that larvae dispersing freely from low-density natural populations should be larger than those from high.

F_1 Adult Cohorts. From each of the six larval cultures, 200 to 400 larvae were isolated at 4, 7, and 10 mo of age ("larval-age-at-metamorphosis") to create the 15 F_1 adult cohorts (there were no 10-mo low-larval-density groups). The mean adult body weight of both sexes of these beetles is shown in Fig. 5 in relation to birth order, larval age at metamorphosis, and F_1 larval culture density. These factors explained 13% of the total variation. Adult body weight increased most strongly in relation to the age of larvae at metamorphosis (F =23.9; df = 2, 714; $P < 0.001$; 44% of explained variation). Males were consistently heavier than females, causing sex to account for 22% of the explained variation ($F = 24.0$; df = 1, 714; $P < 0.001$). Larvae from high-density cultures resulted in lighter adults, and this effect was much stronger for the 4-mo isolations, causing larval density ($F = 5.69$; df = 1, 714; $P < 0.02$) and its interaction with larval age ($F = 4.87$; df = 1, 714; $P < 0.05$) together to account for 12% of the explained variation. The patterns of adult weights in relation to larval age and larval density paralleled the pattern in larval weight in Fig. 2. The differences in weight between high- and low-density cultures were greater for both larvae and the resulting adults at 4 mo than at 7 mo (Figs. 2 and 5).

Reproduction by F_1 Cohort. The F_1 adults resulting from the isolation of larvae at 4, 7, and 10 mo were allowed to breed at either one pair per box or five pairs per box. The sum of the weekly egg counts over the life of each female gave the total eggs produced by each female. The complex response surface of Fig. 6 indicated not only that total eggs declined with birth order and adult density, but that there were complex interactions among several factors. Of the total variation, 44% was explained by the experimental factors, and 28% of this was accounted for by birth order ($F = 12.93$; df = 2, 120; $P < 0.001$), 11% by adult density ($F = 10.8$; df = 1, 120; $P < 0.001$), and 7% by larval age ($F = 3.17$; df = 2, 120; $P < 0.05$). The complex puckering in Fig. 6 was caused by the interactions of density, larval age, and birth order (AD × BO interaction; $F = 4.57$; df = 2, 120; $P < 0.02$); 10% of variation; LA × BO interaction, $F = 4.70$; df = 4, 120; $P < 0.001$; 3%). In general, the most fecund females were those of early birth order and metamorphosis. As both of these factors increased, there was a general decline in the total eggs produced per female. The two points for females from late-birth-order, high-density larval cultures 10-mo old at metamorphosis were higher than predicted by the rest of the response surface, contributing to the strong interaction terms.

The basic shape of the response surface of Fig. 6 was already apparent, though muted, by the time females were 12 wk old, before much mortality had occurred. Therefore, the variation was probably at least partially the result of differences in egg-laying rate, rather than longevity. Of the total eggs at 12 wk, 55% of the variation was explained by the independent factors, and of this, birth order accounted for 25% ($F = 18.1$; df = 2, 120; $P < 0.001$), adult density 19% ($F = 28.6$; df = 1, 120; $P < 0.001$), and larval age 15% ($F = 10.9$; df = 2, 120; $P < 0.001$). Birth order also interacted with larval age to account for an additional 16% ($F = 5.95$; df = 4, 120; $P < 0.001$).

The weekly collections of eggs were allowed to hatch on screens to reduce cannibalism by newly hatched larvae. The proportion of eggs that hatched (arcsine-square-root-transformed data) was consistently lower at high adult density ($F = 174$; df = 1, 120; $P < 0.001$), accounting for 67% of explained variation (Fig. 7). Other factors had significant but much smaller effects: percentage hatched increased with birth order ($F = 4.63$; df = 2, 120; $P < 0.02$; 5% of variation) and larval density ($F = 12.0$; df = 1, 120; $P < 0.001$; 5% of variation). The effects of larval density and adult density also depended upon the birth order, but these interactions together only accounted for 8% of the explained variation. The overwhelming effect of adult density, relative to other factors, gave the response surface in Fig. 7 its puckered appearance.

Because the effects of birth order and adult density on percentage hatched were the opposite of their effects on total eggs, the total larvae per female (the product of total eggs and proportion hatched) produced a more muted version of the response surface for total eggs (eggs, Fig. 6; larvae, Fig. 8). Total larvae per female showed a decline with increasing birth order ($F = 8.75$; df = 2, 120; $P < 0.001$; 23% of variation) and larval age ($F = 3.31$; df = 2, 120; $P < 0.05$; 9% of variation), as did total eggs. These two factors also interacted, accounting for an additional 25%

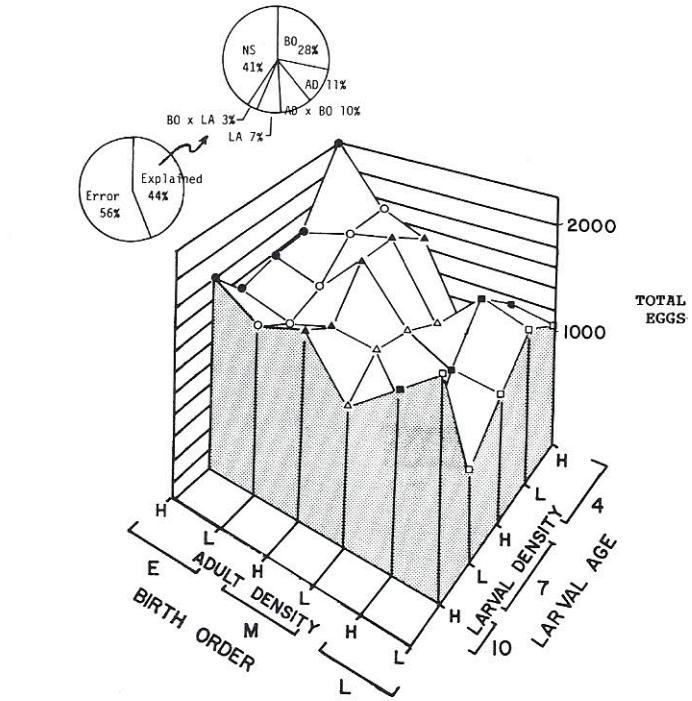

Fig. 6. Lifetime egg production by females in relation to birth order, adult breeding density, larval density, and larval age at pupation. Though the response surface is complex, total eggs declines with birth order and increases with adult density. n = 150 (boxes and pseudo boxes).

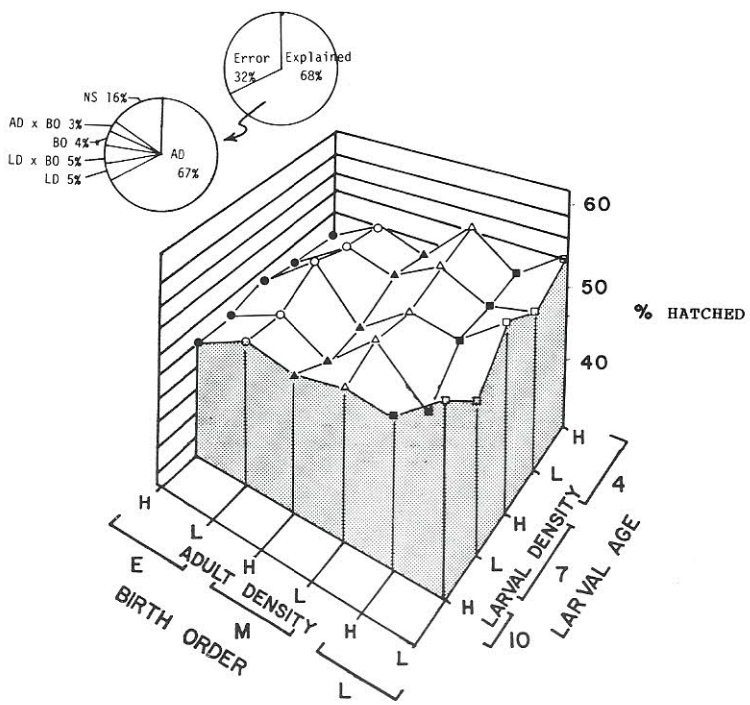

Fig. 7. Percentage of eggs hatching as a function of the experimental factors. Most of the variance is explained by adult density, perhaps linking it to copulation, but other factors also contribute significantly. n = 150.

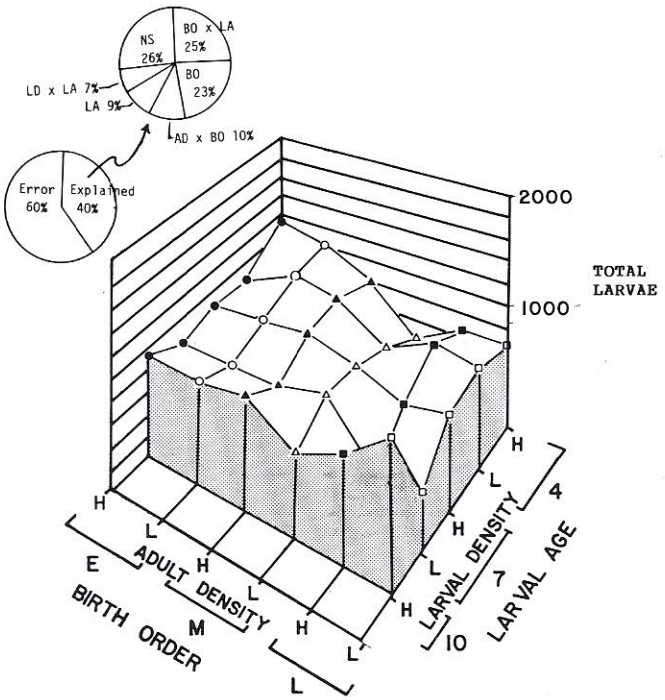

Fig. 8. Lifetime production of larvae as a function of the experimental factors. Birth order and its interactions with larval age and adult density explain the majority of the variance. This response surface is the product of the percentage hatched and the total eggs. $n = 150$.

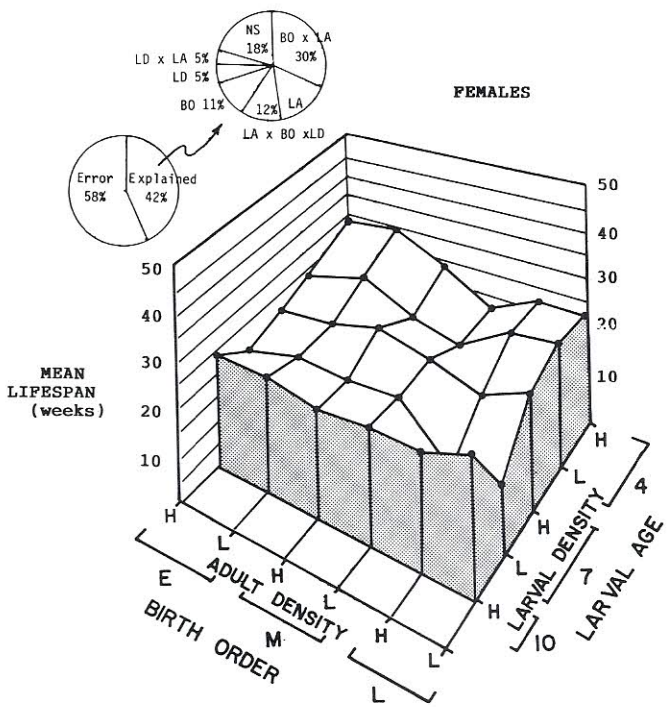

Fig. 9. Female life span as a function of the experimental factors. Female longevity declines with birth order and larval age but is not affected by adult density. The similarity of this response surface to that of Fig. 8 suggests that lifetime larval production is mostly explained by variation in female life span. $n = 750$.

of the explained variation ($F = 4.90$; df = 4, 120; $P < 0.001$). An adult density-by-birth-order interaction contributed 10% ($F = 3.80$; df = 2, 120; $P < 0.05$) and a larval-age-by-larval-density interaction 7% of variation ($F = 5.13$; df = 1, 120; $P < 0.05$). The large interaction terms gave the response surface its complex appearance.

The Role of Longevity. Through what intermediaries might the independent factors be exerting their effects upon fertility and fecundity of females? A clue surfaced when the mean female life span was plotted against the four independent factors, with the same arrangement on the horizontal axes. This response surface (Fig. 9) was very similar to that for total larvae (Fig. 8) and seems to be a more muted version of that for total eggs (Fig. 6). As in these two functions, much of the variation was accounted for by interactions between factors, as expected for the complex surfaces. For mean female life span, the independent factors accounted for 42% of the variation. Life span declined with larval age ($F = 7.95$; df = 2, 120; $P < 0.001$), accounting for 18% of the explained variation, but larval age acted differently according to birth order (BO × LA interaction, $F = 6.54$; df = 4, 120; $P < 0.001$, 30% of variation). Female life span also declined with birth order ($F = 4.74$; df = 2, 120; $P < 0.01$; 11% of explained variation). The remaining 22% of explained variation was accounted for by the larval density and its interactions with larval age and birth order ($F = 5.10$; df = 2, 120; $P < 0.01$).

Male longevity was greatly reduced by high adult density ($F = 662$; df = 1, 60; $P < 0.0001$), perhaps as a result of intermale competition (Fig. 10), giving the response surface its puckered appearance. Adult density accounted for 35% of the explained variation. Male longevity also declined with larval age at metamorphosis ($F = 22.1$; df = 2, 60; $P < 0.001$), accounting for 15% of the explained variation, but there was no birth-order-by-larval-age interaction in males. Male longevity showed a small decline with birth order (10% variation). Other factors, including interactions, accounted for the remainder of the variation. Overall, 25% of the total variation was explained by the independent factors.

For female fecundity (eggs) and fertility (larvae) (Figs. 6 and 8), the complex response surface was greatly simplified if total eggs was divided by the female life span, and the effects of life-span variation were thereby removed. Total eggs per life span (eggs per week, or egg-laying rate; females laid until they died) is shown in Fig. 11. The greatly simplified surface clearly showed that eggs per life span was higher at high adult density ($F = 36.7$; df = 1, 120; $P < 0.001$; 35% of explained variation), declined with birth order ($F = 15.6$; df = 2, 120; $P < 0.001$; 25% of variation), and increased with larval age ($F = 5.64$; df = 2, 120; $P < 0.005$; 11% of variation). The differences in the effects of larval age at different birth orders accounted for another 6% of the variation (AD × BO interaction; $F = 2.55$; df = 4, 120; $P < 0.05$). A total of 49% of the variation was explained by the independent factors.

The decline of the response surface of eggs per life span (Fig. 11) was in the direction opposite to that of proportion hatched (Fig. 7). Because the total larvae per life span was the product of eggs and proportion hatched, Fig. 12 (larvae per life span) showed an almost horizontal response surface, indicating relatively small effects of the treatment factors. Nevertheless, these factors still explained 38% of total variation. The effects of adult density seen in Figs. 7 and 11 were also opposing, so adult density had no significant main effect in Fig. 12. A decline of larvae per life span with increasing birth order ($F = 7.97$; df = 2, 120; $P < 0.001$; 22% of explained variation) remained, however, and was different for the larval ages and densities (LD × LA interaction, $F = 4.31$; df = 1, 120; $P < 0.05$; 16% of variation; AD × BO × LA interaction, $F = 2.62$; df = 4, 120; $P < 0.05$; 14%). Larval age also had a direct effect ($F = 4.52$; df = 2, 120; $P < 0.02$), as well as an interaction with larval density ($F = 4.31$; df = 1, 120; $P < 0.05$) (LA, 12%; LD × LA, 6%).

Another way to view these data on reproduction is to track the decline in the total amount of variation from total eggs to total larvae per life span. A convenient index of variability is the coefficient of variation (COV, SD/mean). For the grand mean of total eggs per female (Fig. 6), this COV was about 16%. This statistic declined to 13.4% for total larvae. For female life span, the factor that covaried so clearly with total eggs and larvae, the COV was 7.3%. Removal of the contribution of life span to the variation in reproduction resulted in a COV of 9.5% for eggs per life span and only 6.2% for larvae per life span.

Analysis of covariance (ANCOVA) confirmed these findings. When female life span was used as a covariate with total eggs, 78% of the explained variance (81% of total variance was explained) was accounted for by the covariate ($F = 409$; df = 1, 119; $P << 0.001$). The share of the variance explained by significant treatment factors dropped from 76% without a covariate to only about 16% ($F = 13.8$; df = 6, 119; $P < 0.001$) with life span as a covariate. In other words, most of the effect of the treatment factors on total eggs operated through their effect on life span. When female body weight was added as a second covariate with life span, the explained variance rose to 82%, of which life span accounted for 82% and body weight 4% ($F = 23.6$; df = 1, 119; $P < 0.001$), leaving the treatment factors to account for only 12% ($F = 2.43$; df = 6, 119; $P < 0.05$).

The same pattern was obtained for total larvae. As with total eggs, most (85%; $F = 358$; df = 1, 119; $P < 0.001$) of the effect of the treatment factors on total larvae operated through the effect

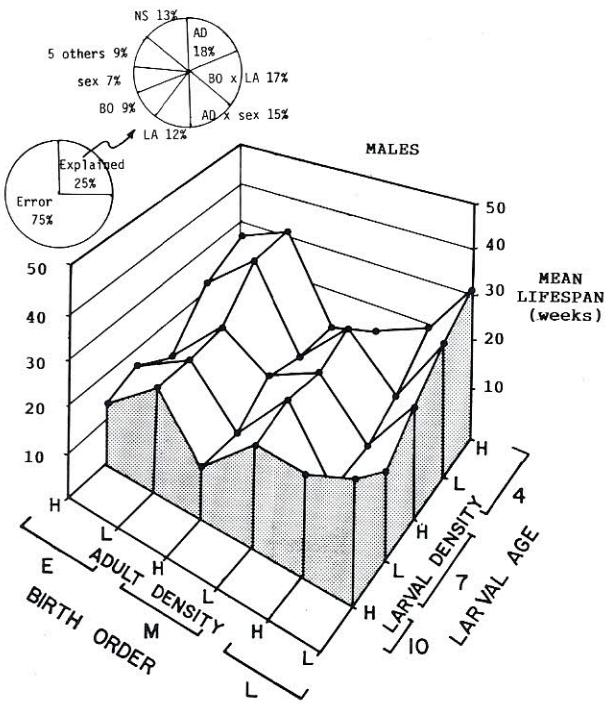

Fig. 10. Mean male life span as a function of the experimental factors. Male longevity declines with adult density, larval age, and birth order. Pie charts are from the ANOVA for both sexes together. $n = 750$.

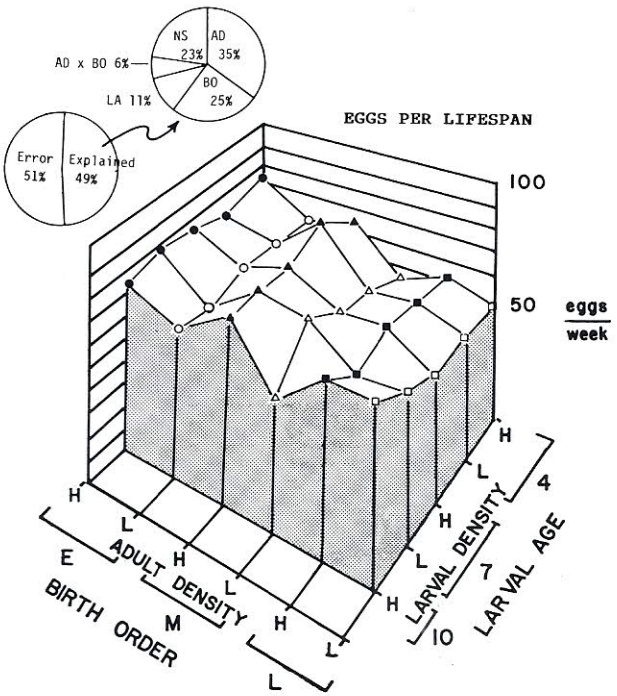

Fig. 11. Eggs per female lifetime as a function of the experimental factors. Lifetime egg-laying rate declines with birth order and increases with adult density. In this response surface, the effect of female life span has been effectively removed. Note the similarity of this estimate of egg-laying rate to that in Fig. 8. $n = 150$.

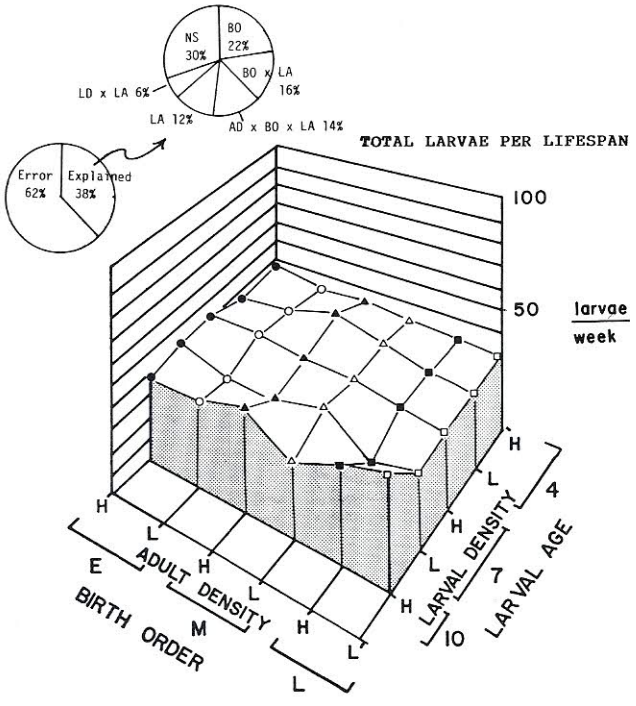

Fig. 12. Larvae per female lifetime as a function of the experimental factors. Most of the variance in Fig. 10 has been removed by adjustment for the variation in female life span, indicating that most of the variation in larval production results from variation in female longevity. The remaining variance is still largely explained by birth order and its interaction with larval age and adult density. n = 150.

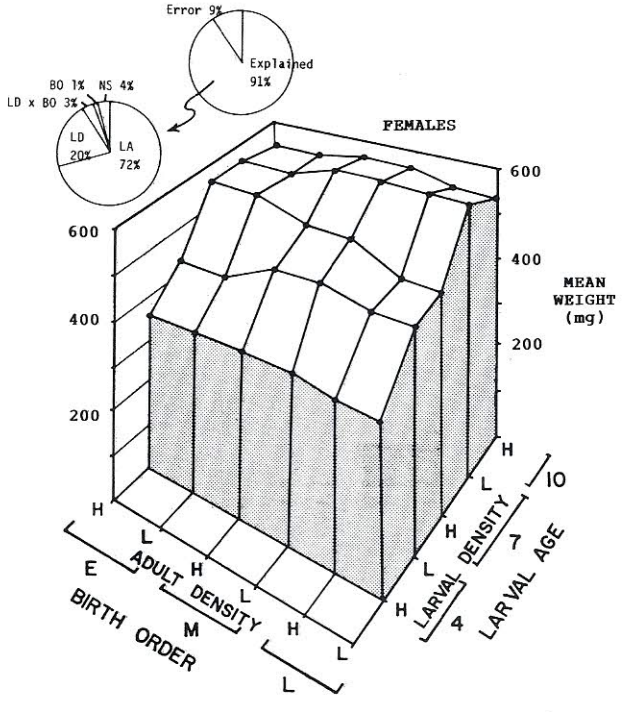

Fig. 13. Mean female body weight as a function of the experimental factors. The negative effect of larval density and the increase with larval age explain most of the variation. n = 30 mean values.

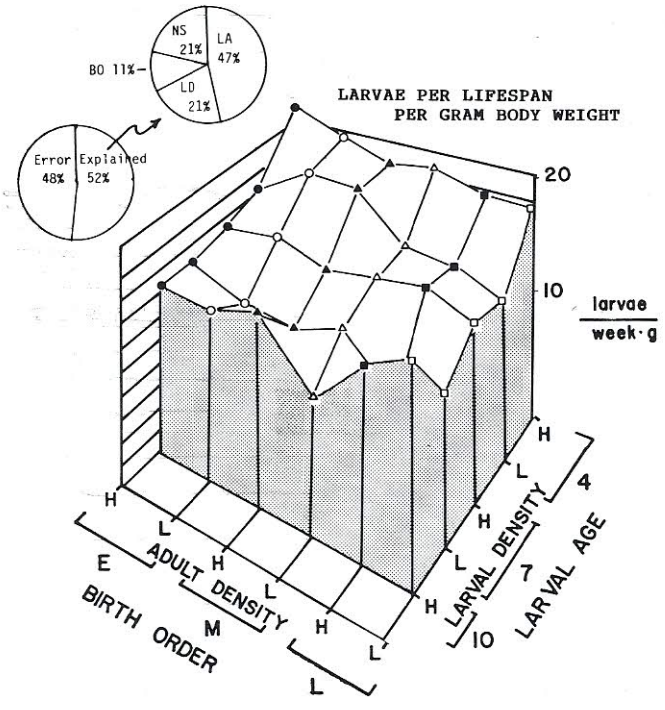

Fig. 14. Larvae per female lifetime per gram body weight as a function of the experimental factors. Because low larval age and high larval density produce smaller females, the production per gram is highest for the smallest, youngest females. This pattern is the opposite of that seen in most animals. Larval age and density explain most variance, but birth order contributes as well. $n = 150$.

of these factors on female life span. In both cases, female body weight made a small contribution ($F = 18.1$; df = 1, 119; $P < 0.001$) because the larger, more fecund females tended to be from the groups derived from older larvae. This finding was supported by an ANCOVA of total eggs per life span using female body weight as a covariate. A total of 48% of the variance was explained, of which body weight accounted for 15% ($F = 17.4$; df = 1, 121; $P < 0.001$). It is interesting that both larval age and its interaction with birth order, which together accounted for 20% of the explained variance without a covariate, fell below the level of significance when body weight was used as a covariate. In other words, larval age operated on total eggs per life span mostly through its effect on female body weight.

ANCOVA of life span revealed no factors with significant effects. The complexity of the relationship between the treatment factors and mean female life span (Fig. 9) must thus be the result of factors not tested in this study.

The Role of Female Body Weight. In many animals, fecundity increases with female body weight, so an analysis of *Z. atratus* female body weight and its relation to fecundity and fertility is of interest. Female body weight increased with larval age at metamorphosis ($F = 524$; df = 2, 120; $P < 0.001$) and decreased with larval density ($F = 298$; df= 1, 120; $P < 0.001$) (Fig. 13). More than 80% of the explained variance (91% of total) in mean female body weight was accounted for by larval age, and another 20% by larval density. No other factor accounted for >3%. The adult body weight of a female was thus related mostly to the length of the larval growth period and the rate of growth (Fig. 2). Birth order and its various interactions accounted for about 14% of the explained variance in larval growth, but only about 8% in the case of body weight. When the lifetime reproductive rate (total larvae per life span) was divided by the female body weight, the result was the larvae per week per gram of female body. This measure increased with larval age, decreased with birth order and larval density, and showed stronger dependence on the treatment factors (Fig. 14) than did larvae per life span. Of the total variance, the treatment factors explained 52%, of which larval density accounted for 21% ($F = 27.3$; df = 1, 120; $P < 0.001$), birth order 11% ($F = 7.05$; df = 2, 120; $P < 0.001$), and larval age 47% ($F = 30.1$; df = 2, 120; $P < 0.001$). This measure of productivity efficiency was thus mostly dependent upon the factors affecting larval growth and body size (LD, LA). There was only one significant interaction, a four-way one ($F = 3.13$; df = 2, 120; $P < 0.05$) accounting for only 5% of explained variance.

An analysis of total eggs per life span per gram female body weight showed similar results except that the effect of larval density was lower, that of birth order was higher, and adult density had a significant effect.

Perhaps because low position in the birth order and low larval age at pupation resulted in lower body weights but higher fecundity, a simple regression of total eggs on body weight was not significant ($R^2 < 1\%$). This situation is unlike that for many other animals, in which female body weight shows a positive relationship to fecundity. There was also no significant relationship between the egg-laying rate (eggs per week) and female body weight. On the other hand, there was a significant positive relationship between the total eggs and the female life span ($R^2 = 66\%$), like the effect of life span seen in a comparison of Figs. 6 and 11 or the ANOVA of total eggs with female life span as a covariate (see above). Female life span is also not related to body weight, as is true of other insects as well (Lawrence 1990, McLain et al. 1990). To achieve their effects on lifetime fecundity, the experimental factors operated largely through their effects on life span rather than those on bodyweight.

Growth of F_2 Larvae. The growth of the F_2 larvae was estimated from their weight at 14 wk of age. The data were analyzed by five-way ANOVA using the experimental factors plus the birth order within the F_2 generation (BO2). The number of larvae in each breeding box was used as a covariate to adjust for the effects of larval density. The relationship of larval growth to the factors was complex; the largest effects resulted from the two birth orders ($F = 54.8$ and 15.9, respectively; df = 2, 308 $P < 0.001$), larval age at pupation ($F = 71.5$; df = 2, 308; $P < 0.001$), and their interactions ($F = 20.3$; df = 4, 308; $P < 0.001$; 71% of total variation was explained). The two birth orders and their interactions accounted for 29% of the explained variation, larval age 19%, and larval age's interactions with the two birth orders 31% ($F = 11.4$ and 29.3, respectively; df = 4, 308; $P < 0.001$). Some patterns were strong: the lightest F_2 larvae were the early offspring of early F_1 larvae, suggesting that the effects of early birth order were additive across generations. As either birth order increased, larvae grew more rapidly up to a limit such that larvae late in both birth orders were not heavier than those late in only one. These birth-order effects would tend to reduce the weight difference (and perhaps the age at pupation) between early larvae and their late siblings. Is there perhaps some advantage to relative synchrony of a group of siblings?

The effects of F_1 larval age at pupation on F_2 larval growth were more complex. For early F_2 larvae, growth rate increased as their mother's age at pupation increased, but this trend reversed for late F_2 larvae. Middle F_2 show a mixed response. For the slower-growing early larvae, this growth-accelerating effect of mother's age at pupation would tend to make the offspring of later-pupated mothers catch up to those of earlier ones. Thus, both the effects of pupating later and those of being later in the birth order tend to be reduced by the consequent increase in larval growth rate.

A comparison of larval weight at 14 wk between F_1 and F_2 larvae confirmed similar patterns. In both generations, larval weight at 14 wk increased with birth order; the differences between both middle- and late-birth-order larvae were much smaller than between early and middle.

Discussion

As a female's own expectation of life and further reproduction (i.e., reproductive value in eggs, v_x) wanes, the quality of her offspring, as measured by the offspring's expected progeny at the beginning of their reproductive lives (v_o), declines. When females first began reproducing, 95% of the cohort was still alive, and the v_o of their earliest offspring was 1,700. At 15 wk, 45% of the P cohort were still alive, and the v_o of their offspring had decreased to 1,500 (88% of the v_o of their first offspring). At 21 wk, 15% of the mothers were still alive, and the v_o of their offspring had decreased to 1,260 (74%). Reproductive value was transferred to offspring, not at a constant rate, but in direct relation to the expectation of the mother's own survival and future reproduction. This asymmetric transfer in relation to birth order is shown in Fig. 15. In the absence of any effect of birth order, offspring of all three birth orders would have similar reproductive values throughout their reproductive lives (Fig. 15, bottom right). With the observed effect of birth order, however, offspring early in the birth order start with and maintain a higher reproductive value (v_x) than those of later birth orders (Fig. 15, top right). Especially for the latest birth order, this v_x is lower throughout life.

Decline of offspring quality with birth order has been reported for a number of species (Mousseau & Dingle 1991). Weighting reproductive investment in favor of early offspring should have important consequences for population dynamics. An allele promoting the birth-order effect would be expected to spread in a population as a result of the greater reproductive success of early offspring. The trade-offs that limit the continued selection for ever greater birth-order effects are unknown. The importance of this phenomenon may be related to competition for local and limited food resources. Early production of higher-quality offspring would lead those genotypes toward monopolization of the food mass. Begon & Parker (1986) analyzed a model for spe-

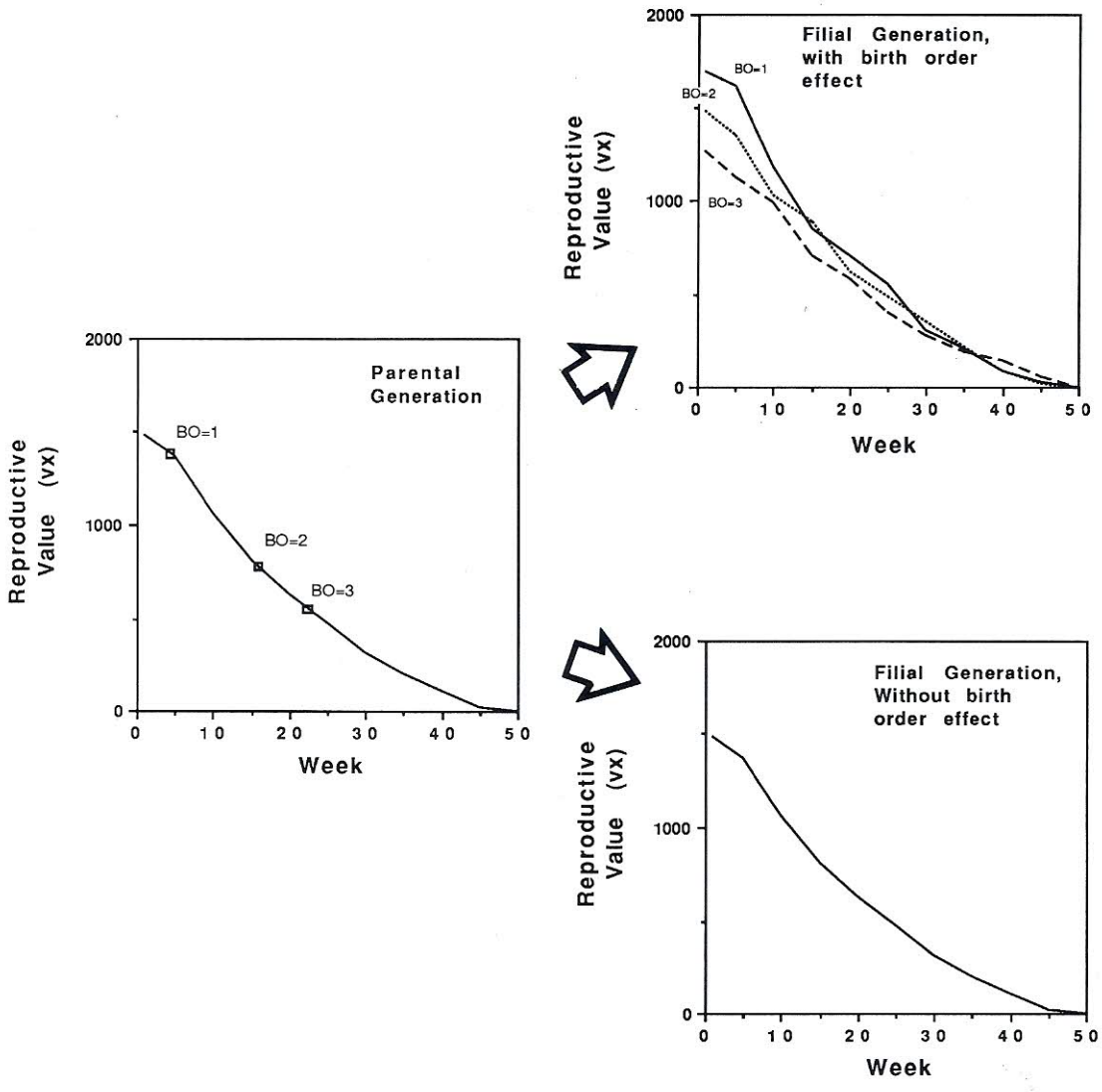

Fig. 15. The decline of reproductive value (v_x, eggs) in the presence and absence of a negative effect of birth order on reproduction. Calculations are based on weekly egg counts averaged for the three levels of birth order.

cies that amass resources before reproducing. When such females are subject to mortality during reproduction, their egg and clutch size (or both) should decline with maternal age, with associated declines in egg fitness. What is not clear from this experiment is whether offspring quality declined at a constant rate with time or was tied to the percentage of the life span lived (i.e., declined more slowly for long-lived than short-lived females). The birth-order effect was determined on the offspring of the P cohort, who, perhaps because of extreme crowding, lived much shorter lives than their offspring. For example, 50% of the P cohort had died by 14 wk, but 50% of their F_1 offspring had not died until 10 wk later. Whether the quality decline of the next generation would have followed that of their parents or would have been slowed by the greater longevity of their parents is unknown. If the decline occurs at a constant rate rather than being correlated with longevity, the last offspring of the F_1 generation would be of much lower quality than those of the P generation.

A possible alternate explanation for the observed effects is that females that lived longer produced a different phenotype of offspring and that the reported birth-order effects are simply the result of differential survival of the mothers, independent of any effect of birth order within the offspring of individual mothers. The experiment does not distinguish these alternates clearly for all characters. However, in both the F_1 and F_2 generations the largest difference in larval growth rate occurred between the first and

second birth orders. Although 45% of the F_1 adults had died by that time, there was very little mortality among the F_2 adults at the time the second-birth-order F_2 larvae were collected (10 wk). At least for larval growth, the effect appears to be related to birth order itself, not differential survival of mothers.

The effect of position in the birth order is programmed in the body of the mother, but, at least for the characters of this study, the program is not played out until her offspring have become adults (Mousseau & Dingle 1991). Only then does the influence of the mother's age become apparent in her offspring, almost a whole generation later. The mechanism is unknown. Maternal age increased growth rate in *Tribolium* larvae (Patterson et al.1983). Ludwig & Fiore (1960, 1961) found that larvae late in the birth order in *Tenebrio molitor* grew faster and pupated earlier, but the resulting adults did not differ in life span. Egg size and offspring fitness did not vary in relation to birth order and thus cannot explain its effects. Egg size and offspring fitness of *Callosobruchus maculatus* (F.) both decreased with parental age, but there was no evidence that egg size itself mediated the observed decrease (Wasserman & Asami 1985). In Z. *atratus*, perhaps maternal cytoplasmic factors transferred to the egg were responsible, but the experiment reported here confounded female and male age, so male or female nuclear factors cannot be ruled out.

The age at which a larva disperses for pupation has important effects on its reproductive future. A direct effect on age at first reproduction is obvious. Given nonzero heritability, as this variable increases, growth rate of the progeny population slows down. In addition, increased age at pupation directly affected reproductive potential of individuals; the highest potential was at intermediate larval age. Reproductive potential decreased monotonically with larval age in the main experiment, but, in a preliminary experiment, 4-mo-old larvae were considerably smaller. When these larvae were isolated for pupation, the resulting F_1 adults had only 20–50% the larval production of the older groups. Larvae of intermediate age had the highest fertility. In this reported experiment, however, larvae were fed a higher-quality food, so they had developed to or beyond the optimum within 4 mo.

Measurements of metamorphosing beetles collected near a natural population indicated a good deal of variation (350–750 mg) in the weight at which larvae disperse for pupation (Tschinkel 1981). Whether this variation resulted from variation in age at pupation, from growth rate, or from both is unknown. In my experiment, dispersion was measured as a group, not an individual, characteristic. As a group, larvae dispersed for pupation primarily in relation to their age, rather than their size. Had they been allowed to disperse at will, the result should have been adults whose weight was primarily a function of larval growth rate and factors that influence it.

Competition among larvae of many species commonly has a delayed effect on populations by reducing the fecundity of the resulting adults (Prout & McChesney [1985] and references therein). Delayed effects could in theory lead to several types of population fluctuations. It appears that Z. *atratus* responds somewhat differently to crowding. High larval density does depress growth rate, but without affecting the timing of dispersal (and presumably pupation). Although this pattern results in smaller adults, it has no effect on fecundity or fertility, both of which are unrelated to larval crowding. This lack of any delayed effect on subsequent reproduction is in striking contrast to the many examples in which such effects are present (Prout & McChesney 1985). The relationship of fecundity to body size is also absent in this species, showing that these two can be uncoupled. Rather, reproduction is related to birth order, adult crowding, and age at pupation.

Crowding in the adult stage had a positive effect on egg laying (fecundity) but a negative one on percentage hatch, so fertility was almost unrelated to adult density. In some species of *Tribolium*, fertility is completely independent of adult density (Park et al. 1961, Lloyd 1968, Young 1970). For many species of insects, fecundity is maximal at an intermediate density, perhaps as a result of the stimulatory effect of repeated mating (Watt 1960). This may be the case in Z. *atratus* as well. Adult crowding reduced longevity of males, but not females, suggesting that males compete with one another, a suggestion in line with the greater body weight of males.

Some effects of the experimental factors were opposed. The negative effect of birth order on fecundity tended to be counteracted by its positive effect on larval growth and percentage hatch. As a result, fertility was less strongly related to birth order than was fecundity. Similarly, the effects of birth order on larval growth in two sequential generations tended to level the differences created by birth order within one generation. Why these leveling effects should exist is unknown. An unexplored aspect of these phenomena is the effect of the experimental factors over several generations. Whether the delayed and direct effects accumulate, cancel, or fade over generations could have important consequences for population dynamics and cycles (Prout & McChesney 1985, Kirkpatrick & Lande 1989, Rossiter 1991). The effects of birth order, crowding, and larval age may also be conditioned by environmental input, but this point was not tested.

What might be the environmental conditions that have shaped the life history of Z. *atratus*?

Larvae exploit the abundant, localized resource provided by accumulations of bat guano but must, as a result, tolerate high densities and probably intense competition. Cannibalism of metamorphosing larvae probably removes competitors and provides a nutritional boost to the cannibal, but it can also lead to the inhibition of pupation by crowding and dispersal for pupation. Adults return to the guano to breed and can be present at substantial densities, making multiple mates possible. The body-size and life-span differences between males and females suggest that males compete for females. Why do early pupating females show the greatest reproductive success, and why do females produce their best offspring among their first clutches? It is tempting to ascribe these traits to the need to exploit a resource that is being replenished at a certain (perhaps variable) rate but exploited by a dense larval population. Females boosting their earliest larvae's performance would get a disproportionate share of these resources. But why not simply boost the early output of eggs? Perhaps the guano diet is not of sufficient quality to allow higher production rates.

The life habits of *Z. atratus* are strikingly like those of stored-product insects. Guano fills the role of stored product. This invites comparison to other stored-product insects, especially the flour beetles, *Tribolium* spp., which are also tenebrionid beetles. Experiments with flour beetles and *Z. atratus* are both carried out in the food medium in confining containers. Both seem capable of growing on a wide range of diets. The adults are rather long-lived, and the generations overlap. The eggs are laid and the larvae live and develop in the medium, where their chief mortality risk (at least in the laboratory) is cannibalism by larvae and adults. Cannibalism seems to have shaped the life history of these species in important ways.

Analysis of *Tribolium* population dynamics has been concerned much with the relative importance of reduced fecundity and cannibalism in population regulation (King & Dawson 1972). Percentage of eggs that hatch is not a prime regulator of population growth and equilibrium. The per-beetle loss of eggs to cannibalism by adults in a growing population tends to increase, thus decreasing the growth rate (Sonleiter 1961). Therefore, in populations dominated by cannibalism, equilibrium level is more strongly a function of cannibalism rate than of reproductive rate (Lloyd 1968, King & Dawson 1973). Once equilibrium has been reached, only enough pupae eclose to offset the loss of adult cannibals by normal mortality. This balance causes equilibrium level in *Tribolium* to be more closely related to cannibalism rate than to reproductive capacity.

Precise comparison of *Z. atratus* with *Tribolium* spp. is not yet possible. Under some conditions, maternal age increased larval growth rate in *Tribolium* (Patterson et al. 1983), as it did in *Z. atratus*. In *Z. atratus*, the importance of egg cannibalism, so dominant in *Tribolium*, is unknown. Pupal cannibalism in *Z. atratus* seems to have led to the evolution of the inhibition of pupation but may not play much role in population equilibrium as long as the population is not confined and pupation sites are not in short supply. Botella & Ménsua (1986) and Laskowski (1986) found that development time was much longer in confined *Tribolium* cultures than in those in which emigration was possible, a situation much like that in *Z. atratus*. Given the chance, larvae of *Tribolium* do emigrate before pupation (King & Dawson 1973, Jasieński et al. 1988), suggesting that the dominant role of pupal cannibalism in population dynamics may be an artifact of confinement. If it is, the primary difference between the two genera would be that *Z. atratus* fails to pupate under crowded conditions, whereas *Tribolium* eventually does and gets eaten. Although little is known about the "natural" habitat of *Tribolium*, *Z. atratus* is not yet a domesticated animal and could serve to illuminate the conditions under which their shared life-history characteristics evolved.

Acknowledgments

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