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Body size selection in *Acanthoscelides alboscuteatus* (Coleoptera: Bruchidae)

I. Entrapment within the fruit of *Ludwigia alternifolia* (Onagraceae)

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Summary. Direct observations and analyses of selection occurring in natural populations are rare. The biology of the bruchid beetle, *Acanthoscelides alboscuteatus*, on its host plant, *Ludwigia alternifolia*, provides an unusual opportunity to study the process of selection on the morphology of an organism under field conditions. *A. alboscuteatus* larvae mature within the variably dehiscent fruit of *L. alternifolia*. At eclosion, adults are confined within indehiscent fruit but are not confined within dehiscent fruit. Beetles can escape from indehiscent fruit only by forcing their bodies through the fruit's apical pore (a circular opening in the top of the fruit). Thus, during the eclosion stage of this beetle's life cycle the relationship between body size and differential fitness appears to be clearly defined.

We examined entrapment of *A. alboscuteatus* within indehiscent *L. alternifolia* fruit in a natural population. Only 8.8% of the beetles that attempted to escape were successful. Smaller beetles were trapped within a narrower range of pore diameters than were larger beetles; and trapped beetles had only limited abilities to enlarge fruit pore diameter. These data suggest (1) that escape from indehiscent fruit is regulated by the relationship between adult body diameter and fruit pore diameter and (2) that adult beetles may experience strong selection for small body diameter (size) within indehiscent fruit.

Key words: Natural selection – Body size – Plant-animal interactions

Few studies have provided adequate descriptions of the process of natural selection acting on the morphology of organisms under field conditions (Endler 1986). This deficiency arises, in part, because the mechanism(s) re-

sponsible for generating fitness differences among phenotypes is seldom obvious in natural populations. Here we begin our description of the mechanism of selection favoring small body size in the bruchid beetle, *Acanthoscelides alboscuteatus* (Horn). This mechanism involves the selective entrapment of adult *A. alboscuteatus* during eclosion within the fruit of *Ludwigia alternifolia* (Onagraceae). The interaction of *A. alboscuteatus* and *L. alternifolia* offers an unusual opportunity to study the selection process because both the prospective target of selection (the specific feature of the organism subjected to selection, i.e. adult body diameter) and the agent of selection (the feature of the organism's environment that leads to differential fitness, i.e. fruit architecture) are clearly identified.

Bruchid beetles are important seed predators of flowering plants in at least 33 plant families (Southgate 1979; Janzen 1980; Johnson 1981). Many bruchids use host plants having fruit that are partially to completely lignified at maturity and tardily dehiscent (Center and Johnson 1974). In addition, the seeds of many host plants are characterized by extremely hard seed coats (Janzen 1969). Lignification, indehiscence, and seed coat hardness present important evolutionary hurdles to bruchid infestation in that larvae must gain access to developing ovules or mature seeds and adult beetles must exit from hard-coated seeds and fruit (Janzen 1969; Center and Johnson 1974). Many bruchids exhibit complex behavioral, morphological, and life history adaptations, however, that enable them to partially or completely counter these host plant defenses (Janzen 1971; Pierre and Pimbert 1981; Jarry and Chacon 1983; Messina 1984; Thiery and Jarry 1985; Highland 1986).

The lignification and delayed dehiscence of *L. alternifolia* fruit present acute difficulties for *A. alboscuteatus* adults at eclosion. In contrast to the typical bruchid life history (see Center and Johnson 1974), *A. alboscuteatus* larvae do not construct windows (opercula) in the host plant's fruit through which adult beetles later exit fruit (Ott 1991). As a consequence, adults eclosing within indehiscent fruit are confined. Once confined, adult *A.*

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alboscutevellatus do not chew through the fruit wall but instead attempt to escape through the fruit's apical pore. This pore arises from abscission of the style and deterioration of subjacent tissue and opens as fruit mature (Raven 1963).

Observations of *A. alboscutevellatus* and *L. alternifolia* populations indicate that (1) fruit often remain indehiscent throughout the period of beetle eclosion, (2) the body diameter of adult beetles on average exceeds the pore diameter of fruit, and (3) those beetles that do not escape from indehiscent fruit die entrapped without reproducing (Ott 1990, 1991).

Here we describe the entrapment of adult *A. alboscutevellatus* within indehiscent *L. alternifolia* fruit in a natural population and provide estimates of (1) the distributions of body and pore diameters of beetles and fruit, (2) the ability of beetles confined within indehiscent fruit to enlarge the fruit's pore diameter, (3) the range of pore sizes within which beetles of each body size are trapped, and (4) the percent of beetles capable of escaping from indehiscent fruit. These data suggest a mechanism of selection: escape from indehiscent fruit is regulated by the relationship between beetle body diameter and fruit pore diameter. Given the distribution of beetle body and fruit pore diameters observed in natural populations, small beetles are more successful than larger beetles in escaping from indehiscent fruit. The pore diameter of *L. alternifolia* fruit may therefore act as a powerful agent of selection on *A. alboscutevellatus* adult body diameter (size), and correlated life history traits (Ott 1990) when beetles eclose within indehiscent fruit.

The study organisms

A. alboscutevellatus is a univoltine, host-specific seed predator of *L. alternifolia* (Hamilton 1892; Bridwell 1935; Bissell 1940; Ott 1991). *L. alternifolia* is a short-lived perennial, common to poorly drained seepage areas and is broadly distributed throughout the eastern United States (Raven and Tai 1979). The geographic range of *A. alboscutevellatus* is coincident with that of *L. alternifolia* (Johnson 1983).

The fruit of *L. alternifolia* is a four-sided capsule, three to six mm in width and four to six mm in depth. During the later stages of development, the walls of the two to three layers of cells immediately beneath the epidermis thicken and lignify, producing a hard woody fruit that remains attached to the plant (Eyde 1981). At maturity the above ground portion of the plant lignifies.

A. alboscutevellatus oviposits on the exterior of developing fruit during the summer months. Larvae bore into the fruit where they feed, develop, and pupate. Adult beetles begin overwintering in cocoons within fruit and eclose from these cocoons the following spring. Up to ten adults can mature within a single fruit.

As in other members of the genus *Ludwigia* (Peng and Tobe 1987), *L. alternifolia* fruit gradually dehisce (the top or one or more sides of the fruit dislodge) during the winter and spring following their maturation. As a result *A. alboscutevellatus* overwinter in two subpopulations. Beetles within indehiscent fruit overwinter in pro-

TECTED environments but may be confined within fruit at eclosion. When fruit dehisce prior to eclosion, beetles are not confined within fruit but encounter greater exposure to winter conditions (Ott 1990). Populations of *L. alternifolia* vary in the percent of fruit that remain indehiscent (range 3% to 58%) (Ott 1990). Additional details of the biology of *A. alboscutevellatus* and *L. alternifolia* are given in Ott (1991).

Methods

Documenting entrapment

To document entrapment of adult *A. alboscutevellatus* within indehiscent *L. alternifolia* fruit, all fruit were removed and examined from a sample of 18 mature plants collected in July of 1984 from a population located near Greenbelt, Maryland. These fruit represented the plant growth and beetle infestation of 1983. At the time of the census, any beetles that were capable of escaping had already done so, and all beetles remaining within fruit were dead.

Fruit were classified as being indehiscent, partially dehiscent, or completely dehiscent. Indehiscent and partially dehiscent fruit were examined for evidence of beetle infestation. Completely dehiscent fruit retained no evidence of infestation and so were not further examined. The number of overwintering cocoons and the number and location of beetles (inside versus outside the cocoon) were recorded for each fruit. Beetles inside cocoons were recorded as having died prior to eclosion from parasitism by either chalcid wasps or the mite, *Pyemotes tritici* (Ott 1991). For indehiscent fruit, beetles found outside cocoons were classified as trapped; if an empty cocoon was found and there was no evidence of parasitism, beetles were classified as having escaped.

For each trapped beetle, the length of each elytron was measured and the sex determined. Mean elytra length (EL) was used to predict each beetle's body diameter (BD), defined as the width of the thorax at its broadest point. Equations relating BD to EL were derived from an independent sample of beetles collected in the Greenbelt, Maryland area. For males, $BD = 0.30 + 0.031EL$ ($R^2 = 0.95$, $n = 197$, $p < 0.0001$); and for females, $BD = 0.005 + 0.032EL$ ($R^2 = 0.94$, $n = 190$, $p < 0.0001$) (Ott 1990).

To estimate the distribution of pore diameters in the population the pores of all indehiscent fruit containing cocoons were measured, and the minimum and maximum dimensions were averaged to yield the pore diameter. To estimate the ability of trapped beetles to enlarge fruit pore diameter, the distribution of pore diameters of fruit containing only beetles that were dead in their cocoons (an estimate of the distribution of pore diameters prior to any enlargement by trapped beetles) was compared to the distribution of pore diameters of fruit that contained trapped beetles. To verify the status of beetles classified as trapped, the body diameter of each presumptively trapped beetle was compared to the pore diameter of the fruit in which the beetle was found.

To estimate the distribution of body diameters of live adult beetles in the population, a sample of 119 beetles was collected from the flowers and foliage of *L. alternifolia* during July, 1984. The sex of each beetle was determined, and the beetle's body diameter was predicted based on its elytra length.

All measurements were made using a stereo dissecting microscope fitted with an ocular micrometer. Measurements of pore diameters and elytra lengths were recorded to the nearest ocular unit (0.0183 mm).

Results

Distribution and fates of beetles among fruit

A total of 2,942 fruit were examined from the sample of 18 plants. Thirty percent of these fruit were indeh-

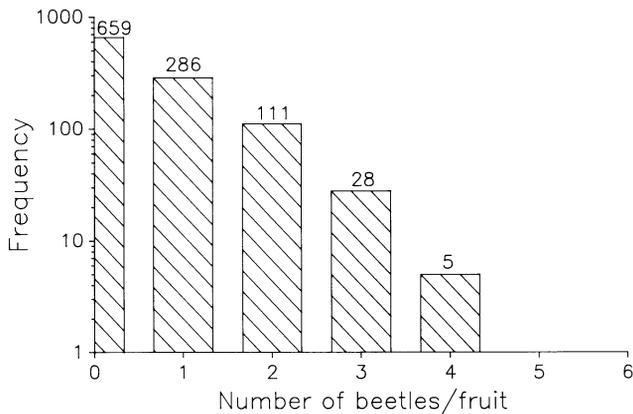


Fig. 1. The distribution of beetles among fruit. The presence of beetles in fruit was established by the presence of overwintering cocoons constructed by late instar larvae prior to parasitism by chalcid wasps and the mite, *Pyemotes tritici*. The numbers accompanying the bars are the observed frequencies

iscent and thus constituted potential traps for eclosing adults, 7% of fruit were partially dehiscent, and 63% of fruit were completely dehiscent.

Thirty-nine percent of the 1,089 partially dehiscent and indehiscent fruit contained evidence of infestation by *A. alboscuteatus*. A total of 612 beetles (based on the presence of overwintering cocoons) were distributed among these fruit (Fig. 1). An average of 1.4 beetles were present in those fruit that contained beetles. Within indehiscent fruit, which provide the most reliable information on the fates of beetles developing within them, 511 beetles were represented. Of these beetles, 217 (42%) died in their cocoons prior to eclosion as a result of parasitism. A total of 239 beetles (47%) survived through eclosion. An additional 55 adult beetles (11%) died within indehiscent fruit but their position with respect to the overwintering cocoon (within versus outside the cocoon) was ambiguous.

Documenting entrapment

Only 21 of the 239 beetles (8.8%) that eclosed within indehiscent fruit successfully escaped through the pores of these fruit. In virtually all observations in which a beetle was found trapped, the beetle's body diameter exceeded the pore diameter of the fruit (Fig. 2). These data demonstrate that (1) entrapment within indehiscent fruit is determined by the diameter of the beetle in relation to the diameter of the fruit's pore and (2) larger beetles are trapped within a wider range of fruit pore diameters than are smaller beetles. Mortality due to entrapment accounted for 44% of the overall mortality observed within indehiscent fruit. If the 55 beetles whose fates were ambiguous were actually trapped, then 21 of 294 beetles (7.1%) eclosing within indehiscent fruit escaped, and entrapment accounted for 63% of the mortality in indehiscent fruit. Similarly, if these beetles died prior to eclosion, then preeclosion mortality was 53%.

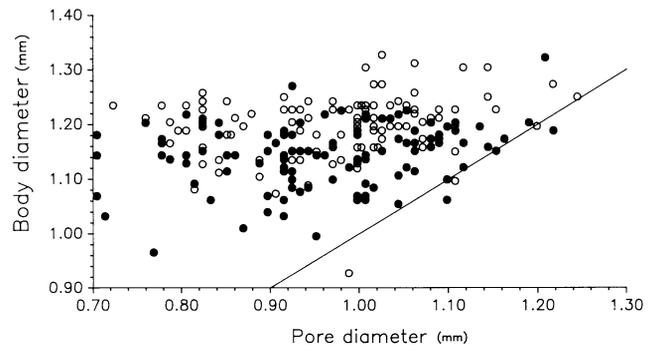


Fig. 2. The relationship between the body diameter of trapped beetles and the pore diameter of the fruit in which beetles were trapped. Males are represented by solid circles, $n=107$; females by open circles, $n=95$. The diagonal is the body-pore isodiametric line. Paired measurements of beetle body and fruit pore diameters were obtained for 202 of the 218 trapped beetles

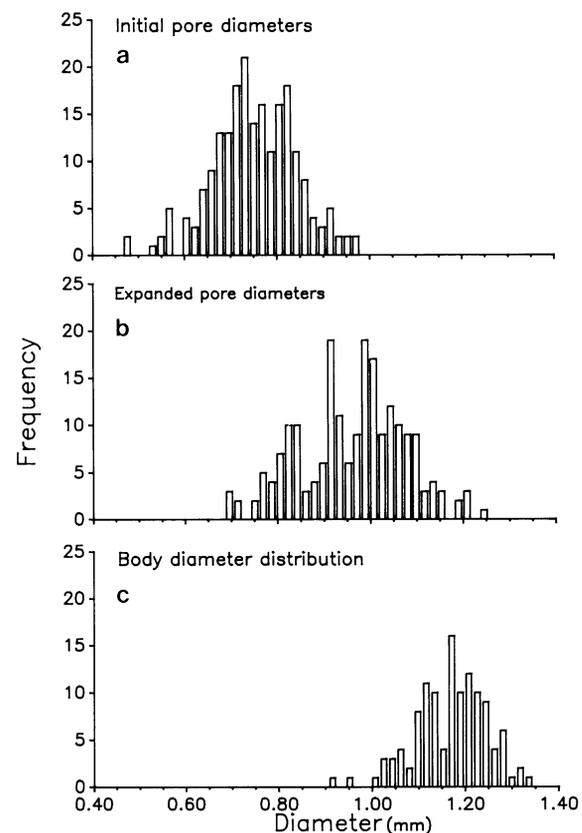


Fig. 3a-c. The distribution of fruit pore diameters prior to enlargement (a) and following enlargement by trapped beetles (b) in comparison to the distribution of adult beetle body diameters (c). Means ± 2 se and sample sizes are: (a) 0.76 ± 0.012 , $n=210$; (b) 0.97 ± 0.016 , $n=202$; (c) 1.17 ± 0.014 , $n=119$. The distribution of body diameters of the 119 live beetles provides a reasonable estimate of the preeclosion adult body diameter distribution because (1) the sample was composed primarily of beetles liberated by the dehiscence of 70% of the fruit in the population (an unbiased sample with respect to body diameter) and (2) the contribution of beetles that escaped from indehiscent fruit to this sample was negligible: only 30% of fruit were indehiscent and only 8.8% of beetles (potentially biased toward smaller beetles) escaped from indehiscent fruit

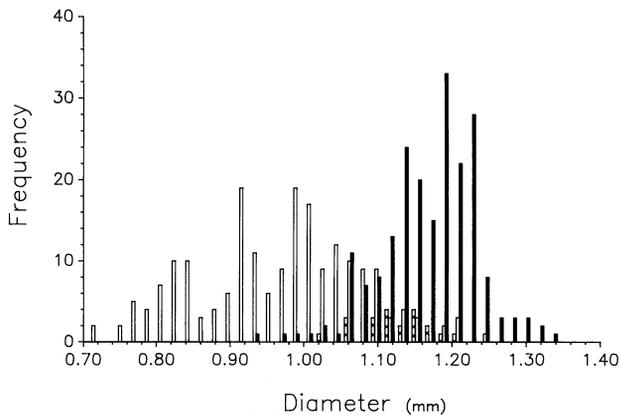


Fig. 4. The distributions of pore diameters of fruit that trapped beetles (*open bars*), fruit from which beetles escaped (*solid bars*) and the distribution of body diameters of trapped beetles (*hatched bars*). The means ± 2 se and sample sizes for the distributions are: trapped fruit 0.97 ± 0.016 , $n=202$; escaped fruit 1.12 ± 0.02 , $n=21$; trapped beetles 1.17 ± 0.009 , $n=208$. The distribution of fruit pore diameters from which beetles escaped (solid bars) provides an estimate of the distribution of body diameters of the beetles that escaped from indehiscent fruit (see text)

Distribution of pore and body diameters

In all fruit in which beetles had been trapped, the pore showed signs of abrasion and enlargement. The mean pore diameter of fruit containing trapped beetles was significantly greater than the mean pore diameter of fruit containing only beetles that had died prior to eclosion ($t=20.73$, $df=410$, $p<0.0001$, Fig. 3a, b) demonstrating that trapped beetles can enlarge pores.

Comparison of the distributions of live adult *A. alboscuteallatus* body diameters and *L. alternifolia* fruit pore diameters highlights the problem that adult beetles face at eclosion (Fig. 3a–c). The distribution of adult body diameters (Fig. 3c) displays only marginal overlap with the distribution of preeclosure (unmodified) pore diameters (Fig. 3a) and more, but still limited, overlap with the distribution of pore diameters following enlargement by trapped beetles (Fig. 3b). Average adult body diameter exceeded mean preeclosure pore diameter by 54% and exceeded the mean diameter of enlarged pores by 21%.

Selective entrapment hypothesis

The above results suggest that only those beetles with the smallest body diameters escaped from *L. alternifolia* fruit having the largest pore diameters. Two specific predictions follow: (1) the mean pore diameter of fruit from which beetles escaped should exceed the mean pore diameter of fruit that trapped beetles, and (2) the mean body diameter of trapped beetles should exceed the mean body diameter of escaped beetles.

Prediction one was tested by comparing the pore diameters of the 221 fruit that trapped beetles to the pore diameters of the 21 fruit from which beetles escaped. The mean pore diameter of fruit from which beetles es-

caped was significantly greater than the mean pore diameter of fruit that trapped beetles (t , adjusted for unequal variances, $=6.26$, $df=221$, $p<0.0001$, Fig. 4).

The second prediction cannot be tested directly since the body diameters of escaped beetles were unavailable. The body diameters of these beetles, however, can be estimated. The body and pore diameter coordinates of trapped beetles (Fig. 2) demonstrates that beetles are trapped when their body diameter exceeds the fruit's pore diameter. Consistent with this observation is the inference that beetles escape only when their body diameter is equal to or less than the fruit's pore diameter. The pore diameter of each fruit from which a beetle was judged to have escaped therefore represents the maximum possible body diameter of the beetle. Comparison of the body diameter distributions of escaped and trapped beetles supports the selective entrapment hypothesis: escaped beetles are on average smaller than trapped beetles ($t=3.08$, $df=227$, $p<0.002$, Fig. 4).

Discussion

Entrapment and mortality within fruit

This study demonstrates that adult *A. alboscuteallatus* that have eclosed within indehiscent *L. alternifolia* fruit can become trapped and die. Moreover, this study demonstrates that the phenomenon of entrapment occurs because the body diameter of some beetles exceeds the pore diameter of the fruit in which they eclose, and because the ability of beetles to enlarge the fruit pore diameter is limited.

The dilemma faced by *A. alboscuteallatus* eclosing within indehiscent fruit is apparent when the distributions of adult body diameter and fruit pore diameter are compared. This comparison shows that, on average, the body diameter of beetles exceeds the pore diameter of fruit. This pattern of limited overlap is corroborated by comparison of pore and body diameter distributions from multiple populations in the Greenbelt, Maryland area (Ott 1990). The marginal overlap of the distributions suggests that only a few percent of the beetles that eclose within indehiscent fruit should escape. For the sample of fruit examined in this study only 8.8% of beetles escaped from indehiscent fruit.

That 91% of beetles failed to escape from indehiscent fruit suggests that entrapment can be a major source of mortality among beetles within indehiscent fruit. Entrapment accounted for 44% to 63% of the overall mortality within indehiscent fruit, while preeclosure parasitism by chalcid wasps and the mite, *Pyemotes tritici* accounted for the remaining 42% to 53%. Entrapment may be a particularly important source of mortality because the extent of mortality due to entrapment will be governed strictly by the overlap of the body and pore diameter distributions and will not be affected by variation in the magnitude of other sources of preeclosure mortality. In a related series of experiments and simulations (Ott 1990) the contribution of entrapment to total mortality among beetles in both indehiscent and deh-

iscent fruit has been shown to be a function of (1) the ratio of indehiscent to dehiscent fruit, (2) differences in preeclosure mortality schedules of beetles overwintering within indehiscent fruit as opposed to overwintering in environments created by fruit dehiscence, and (3) the overlap of the beetle body and fruit pore diameter distributions.

Selective entrapment

Selection favoring beetles of small body diameter will occur when adult *A. alboscuteatus* eclose within indehiscent *L. alternifolia* fruit if escape from indehiscent fruit is selective with respect to body diameter. Four lines of evidence presented herein suggest that the probability of a beetle's escape from an indehiscent fruit should be a negative function of its body diameter. These lines of evidence are (1) the marginal overlap of the pore and body diameter distributions (Fig. 3a and c), (2) the relationship between the body diameter of trapped beetles and the pore diameter of the fruit in which the beetles had been trapped (Fig. 2), (3) the limited ability of trapped beetles to enlarge the fruit's pore diameter (Fig. 3a and b), and (4) the low success rate of beetles escaping from indehiscent fruit.

The selective entrapment hypothesis can be directly tested either by determining the range of pore diameters through which beetles of each body diameter class can and cannot escape or by establishing the functional relationship between body size and the proportion of beetles that escape from indehiscent fruit. While the present study provides data on the range of pore diameters in which beetles are trapped, the range of pore diameters through which beetles of each body size can escape can only be inferred. Moreover, the probability of escape from fruit cannot be established using the present data since by design beetles that escaped from fruit were not available. Two predictions of the selective entrapment hypothesis, however, were tested using data provided by the present study. The prediction that the mean pore diameter of fruit from which beetles escape should exceed the mean pore diameter of fruit that trap beetles, as well as the prediction that the mean body diameter of trapped beetles should exceed the mean body diameter of escaped beetles were supported. A direct test of the selective entrapment hypothesis and estimates of the intensity of selection for reduced body diameter (size) are presented in Ott (1990).

Escape behaviors

The fruit and seeds of many plants attacked by bruchids exhibit physical and chemical barriers to entry to and/or escape from the site of adult development (Janzen 1969; Center and Johnson 1974; Thiery 1984; Annis and O'Keefe 1984; Osborn et al. 1988). Most species of bruchids, however, seem to effectively counter the defenses presented by their host plant(s) (Center and Johnson 1974; Rosenthal et al. 1977; Messina 1984).

Given the disparity between body and pore diameter distributions observed in natural populations of *A. alboscuteatus* and *L. alternifolia*, the evolution of behavioral and morphological mechanisms enabling adult beetles to extricate themselves from indehiscent fruit might be expected. These expectations are only partially borne out by observations of trapped beetles in nature. When confined within fruit, beetles repeatedly force their bodies into the fruit's pore and chew the pore's margins (pers. obs.). The ability of beetles to enlarge the pore diameter is, however, clearly limited. Considered at the population level, the effect of the beetles' abilities to expand pores is to increase the degree of overlap between adult body and fruit pore diameter distributions. This behavior effectively increases the percent of beetles capable of escaping fruit (Ott 1990). The limited overlap of the distributions of beetle body and preeclosure fruit pore diameters suggests that if beetles could not expand pores, almost no beetles would escape from indehiscent fruit (Ott 1990).

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