BIOLOGICAL ACTIVITIES OF THE VETCH BRUCHID, *Bruchus brachialis* Fahraeus

By

Elvis Arnie Dickason

A THESIS

Submitted to the School for Advanced Graduate Studies
of Michigan State University of Agriculture and
Applied Science in partial fulfillment of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

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ABSTRACT

A study of the biological activities of the vetch bruchid, Bruchus brachialis Fahraeus, was conducted in Michigan in 1956, and in Oregon in 1957 and 1958. In addition, an attempt was made to clarify the problem involved in the correct nomenclature for the seed beetles. The family name Bruchidae and generic name Bruchus are accepted and defended, although strict adherence to the International Code of Zoological Nomenclature apparently would not permit the use of any of the commonly accepted names, Bruchus, Mylabris, or Laria.

Adults were found to overwinter in vetch seed storage facilities, and in the moss on oak trees. Males entered vetch fields approximately one month before pods appeared, and a sex ratio of 1:1 was found prior to the appearance of vetch pods. Mating occurred from the first flowering of vetch until males were no longer present in vetch fields. An attempt was made, through adult dissections and cage experiments, to determine the biotic potential of the species.

The incubation period of the egg stage varied from 12 to 18 days. The activities of the four larval instars within the vetch seed are discussed. These stadia, collectively, required from 45 to 67 days, and the pupal stage 9 days. Thus, from egg to adult required from 55 to

91 days, with an average of 72 days.

A life table, and mortality factors, are presented for the immature stages of the vetch bruchid. Although several mortality factors are presented, approximately three-fourths of the mortality resulted from eggs being lost from the pod, failure of first instar larvae to enter a seed, and mortality of larvae within a seed. This latter is to be expected, because several larvae enter a seed and only one adult can be produced per seed.

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INTRODUCTION

The vetch bruchid, Bruchus brachialis Fahraeus, is an insect pest of European origin that was first found in the United States in 1930 (Bridwell and Bottimer 1933). Since that date it has become distributed throughout most of the areas of the United States producing vetch seed (U.S.D.A. 1956). It is generally believed to have been transported from one area (or country) to another in infested vetch seeds. It is principally a pest of hairy vetch, Vicia villosa Roth, although it attacks woolypod vetch, V. dasycarpa Ten., and at times other vetches and commercial lentils. In areas where it has become established, the vetch bruchid is usually considered one of the major insect pests of vetch seed production.

Since the insect is so widespread in the United States, and because of the economic importance of the insect to vetch seed production, a study of the biological activities of the vetch bruchid was undertaken. The investigations reported herein were initiated in 1956 in Michigan, and concluded during 1957 and 1958 in Oregon.

During the course of these investigations major attention was given to evaluating those activities not previously reported in detail by other workers. As a result of this particular research, a life table was established wherein mortality factors were evaluated for each of the immature

stages, from egg to emerging adult.

A discussion of the nomenclatorial controversy over the correct generic name (Bruchus, Mylabris, or Laria), and the correct family name (Bruchidae, Mylabridae, or Lariidae), for the seed beetles is essential to an understanding of the nomenclature accepted in this thesis.

REVIEW OF LITERATURE

The vetch bruchid was described as Bruchus brachialis by Fahraeus in 1839 (Schoenherr 1839). Insects, which were later shown to be synonyms of the species, were described by Mulsant and Rey (1858), Mulsant (1858), and Allard (1867-8): and generic changes for the species were first proposed by Baudi (1886) to Mylabris, and Bedel (1889-1901) to Laria. A controversy exists today over the choice of the proper generic names (Bruchus, Mylabris, or Laria), and the proper family name (Bruchidae, Mylabridae, or Lariidae) for the seed beetles. The literature concerning this controversy is too involved to present in this review of literature, but is discussed in the section on Nomenclatorial Controversy.

The world distribution of the species was summarized by Pinckney (1937) and the U. S. distribution by the United States Department of Agriculture (1956).

There are two records of the vetch bruchid infesting seeds of a plant outside of the genus Vicia, the true vetches (Zacher 1936 and Schopp 1953). The common hosts for the larval stages are Vicia villosa and V. dasycarpa, although the susceptibility or resistance of other vetches was evaluated by Bridwell and Bottimer (1933), Pinckney (1937), Pinckney and Stitt (1941), Weimer and Bissel (1942) and Rockwood et al (1946). Seed analysts (Wertman 1951 and Pierpoint 1952) have attempted to classify bruchid injured

seed.

Various aspects of biological activities have been described by several workers. Adult overwintering was discussed by Rockwood et al (1946) and Steinhauer (1955). The egg stage was described by Bridwell and Bottimer (1933), Pinckney (1937), Steinhauer (1955), and Randolph and Gillespie (1958). These writers all consider the biology or life history of the insect in a general way, and some workers consider certain phases in detail. Experiments to determine the biotic potential of female bruchids were conducted by Steinhauer (1955) and Randolph and Gillespie(1958). Incubation period of the egg stage and temperature relationships were studied by Steinhauer (1955).

The activities of larvae within the vetch seed have received very little attention. Bridwell and Bottimer (1933) determined there were four larval instars, and Steinhauer (1955) and Randolph and Gillespie (1958) confirmed this by larval head capsule measurements.

The larval stages were first described by Pinckney (1937), and Bridwell and Bottimer (1933) have given the most complete description of the adult stage. These two references give accounts of parasitic insect species reared from vetch bruchids.

METHODS AND MATERIALS

Field Procedure

Observations of the activities of the vetch bruchid and its various life stages under natural conditions in hairy vetch fields was the primary procedure followed in this study.

Adult populations were sampled and collected by sweeping vetch plants with a standard 15-inch insect net.

All plant material was collected by carefully placing the entire above-ground portion of the plant in individual boxes for later sub-sampling of the desired materials. This procedure was necessary to prevent loss of insect eggs from vetch pods during sampling and subsequent handling. Samples of vetch pods for vetch bruchid mortality studies were taken immediately following the maturity of pods in the field, and prior to dehiscence of the most mature pods.

Laboratory Procedure

During the 1957 season adults were maintained in cages in an insectary. The insects did not live under caged conditions in the insectary any longer than they did under caged conditions (out of direct sunlight) in the laboratory. For this reason, all of the 1958 cage studies were conducted in the laboratory where the insects could be kept under closer

and more constant observation.

Adults were confined in petri dishes, or in cages constructed by capping glass lamp chimneys with a double layer of cheesecloth. In either type of cage, the plant material was maintained in a fresh condition by wrapping the stem with cellucotton and forcing it into a shell vial filled with water. In the oviposition experiments a single pod (usually the basal pod on the raceme) with a short section of stem and adjacent leaf was placed in each cage with the adult. For these experiments pods of uniform maturity were selected and all field-laid eggs were removed.

Harvested seed samples for rearing studies of the vetch bruchid (and parasite) were maintained in pint, or one-half pint, cardboard cartons.

Material used for the mortality studies of the immature stages of the vetch bruchid was collected in the field and returned to the laboratory for examination. Each pod was examined under a microscope (40X) and the number and condition of the eggs (lost from pod, sterile, embryo dead, eaten by female bruchid, or hatched), and the number of larval entrance holes into the pod were recorded. The seeds were harvested, examined under a microscope, and the number and position of larval entrance holes (hilum or side of seed) recorded. These seeds were kept separate in individual paper envelopes and retained for adult emergence.

Field collected material was used in almost all dissections.

Early instar larvae were easily dissected from the soft immature seeds. Later instar larvae and pupae were dissected from hardened seeds after softening the seeds for ten minutes in boiling water. This procedure prevented crushing the insect stages during dissection, and permitted a study of the pattern and extent of feeding within the hardened seeds.

All measurements were made under a dissecting microscope (20X or 40X) with a callibrated micrometer disc in the eyepiece.

Locations of Study

The 1956 study was conducted on material collected from a hairy vetch field near East Lansing, Michigan. The 1957 and 1958 phases were conducted in hairy vetch fields near Corvallis, Oregon. All observations and collections were made in fields where no insecticidal control practices were followed.

Identification of Insects

Confirmation of identification of Michigan and Oregon collected material as Bruchus brachialis Fahraeus was made by the Insect Identification and Parasite Introduction Laboratories, U.S.D.A., Beltsville, Maryland. This agency also identified the parasites reared from the Michigan collected bruchids

as Bruchobius mayri (Masi.), a member of the family Pteromalidae (superfamily Chalcidoidea) and order Hymenoptera. The Insect Pathology Laboratories, U.S.D.A., Beltsville, Maryland, identified the fungus attacking some of the vetch bruchids as an Entomopthorales.

DATA AND DISCUSSION

Systematic Position

The insect was originally described by Fahraeus in 1839 as Bruchus brachialis from specimens collected in France (Schoenherr 1839, p. 79).

The male of the species was described in two separate publications by Mulsant in 1858 as Bruchus pallidicornis. The correct reference for the description is questionable. Mulsant (1858) described the species in Opuscules Entomologiques, and Mulsant and Rey (1858) described it in Memoires de L'acadamie Imperiale des Science, Belles-Lettres et Arts de Lyon. There is no way of determining which publication has priority, or why Mulsant chose to publish the same article in two periodicals, or why Rey was included in one and not the other. The first workers to place B. pallidicornis in synonomy cited Mulsant as the author of the species (Allard 1867-8, Baudi 1886, Bedel 1889-1901), but some of the later publications (most recently, Bridwell and Bottimer 1933) cite B. pallidicornis Mulsant and Rey. Further, they not only cite Mulsant and Rey, but they also cite the Opuscules Entomologiques reference. There was no explanation given for including both authors under the Opuscules Entomologiques reference. The earliest reference found which cites both authors (Mulsant and Rey) under Opuscules Entomologiques was Hagen's Bibliotheca Entomologica (1862, p. 562), and possibly

subsequent workers have cited from this well-known publication.

Allard (1867-8, pp. 103-4) renamed Bruchus pallidicornis Mulsant as B. ruficornis, stating the name B. pallidicornis was occupied by a species (presumably a homonym) of Schoenherr's. According to Perris (1876, p. 237), Allard later acknowledged to him B. ruficornis Allard was the male of B. brachialis Fahraeus.

Baudi (1886a, p. 16, 1886b, p. 393), for nomenclatural reasons, changed the name to Mylabris brachialis Fahraeus= ruficornis All., pallidicornis Muls. Baudi unexplainably published the same article in two periodicals in the same year; one in Italian in a Sicilian periodical (1886a) and one in Latin in a German periodical (1886b). According to the Zoological Record for 1886 (Sharp 1888, p. 4), the Italian (Baudi 1886a) article has priority.

Bedel (1889-1901, p. 357) changed the generic name to Laria and recognized the synonomy outlined by Baudi. Other than these questionable changes in the choice of generic names, the original name of the species has not been placed in synonomy.

In this thesis the species is recognized as Bruchus brachialis Fahraeus, a member of the family Bruchidae and order Coleoptera.

Nomenclatorial Controversy:

A summary of the nomenclatorial controversy is essential

to an understanding of the choice of nomenclature accepted for this thesis. There is considerable controversy, and very little agreement, among entomologists as to the proper generic and family names for the group of insects commonly called seed beetles. They have been referred to under the family names Bruchidae, Mylabridae, or Lariidae; and accordingly, under the generic names Bruchus, Mylabris, or Laria.

According to Neave's Nomenclator Zoologicus (1939a, 1939b, and 1940) the history of these genera is as follows:

Bruchus
(as summarized by Neave, 1939a, vol. 1, p. 491)

Geoffroy 1762, Hist. Insect Paris, I. 163.
Mueller 1764, Fauna Ins. Fridrichsdal., XV- Col. (Ptinid).
Linnaeus 1767, Syst. Nat. ed. 12, 604- Col. (Bruchid).

Laria
(as summarized by Neave, 1939b, vol. 2, P. 869)

Scopoli 1763, Ent. Carn., 21,- Col.
Schrank 1802, F. Boica, 2(2) 150.- Lep.
Gray 1867, Ann. Mag. Nat. Hist. (3) 20, 276- Mamm.

Mylabris
(as summarized by Neave, 1940, Vol. 3, p. 239)

Geoffroy 1762, Hist. Insect Paris, I, 266.
Mueller 1764, Fauna Ins. Fridrichsdal., XIV- Col (Bruchid).
Fabricius 1775, Syst. Ent., 261- Col. (Meloid).

The name Bruchus was adopted by early workers as a result of the use of this generic name by Linnaeus in 1767. According to Bridwell (1946), Bruchus was first used by Baeckner in 1752 to describe two bruchids. Bridwell points out that Opinion 5 of the International Commission of Zoological Nomenclature states that names prior to 1758,

which are cited in synonomy in 1758 or later, are not available; and that Linnaeus treating the pea weevil in the genus Dermestes in 1758 places Bruchus in synonomy and it is no longer available.

The use of Bruchus Mueller in 1764 was in reference to the family Ptinidae, but this genus of spider beetles is referred to as Ptinus at the present time.

The use of Bruchus Geoffroy in 1762 is invalid because Geoffroy's 1762 publication is included in the Official Index of Rejected and Invalid Works in Zoological Nomenclature (1958). The publication was rejected by Opinion 228 of the Commission because the author failed to follow principles of binomial nomenclature (International Commission of Zoological Nomenclature 1954).

The change to Mylabris was based on the 1762 publication of Geoffroy. As mentioned in the previous paragraph, this publication has been declared invalid, thus invalidating the name Mylabris Geoffroy. Prior to this action of the Commission, some concern had been expressed over the validity of Mylabris Geoffroy because the author did not designate a genotype. An exception to the origin of the use of Mylabris in relation to seed beetles was noted. Leng (1920, p. 304) uses Mylabris Mueller in his Catalogue of Coleoptera. However, Blackwelder (1948, p. 44) in the Fifth Supplement to the Leng Catalogue of Coleoptera cites Mylabris Geoffroy.

Since Geoffroy's 1762 genera are not available, the

1763 publication of Laria by Scopoli has priority. Some entomologists accept Laria Scopoli and the family name Lariidae. However, Bridwell (1932) designated Laria dulcamarae Scopoli=Pria dulcamarae auctorum as the genotype for a genus of Nitidulidae. This designation by Bridwell has been accepted (Barber 1942, p. 9), thus making Laria a genus in the family Nitidulidae and the name is no longer available for Bruchidae.

According to the rules of zoological nomenclature it is doubtful if any of these generic names are available. Bridwell (1946) suggests the International Commission of Zoological Nomenclature could invoke the plenary power to suspend the rules and arbitrarily validate Bruchus Linnaeus as of 1758. A review of available publications of the International Commission of Zoological Nomenclature did not reveal any request in reference to Bruchus, Mylabris or Laria. A ruling by the Commission offers the only valid solution to the nomenclatorial problem.

As mentioned earlier, Bruchus and Bruchidae are the designations chosen for this thesis. These are the designations approved by the Entomological Society of America in their list of approved common names of insects (1955, p. 18, 32). However, this list has no official standing outside of the Entomological Society of America, and entomologists are not obligated to follow this nomenclature unless publishing in the Journal of Economic Entomology. It is the designation

used by the Insect Identification and Parasite Introduction Laboratories, U.S.D.A., because specimens sent in for identification during the present study were identified as Bruchus brachialis Fahraeus. The effect has been that the majority of American writings in recent years have used Bruchus and Bruchidae. European writers have, for the most part, considered Laria as the generic name, but Mukerji and Chatterjee (1951) published under Bruchus at the suggestion of the Director, Commonwealth Institute of Entomology, London.

Mayr, Linsley, and Usinger (1953, pp. 212-20) attach considerable importance to usage as a criterion in acceptance of names in their text on Methods and Principles of Systematic Zoology. Their attitude is that the majority of modern systematic zoologists are quite conservative in suggesting changes in well-known names. Usage is an important factor in nomenclature because it tends to establish stability, and strict application of priority frequently results in greater confusion than uniformity.

Bradley (1946) published a paper with "Mylabridae seu Bruchidae" in the title, with the explanation that the use of Bruchus or Bruchidae had not been validated. However, in personal correspondence (Sept. 6, 1957) Dr. Bradley suggested that Bruchus and Bruchidae could be used in this thesis because the present attitude and ruling of the International Commission of Zoological Nomenclature is that names of long

and almost universal usage should not be disturbed until the Commission has ruled upon them.

The most recent textbook in the field of entomology presents a nomenclature quite different from that presented in this thesis. Essig (1958, pp. 482-487) gives the family name as Lariidae, Lariidae Mylabridae (Bruchidae). Obviously the author considers Bruchidae a synonym of Lariidae, but the combination of Lariidae Mylabridae is unexplainable. Although the text does not list the vetch bruchid, a generic approach to the nomenclature of the seed beetles is presented that differs from any previously found. For example, the pea weevil is cited as Mylabris pisorum (Linn.)(Bruchus, Laria) and the broad bean weevil as Laria rufimanus (Boheman) (Bruchus, Mylabris). This approach is unexplainable because pisorum and rufimanus are congeneric species. Hence, in spite of this different approach in recent American literature, the use of Bruchus and Bruchidae is maintained in this thesis for previously stated reasons.

Distribution

The vetch bruchid is believed to be a native European species (Zacher 1936). No recent literature was found on world distribution, but Pinckney (1937) summarized the world distribution, from literature and records of vetch bruchids found in shipments of vetch, as follows: Algeria, Asia Minor, Austria, Czechoslovakia, France, Germany, Italy, Hungary, Palestine, Poland, Spain, and the United States. Because of the ease with which this insect can be transported in vetch seed, this known distribution is undoubtedly incomplete.

The vetch bruchid was first found in North America in 1930 at Haddon Heights, New Jersey (Bridwell and Bottimer 1933). The insect was undoubtedly introduced in shipments of vetch seeds from abroad. Since this original recovery the vetch bruchid has spread into many of the vetch growing areas of the United States. The following U. S. distribution, computed by the Economic Insect Survey Section (U.S.D.A. 1956), is based on reports from state agencies and Agriculture Research Service records: Alabama, Arkansas, California, Connecticut, Delaware, Georgia, Idaho, Indiana, Maryland, Michigan, Mississippi, Missouri, New Jersey, North Carolina, Oklahoma, Oregon, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, and Washington.

Host Plants

Host plants, as used here, refer to those plants upon which larval development of the vetch bruchid is completed. Adult feeding, if it exists, has not been reported and was not definitely established during the present study.

Table 1 is a summary of host records compiled from the literature and observed during the course of this study. It is not a complete reference to the numerous accounts of the insect attacking the two common hosts, Vicia villosa Roth (hairy vetch) and V. dasycarpa Ten. (woolypod vetch). There is complete agreement between previous reports and the present study on these two species of vetch. The differences between observations reported in the literature on V. pannonica Crantz, V. atropurpurea Desf., and V. sativa L. and the negative findings reported in this study are difficult to explain, because all of the species studied were in replicated nursery-row plantings, and adults oviposited freely on pods in rows containing the previously mentioned common hosts, V. villosa Roth and V. dasycarpa Ten.

There are two accounts of the insect maturing in seeds from plants in a genus other than Vicia, the true vetches. Zacher (1936) recorded the species attacking Ervum lens L., which is a synonym of Lens culinaris Medic., the common commercial lentil. Schopp (1953) published an account of adults reared from lentil seeds (presumed to be L. culinaris)

Table 1, Summary of species of vetch susceptible or resistant to the vetch bruchid.

Species	Bridwell: Bottimer: 1933	Pinckney: Pinckney 1937	Pinckney: Stitt 1941	Weimer: Bissell 1942	Rockwood: et al 1946	O.S.C.: unpublished	Present study
Vicia villosa Roth	+	+	+	+	+	+	+
V. dasycarpa Ten.	+	+	+	+	+	+	+
V. cracca L.	+					*	
V. pannonica Crantz	+	#	#		o		o
V. atropurpurea Desf.			+	o	o	o	o
V. caroliniana Walt.			+				
V. sativa L.		#	#	o	o	o	o
V. melanops Sibth. & Sm.			#				
V. angustiflora L.	o	o	o		o	o	
V. monanthos (L.) Desf.		o	o	o			
V. grandiflora Scop.			o	o			
V. ludoviciana Nutt.		o	o				
V. ervilia (L.) Willd.		o	o				
V. hycranica Fish. & Meg.			o				
V. hybrida L.			o				
V. noeana Boiss			o				
V. lutea L.			o				
V. lutea var. hirta Loisel			o				
V. serratifolia Jacq.			o				
V. tetrasperma Moench			o				

+ symbol, insect capable of completing life history in species
o symbol, insect not infesting species
* symbol, entrance holes noted in seed, no adults produced
# symbol, eggs noted on pod, no adults produced

in an area where vetches were delayed by late cultivation or killed with herbicide sprays.

Although several of the vetches may be infested by the vetch bruchid (Table 1), hairy vetch and woolypod vetch are the most commonly and severely attacked. Pinckney (1937) stated that these vetches were both readily infested, but only 50 per cent of the infested seeds of woolypod vetch produced adults in contrast to 80-90 per cent of the infested seeds of hairy vetch.

In 1957 pod samples were collected from a mixed stand of these two species of vetch, identified as to species, and seed harvested and saved for adult emergence (Table 2). In the hairy vetch samples, 54 per cent of the seeds were infested, and 61 per cent of these produced adults. In the woolypod vetch samples, 72 per cent of the seeds were infested, and 38 per cent produced adults. The percentages of adult emergences varied from those reported by Pinckney, but the ratio of emergence for the two species was comparable. Twice as many eggs were laid on pods of woolypod vetch (Table 2) as on pods of hairy vetch when the species were grown in a mixed stand.

Injury to Seeds:

Injured seeds were characterized by one or more larval entrance holes, and when insect development was complete, either a ring was cut on the inside of the seed coat for adult emergence, or a cavity was exposed in the seed where

an adult had emerged.

Table 2, A yield comparison of vetch bruchid from the two common host species of vetch, Vicia villosa Roth, hairy vetch, and V. dasycarpa Ten. woolypod vetch.

Entry	Hairy vetch	Woolypod vetch
Number of eggs laid on pods (34 pods in sample) (29 pods in sample)	174	288
Number of seeds in sample	52	65
Number of seeds with larvae	28	47
Number of larval entrance holes in seeds	47	99
Number of adults produced	17	18
Percent of infested seeds producing adults	61	38

The effect of bruchid-infested seed on germination, and the evaluation of inert matter in purity analysis, has been a problem to seed analysts for several years. Seeds from which adults emerge are usually not viable and are considered inert matter. Seeds having one or more larval entrance holes, but incomplete larval development, present a problem in evaluating injury. Wertman (1951), a seed analyst, concluded it was not necessary to remove all infested seeds as some seeds produced normal seedlings. In an attempt to classify seeds in which larval development was not complete, Pierpoint (1952) tested seed viability in relation to larval

entrance holes. Germination tests showed the number of normal sprouts decreased as entrance holes increased. The course traveled by the larvae after entering the seed, and subsequent larval development, effected the resulting damage to the seedling.

Adult Activities

Overwintering:

The vetch bruchid was found to overwinter as an adult in seed storage facilities in association with harvested seed or in moss on oak trees, which is presumed to be a natural or innate habitat.

There are numerous accounts of adult recovery from harvested seed. Undoubtedly this habit of remaining in or among harvested seed accounts for the wide distribution of the insect.

Storage facilities in western Oregon were noted to have adults overwintering among sacks of vetch seeds. Further, limited observations at seed-cleaning time in the fall of the year suggested many adults fly free during seed processing. If these adults escape from the buildings it is possible they overwinter in natural habitats.

There are two accounts in the literature of habitats other than those associated with harvested seed. Rockwood et al (1946) found adults in lichens on trees, and Steinhauer (1955) found adults under lichens and loose bark on trees, cracks in fence posts, and in trash and weeds in fence rows. Both of these records are from areas in Oregon where the present study was conducted. During this study adults were recovered during winter months from samples of moss collected on oak trees growing near hairy vetch fields. Samples of

moss approximately one-half cubic foot by volume yielded only one to three vetch bruchids per sample. Adults were collected from this habitat in 1957 and 1958 by forcing the insects out of the samples with heat in a Berlese-type funnel.

All of the previously mentioned habitats (Rockwood and Steinhauer) were sampled, as well as extensive sampling of field debris in and adjacent to vetch fields, and no adults were recovered. No adults were found remaining in the seed under natural conditions in surface debris in the field. Because of the numerous negative recoveries, and low numbers of adults found in moss on oak trees, an overwintering habitat not detected or seed storage facilities must have accounted for the large populations of insects that migrated into vetch fields in the spring of the year.

Habitats, similar to those described, were sampled in March and April of 1956 in Michigan. No adults were recovered, but a possible limitation to the study was the method of evaluating samples. Samples were hand-separated and inactive adults were possibly easily overlooked.

Spring Emergence:

Adults left their overwintering habitats and appeared in vetch fields approximately one month prior to the first appearance of pods, Table 3. This emergence period was approximately 2 weeks prior to the appearance of recognizable racemes, and 3 weeks prior to the development of open florets.

Table 3, Period in days between the first appearance of vetch bruchids in hairy vetch fields and the first appearance of vetch pods and insect eggs.

Year	Area	First Appearance		Period in days
		Adults	Pods & Eggs	
1956	Michigan	May 21	June 21	31
1957	Oregon	April 29	June 4	36
1958	Oregon	May 5	June 3	29

Sex Ratio:

The vetch bruchid, in general, had a 1:1 sex ratio. However, there was only a short period during which this ratio existed in the field during the activity period of the insect. Table 4 includes a summary of 1958 male and female recoveries in the field, as well as laboratory-reared results for 1957 and 1958. Steinhauer (1955) tabulated sex ratios from mid-season on to the period of inactivity, and these data agree with the data from mid-season to the period of inactivity presented in Table 4.

An approximate 1:1 ratio of sexes was found immediately prior to the first set of vetch pods (May 26, Table 4) under natural conditions. The percentage of females in the population increased from the period of pod appearance until termination of insect activity. An approximate 1:1 ratio of sexes was obtained from laboratory reared adults in 1957 and 1958. This ratio agreed, in general, with that found in the

field during mid-season of 1958, and the ratio reported for reared adults by Pinckney (1937).

Table 4, Sex ratio computed from laboratory-reared adults in 1957 and 1958, and from field-collected adults during the 1958 vetch bruchid activity period.

Collection (or rearing) Date	Percent Male	Percent Female
Adults reared in the laboratory from field-collected vetch. 1957	43	57
Field-collected adults. 1958		
May 5	100	0
May 12	76	24
May 20	63	37
May 26	49	51
June 3	23	77
June 10	23	77
June 16	28	72
June 23	2	98
June 30	9	91
July 5	0	100
Adults reared in the laboratory from field-collected vetch. 1958	49	51

Mating:

There are two accounts of mating of the vetch bruchid recorded in the literature. Pinckney (1937) reported that mating took place during the period of oviposition, and at no other time of the year. Steinhauer (1955) reported mating took place before pods were formed, and at no other

time of the year. The results of the present study agree, in part only, with the above statements.

Mating during this study was noted to take place on warm, bright days, from the first appearance of open florets until males were no longer present in the field. Thus, the observations agreed with Steinhauer that mating took place before the pods were formed, but did not cease with pod formation as reported by Steinhauer. The observations agreed with Pinckney that mating took place during the period of oviposition, but did not last because males were not present the entire period. As the numbers of males declined after mid-season (Table 4) it undoubtedly altered the mating activities. It was not possible to observe any changes under field conditions, and all attempts to determine mating under laboratory conditions failed. Adults maintained in close contact failed to mate under caged conditions, even among specimens collected when mating was common under field conditions.

Mating then, during 1957 and 1958, extended from approximately one week before the appearance of pods until three or four weeks after the appearance of pods, depending on the year. It is possible mating took place at an earlier date in the spring because well-formed oocytes were dissected (table 6) from females one week prior to pod appearance, and a period of development following fertilization is usually necessary. However, the observations on mating at flowering

time were approximate, because recognizable oocytes were not found two weeks prior to pod formation (Table 6), which was approximately one week prior to flowering of the vetch. This period also fell during a time when an approximate 1:1 ratio of sexes occurred in the field (Table 4). Possibly this ratio was not a requisite to mating, because field observations did not reveal any maximum mating activity period.

Field Studies of Oviposition:

Oviposition has been observed and described by Bridwell and Bottimer (1933), Pinckney (1937), Rockwood et al (1946), Steinhauer (1955), and Randolph and Gillespie (1958). These accounts agreed, in general, with the observations made during this study. Briefly, the female assumed an immobile position for a few seconds with the body parallel to the longitudinal axis of the vetch pod. The tip of the abdomen was then curved downward, and by a rhythmic motion of the abdomen the egg was deposited. The egg was covered with a viscous substance, which upon drying, fastened the egg to the surface of the pod. Invariably the adult flew or crawled away from the pod following oviposition, and then either returned to the same pod, or another pod, for subsequent oviposition. When females were confined in lamp chimney cages in the laboratory they rarely laid more than a single egg without leaving the pod and crawling about for 1 to 3 minutes.

A vetch pod from the time it appeared, or was even

visible in the drying floret, seemed apparently satisfactory for adult oviposition. Eggs were not found on any part of the plant except the pods. Vetch stems and leaves were placed in lamp chimney cages with females, and no eggs were deposited on the plant material. Under confined conditions in the laboratory eggs were sometimes deposited on the walls of the cages, even when vetch pods were available for oviposition.

The search by females for a suitable oviposition site appeared to be related to some sense associated with the labial palpi. As the female crawled about on the plant the palpi were kept in constant motion and erratic contact with the surface of the plant. A simple experiment was designed which, by circumstantial evidence only, demonstrated the possibility of this palpal sensory relationship or association. A single female was introduced into each of six cloth-capped glass chimney cages containing vetch stems, leaves, florets, and a single pod. Three of the cages were immediately covered with cardboard cylinders closed at the top to insure complete darkness within the cages. At the end of 24 hours, eggs were found on the vetch pods in all six cages, and on no other plant parts (Table 5). Thus, in complete darkness the females were capable of determining the correct oviposition site.

Egg Development:

An attempt to determine egg development in 1957 failed

Table 5, Summary of oviposition habits of female vetch bruchids in total darkness and in normal diurnal-nocturnal conditions.

Condition	Total Eggs Deposited			
	Stems, Leaves, or Florets	Pods (by cages)		
		I	II	III
Complete darkness	none	14	5	7
Diurnal-nocturnal 1/	none	0	12	3

1/ Eggs were noted, but not counted, during the first few hours of the experiment under natural daylight.

because alcohol preserved specimens were not satisfactory for dissection. Female bruchids were collected in the field in 1958 and dissected while fresh. This procedure necessarily limited the number of specimens that could be dissected because of the limited time available for immediate dissection during the period of activity of the insect. Steinhauer (1955) dissected females and found that they contained as many as 20 mature eggs in the oviducts and a great many more developing.

Considerable difficulty was encountered in determining which eggs to include as fully-formed or fully-developed. Strictly speaking, they were not eggs but ovarial oocytes, and not fully developed until oviposited. A decision was made to score the series of larger oocytes in the lateral oviducts, or egg chambers, as developed eggs. There was a distinct reduction in size between these oocytes and those in earlier stages of development.

Table 6, Number of developed eggs (or oocytes) dissected from female vetch bruchids during 1958.

Date	Number of Eggs Per Female					Average Number Eggs Per Gravid Female
May 12	0	0	0	0	0	-
May 20	0	0	0	0	0	-
May 26	0	18	2	14	4	9.5
June 3 1/	16	4	10	6	4	8.0
June 10	14	8	10	28	12	14.4
June 16	14	10	8	14	0	11.5
June 23	20	6	12	10	10	10.6
Average number per gravid female						10.9

1/ First pods noted in field where insects were collected.

Table 6 summarizes the results of the dissections. The first developed eggs were found approximately one week before the pods appeared in vetch fields. The average number of developed eggs (as previously defined) per gravid female was 10.9. These data are not a reflection of the egg laying potential, but an indication of the number of eggs produced by an individual female at given times throughout most of the egg deposition period. A later collection was made (June 30, 1958), but there was no opportunity to complete the dissections while material was still in a fresh state.

A series of adults was selected for collateral studies from the population that was collected for dissection studies.

Laboratory Studies of Oviposition:

Adults selected for collateral studies were confined in lamp chimney cages for oviposition studies (Table 7).

Table 7, Number of eggs laid per female bruchid confined in lamp chimney cages with vetch pods. Each entry represents total number of normal appearing eggs laid in 48 hours, and entries in parentheses refer to non-viable eggs laid in a 96 hour period.

(Number of Eggs Laid with Males Present in Chimney Cages)

	June 10	June 16
	26	2(2)
	22	17(4)
	0(1)	0(1)
	4	4
	14	0(1)
Av. 1/	16.5	7.6

(Number of Eggs Laid Without Males Present in Chimney Cages)

	June 10	June 16	June 23	June 30	July 5
	10	17	28	5	0
	23	8	13	7	0
	3	10	22	1	3
	4	4(1)	24(1)	13	1
	12	3	22	2	
			27(3)	10	
			0	5	
			8	2	
			17	2	
			34	1	
Av. 1/	10.4	8.4	21.7	4.8	2

1/ Average computed from number of female bruchids laying normal appearing eggs.

A female was placed in each cage, and in two of the experiments, a male was admitted with the female in one-half of the replications. This procedure was not possible in subsequent experiments because males were, for the most

part, unavailable in the fields after mid-May.

The pods were examined under a microscope, after exposure to the adults, at 24, 48, 72, and 96 hours, and then retained for several days to verify the number of normal, or eggs which hatched. The totals in Table 7 for normal eggs are based on the 48 hour counts, and the totals for sterile eggs are based on the 96 hour counts. The counts for 48 hours are given because adult mortality was very high under artificial (caged) conditions. Adult mortality was noted prior to the 72 hour counts, and in one experiment (Table 7, June 16 experiment) all adults were dead at the 96 hour count. This 48 hour limitation does not impair the validity of these data because 91.3 per cent of the eggs were laid in the first 24 hours of all experiments, and in approximately 40 per cent of the chimneys, adults survived the life (96 hours) of the experiments.

The peak of oviposition occurred during the experiment established June 23, and following this date the rate of oviposition dropped rapidly. The peak period occurred during a period when males were extremely scarce in the field (Table 4). The numbers in parentheses in Table 7 refer to sterile, or non-viable eggs. There were more sterile eggs laid early in the season than at the peak of oviposition or later in the season. In the section on mating, the possibility was mentioned that late-season mating was not taking place under field conditions, and could not be observed

under laboratory conditions. The peak oviposition period was also a period of low numbers of sterile eggs, as well as a period of low male populations, and followed an extended period (Table 4) when males had been in an approximate 1:3 ratio. Thus, the data offered circumstantial evidence supporting the suggestion that late-season mating may not have been essential.

Females, which produced a single sterile egg, and no normal eggs, did not oviposit the first 72 hours of confinement. Similarly, those which produced both normal and sterile eggs, laid only sterile eggs after 72 hours of confinement.

The average number of eggs produced per female, laying normal appearing eggs, was 10.2 in 48 hours. This figure was surprisingly close to the average number of developed eggs (10.9) reported for the season from dissected individuals (Table 6). However, this relationship existed only on seasonal averages computed from Tables 6 and 7. An average comparison by dates, revealed that during the peak oviposition period twice as many eggs were laid as were noted in dissected adults from the same population. Possibly this was a reflection of inadequate numbers used in both experiments, or an error in designating mature oocytes in dissections. It was possible, because of the stress of the unfavorable environmental conditions, and presumed premature death of adults, that females were stimulated to lay eggs more

rapidly than normal. The latter possibility was suggested by the fact that unfertilized females in the oviposition experiments laid sterile eggs after a long confinement period. Conversely, countless insects were killed and preserved in various ways over the three year period and no attempt to promiscuously discharge eggs was noted.

Table 8, Total eggs arranged by classes and total females laying normal (and non-viable) eggs in each class. (Data are adapted from Table 7)

Total Normal Eggs (by classes)	Total Females	Percent of Total Ovipositing in Each Class
none	6	-
1-5	16	42
6-10	6	16
11-15	4	10
16-20	4	10
21-25	5	13
26-30	2	5
31-35	1	2
non-viable (only egg laid)	3	-
non-viable (plus normal eggs laid)	5	-

Table 8 is a tabulation of oviposition, arranged by classes, to illustrate frequency of total eggs per ovipositing female. The grouping by classes simplified the presentation of data, and has no known biological significance. The table illustrates the high percentage of females ovipositing in the 1-5 egg class (42 per cent), and the

distribution of entries in the four subsequent classes, which accounted for almost 50 per cent of the total of normal eggs deposited.

Steinhauer (1955) caged adults and reported the number of eggs deposited to range from 0 to 62, with an average of 24 per adult, during a period of 3 to 13 days.

In a recent paper Randolph and Gillespie (1958) reported the average number of eggs laid per female as 8.5 per day when caged in the field, and 5 per day when caged in the laboratory. The results obtained for field caged adults (8.5 per day) by Randolph and Gillespie approached the results (10.2 per 48 hours with 91.3 per cent of 9.2 eggs laid in the first 24 hours) in laboratory studies during this study, Table 7. In comparing laboratory results there were considerable differences in the number of eggs laid per day in their experiments and the present study. Although the workers did not describe their procedure, they mention eggs present on the walls of vials that were used for isolating female bruchids. Thus, it is possible the oviposition of vial-confined adults cannot be compared to the lamp chimney technique employed in the present study because of the obviously great differences in the physical factors of the two environments.

It was not possible, as a result of the data collected during this study, to resolve a valid egg-laying potential for the vetch bruchid. It would be possible, however, by

extrapolation of the presented data to compute a hypothetical egg-laying potential for the insect. This is of questionable value because it would assume that an individual would live and oviposit during the entire season in an uninhibited environment. If computed from results presented in Tables 3, 4, and 7, it would not consider the possible necessity of a recovery period following oviposition and prior to subsequent oviposition.

Egg Stage

The egg of the vetch bruchid has been described in detail by Bridwell and Bottimer (1933), Pinckney (1937), Steinhauer (1955), and Randolph and Gillespie (1958). Observations on the descriptive phase of the egg stage agreed with published accounts. The freshly laid egg was pale yellow, the chorion was delicately sculptured with a network of fine, irregular reticulations, and ranged from 0.6 mm. to 0.7 mm. in length and from 0.2 to 0.25 mm. in width. About 72 hours after oviposition two dark transverse bands appeared visible through the chorion, and as the embryo developed, these bands lost their identity and the head of the developing embryo appeared as a darkened area through the chorion. As pigmentation continued the head became clearly visible through the semitransparent chorion.

The incubation period was 18 days under field conditions in Oregon in 1957 (average temperature, 60° F.), and 12 days under field conditions in Oregon in 1958 (average temperature, 61.4° F.). Both of these accounts refer to the duration of time required for the first laid eggs to hatch, incubation time for eggs subsequently laid was not satisfactorily determined. In spite of difficulties in scoring hatching under field conditions, it appeared quite definite that no eggs hatched in less than ten days after oviposition. This was considerably different than the 4-5 day incubation period reported from Texas (Randolph and Gillespie 1958), or the eight day average reported from North Carolina (Pinckney 1937).

The most extensive studies and experiments on incubation were made in Oregon by Steinhauer (1955). This worker conducted incubation trials early and late in the season, and found that eggs deposited early in the season hatched in (average) 14.6 days, and eggs deposited late in the season hatched in (average) 11.9 days. Upon plotting incubation period against mean temperatures he obtained a straight line relationship, suggesting that increased temperatures reduced the incubation period. These durations agreed closely with the results obtained during the present study. Possibly the temperature relationship to the incubation period is an explanation, or a factor in an explanation, for the wide differences in incubation period reported in the literature.

Larval Stages

Bridwell and Bottimer (1933) were the first to establish that there were four larval instars in the developmental period of the vetch bruchid. Steinhauer (1955) and Randolph and Gillespie (1958) confirmed the number of instars by head capsule measurements of the various stadia. During this study the average width of the head capsule of the four larval instars was found to agree within 0.02 mm. of published accounts (I= 0.13 mm., II= 0.25 mm., III= 0.42 mm., IV= 0.62 mm.).

The activities of larvae are mentioned by Bridwell and Bottimer (1933), Pinckney (1937), Steinhauer (1955), and Randolph and Gillespie (1958). Discussions on activities are limited to statements, in effect, that larvae completed development by feeding within a vetch seed, and that the last instar larva cuts a cap in the seed prior to pupation to permit the escape of the adult. Duration of larval stages is mentioned in two articles. Pinckney (1937) found the four instars required two weeks for development in North Carolina, but no mention was made of the duration of individual stadia. Steinhauer (1955), working in western Oregon, found each stadia to average about two weeks in duration.

The writer conducted a series of dissections of field-collected vetch seeds in 1957 and 1958 in an attempt to extend the known data on larval activities and duration.

Any attempt to investigate or observe individual larvae (such as opening a pod in the case of first instar larvae, or dissecting a seed in the case of second, third, or fourth instar larvae) killed the individual, or individuals, thus exposed and terminated the observation. As a result, this discussion is necessarily based on the population under observation at any one time. Inference related and interpreted from observations, such as these, can be subject to large errors.

First Instar Larvae:

It was found that the first instar larva chewed its way through the ventral surface of the chorion and into the valve of the pod. Thus, the larva did not leave the egg to the outside, but remained protected by the egg as it bored through the valve into the pod. Based on the first appearance of recognizable frass in the egg shell, until larval entrance into the pod, the period from eclosion until pod entry was at least three days.

Once inside the pod the larvae crawled about, apparently at random, before gaining entry into a seed. Larvae appeared capable of entering at any point on a seed, including the hilum. Observations indicated that a point of purchase was necessary for seed entrance. That is, larvae appeared to enter where seeds were adjacent to each other, or where seeds touched the walls of the valve. Those which entered through the hilum mined in the

funiculus, which afforded an excellent point of purchase for boring into the seed.

The period from boring through the valve until seed entrance varied from overnight (less than 12 hours) to 2 or 3 days. Larvae in premature pods, collected in the field and maintained under laboratory conditions, mined in the inner surface of the valve. This type of mining was never observed under field conditions.

Following entrance into the seed, the first instar larvae either molted and immediately tunneled into the seed, or mined from 1 to 3 days between the seed coat and endosperm. These mines were never over 1 mm. in length. The duration of the first larval instar, based on these observations, ranged from 4 to 9 days. However, since some larvae did not mine in the seed before molting, it is possible they had a longer free-living period in the pod. This conclusion, if valid, would make the duration of the first stadia range from 7 to 9 days.

Second and Third Instar Larvae:

The study of activities of subsequent instars had to be based on inference because if a seed was opened the larva or larvae within soon died. All attempts to rear larvae in any habitat other than entire seeds failed. Seeds were easily dissected in early stages of their development, but after they had hardened it was necessary to immerse them in boiling water for at least ten minutes to soften them enough

for dissection.

Second instar larvae bored towards the center of the seed, almost at right angles to the seed wall. If larvae entered through the hilum they usually remained oriented in the area between the cotyledons and fed on both cotyledons. If the larvae entered from any other point on the seed, they fed a short distance inwards and turned to feed parallel to the seed wall, or fed in the area where the cotyledons were contiguous.

Third instar larvae continued feeding in the central portion of the seed. The feeding during this stadia was more general and a central cavity was formed in the seed. This latter pattern of feeding suggested that the larvae no longer burrowed or tunneled, but fed on the perimeter of the central cavity.

The collective duration of second and third instar larvae was 25 days. Difficulty was encountered in determining the duration of individual stadia. The second stadia apparently exceeded 13 days, and it appeared that the third stadia ranged from 12 to 15 days.

Fourth Instar Larvae:

Fourth instar larvae continued to enlarge the central cavity. This stadia ranged from 13 to 23 days, with an average duration of 18 days. When ready to pupate, larvae cemented frass around the wall of the cavity to form a pupal cell. They also cut a circular groove or ring in the

seed coat which produced the "cap" or "lid" by which the adult escaped from the seed. This groove was apparent externally as a narrow light green ring. Occasionally a small circular area in the center of the cap was thinned out, which gave the appearance of a light green circular area, surrounded by a dark green and a light green concentric rings. Based on an examination of 150 seeds, the cap was cut at a point along the line of cleavage of the cotyledons (other than in the hilum) in 80 seeds; and at a point other than the line of cleavage (or hilum) in the remaining 70 seeds. The cap was never cut through the hilum or around an existing larval entrance hole.

Prior to pupation, fourth instar larvae went through a transformation stage. The abdomen became greatly distended and it gradually assumed pupal characters. The initiation of these late-stadia characters was not clear-cut. There were recognizable, gradual changes, and then suddenly an apparent assumption of pupal characters in a period of less than 48 hours.

Pupal Stage

The pupal stage lasted 9 days. The fourth instar larval exuviae remained as a small disk, or pad, on the ventor of pupae throughout pupation. The newly formed adult body was teneral for approximately one day, and then hardened

and assumed adult colors.

Adult Stage

Newly matured adults forced open the previously described cap or lid, which the fourth instar larvae had cut in the seeds, and then remained quiescent within the seed or left the seed. Frequently adults left the seed for a short time, and then returned to the same seed, or another seed, and remained quiescent. Adults were unable to escape from the pod unless the valves dehisced.

The total time for development from egg to adult ranged from 55 to 91 days, with an average duration of 72 days. Steinhauer (1955) worked on the vetch bruchid in Oregon and found the duration to be 67 to 75-plus days. Randolph and Gillespie (1958) found the development period to range from 22 to 43 days in Texas, and Bridwell and Bottimer (1933) found the development period to be 30-plus days in New Jersey. The exact developmental period for the material collected in 1956 in Michigan was not satisfactorily determined, except that the minimum duration was in excess of 41 days.

Previous workers noted the great range in size of vetch bruchids. Bridwell and Bottimer (1933) gave the adult range in length as 2.0 to 3.5 mm., and Pinckney (1937) gave the length as 3.0 to 3.5 mm., however neither paper reported

which sex was measured. Steinhauer (1955) gave the range in length of the female as 2.5 to 3.5 mm., and stated the male was similar to the female. Randolph and Gillespie (1958) gave the following average sizes: male, length 2.92 mm., width 1.84 mm.; female, length 3.01 mm., width 1.90 mm.

During the present study a sample of 36 males and 37 females was measured (Table 9). Although there was considerable variation in size, the average fell within measurements reported in previous accounts. The female was larger than the male in all measurements.

Table 9, Minimum, maximum, and average length and width measurements (in mm.) of male and female vetch bruchids.

Measurement	(in mm.) Male	Female
Minimum length	2.3	2.8
Maximum length	3.5	3.7
AVERAGE LENGTH	3.02	3.15
Minimum width	1.3	1.6
Maximum width	2.0	2.1
AVERAGE WIDTH	1.78	1.9

Bridwell and Bottimer (1933) noted that small, poorly developed seeds, produced small adults. Similar observations were made during this study, and Figure 1 is a scatter diagram of adult length (by sexes) and maximum diameter measurements of hairy vetch seeds from which the adults emerged.

These data were not calculated for regression coefficience because of the low population involved. However, the measurements revealed that adult size was related to the size of seed in which development took place. There appeared to be a closer relationship between seed size and adult size among the males than among the females (Figure 1). The males tended to fall along a straight line from lower left to upper right of the scatter diagram, whereas females produced from seeds in excess of 3.4 mm. tended to be grouped along a line perpendicular to adult length. The relationship of increased insect size to increased seed size was reversed in large seeds, and smaller adults of both sexes were produced from seeds in excess of 4.2 mm.

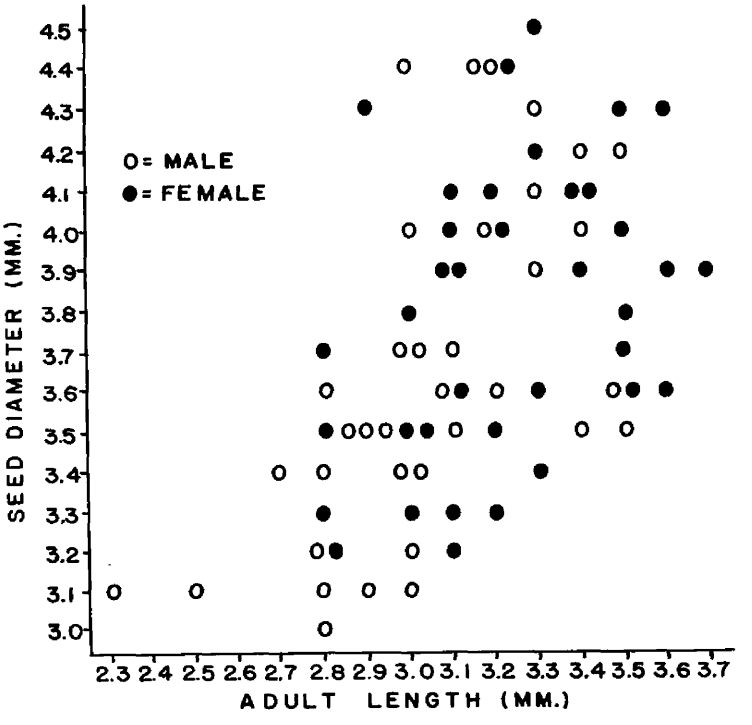

Figure 1, Scatter diagram showing adult size (by sexes) of the vetch bruchid in relation to diameter of hairy vetch seeds from which adults emerged.

Immature Mortality Studies

The literature in all fields of biology contains teliological-like statements concerning the wasteful or haphazard methods nature has in perpetuating herself. The oviposition habits of the vetch bruchid appeared, by man-made observational standards, to be very wasteful and inconsistent with the presumably advanced type of host relationship previously described. As a result of this observation, a study of mortality and mortality factors of the immature stages was conducted in 1957 and 1958. Only the 1958 data are presented because of refinements in methods adapted from knowledge gained in the initial (1957) study.

There are previous accounts of mortality observations on the vetch bruchid reported in the literature. In vetch pods caged in the field, Pinckney (1937) obtained a 75.7 per cent hatch of bruchid eggs (53 out of 70 eggs), and a 70 per cent hatch in the laboratory (56 out of 80 eggs). Steinhauer (1955) reported an 82 per cent hatch in laboratory rearing trials (271 out of 331 eggs). Steinhauer also noted that under field conditions as high as 50 per cent of the eggs on some pods dried up a few days after being laid.

Pinckney (1937) noted that some larvae died within the pod before finding a seed, or while effecting entrance into the seed. He commented on more than one larval entry per seed, and stated that generally the stronger and more

aggressive larvae destroyed the weaker specimens when they met in a seed. Bridwell and Bottimer (1933) noted up to 7 larval entries per seed. Randolph and Gillespie (1958) reported that out of 297 larvae removed from seeds, in only a few instances was there more than one per seed, and they were not developed beyond the second instar. All of these accounts agreed with the present study in that only one adult was produced per seed.

Life Table for Immature Stages:

Data for life tables of natural populations are extremely difficult to obtain. Deevey (1947), in a review of life tables as a tool in the study of natural populations, outlined various methods of obtaining life table data. The procedure followed in this study, direct observations of the number of survivors out of a definite initial population, was considered by Deevey to be the most valid approach.

Table 10 is a summary of immature mortality factors and numbers dying in the finite population under observation. It was not possible to measure mortality after adult emergence from the seed, but it was not necessary to measure all factors in order to obtain a useful picture of the delimited population mortality. Some limits, for practical experimental procedure, had to be imposed.

In this study approximately one-third of the total mortality was caused by eggs dropping off the pods. The data collected showed that 29.7 per cent of the eggs

Table 10, Life table and mortality factors for immature stages of the vetch bruchid. (Based on 4,333 eggs on 188 pods and 559 out of 620 seeds infested.)

Age Interval	Number Surviving	Mortality Factors	No. Dying	% Mortality $\frac{D}{I}$ 1/	% Mortality $\frac{D}{S}$ 2/
Eggs	4,333	Eggs lost from pod	1,286	29.7	29.7
		Embryo dead in egg	370	8.5	8.5
		Sterile (non-viable) eggs	173	4.0	4.0
		Egg eaten by female bruchid	73	1.7	1.7
Larval stages	2,430	Failure to gain entrance into seed. Instar I (early stadia)	941	21.7	34.6
		Failure to mature in seed. Instar I (late stadia), II, III, IV (early stadia)	1,018	23.5	41.9
		Instar IV (late stadia) prepupae	6	<1.0	<1.0
Pupae	465	None	-	-	-
New adults	465	Failure to escape from seeds	4	<1.0	<1.0
TOTAL ADULTS	461	TOTAL MORTALITY		89.1%	

1/, $\frac{D}{I}$= number dying divided by number in initial population

2/, $\frac{D}{S}$= number dying divided by number surviving each mortality factor

(Table 10) or 1,286 eggs out of the initial population of 4,333 were lost from the pod. Eggs which drop from the pod could have exhibited any of the mortality factors given in Table 10. It was impossible to designate these factors after the eggs were lost, but fortunately it was not essential to these data. The dropping of eggs from pods, regardless of their condition, was the major mortality factor.

Some of the factors found to cause eggs to drop from the pod, were adults brushing or knocking the eggs off the pod as they crawled about during oviposition, and some eggs appeared to be weakly cemented to the pod and fell off shortly after oviposition. Possibly a great many were brushed off by any factor that brought about plant movement and plant contact in the field.

Identification of this mortality factor was based on examinations of field collected pods under binocular (40X) magnification. The presence of a slightly chewed area, sometimes darkened, or remnants of the dried and somewhat shiny adhesive substance easily indicated a lost egg. If there was a completed larval entrance hole in the valve, the egg was not scored as lost from the pod because this type of loss was not a mortality factor. It indicated a larva had successfully entered the pod before the egg was lost.

Figure 2, B, indicates the frequency at which this mortality factor occurred. The importance of this factor was

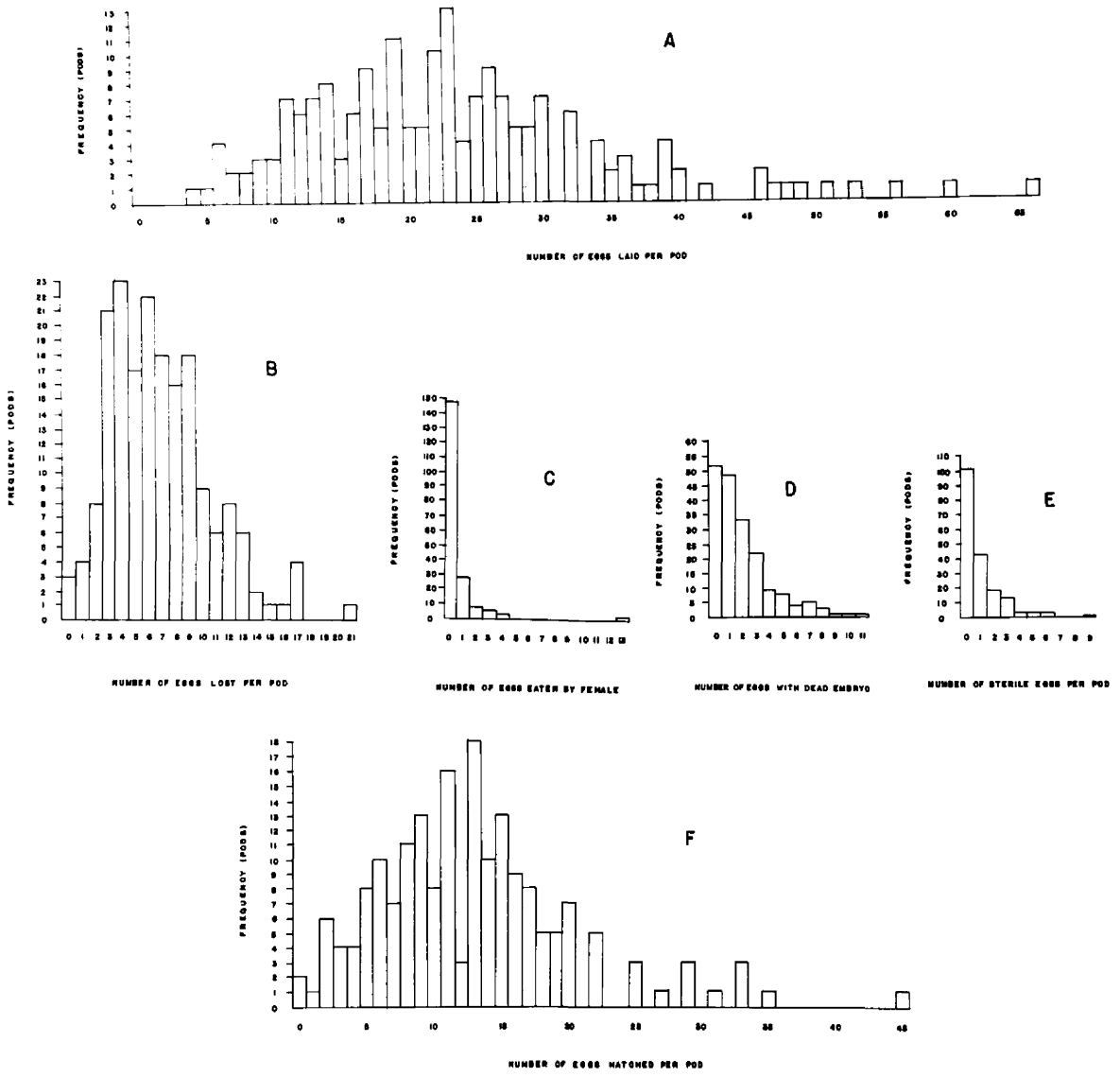

Figure 2, Histogram showing frequency of mortality factors for the immature stages of the vetch bruchid in hairy vetch.

established, since only 3 out of 188 pods retained all eggs. From 3 to 9 eggs were lost from 135 out of the 188 pods in the sample (Figure 2, B), or by comparison to histogram A (Figure 2), approximately one-third of the total eggs in the samples.

Eggs with dead embryos accounted for 8.5 per cent of the mortality, or 370 of the initial 4,333 eggs had dead embryos (Table 10). The cause of embryo mortality was not determined. Possibly it was a result of some physical factor in the environment, or a genetic feature of the particular eggs. This factor occurred in small numbers among approximately two-thirds of the pods sampled (Figure 2, D).

Sterile, or non-viable, eggs accounted for a 4 per cent mortality, or 173 eggs out of the initial 4,333. The frequency of sterile eggs was low (Figure 2, E) in contrast to the previously mentioned factors. In these eggs no embryonic development took place, and the eggs were empty and transparent.

Individual females eating their eggs following oviposition accounted for 1.7 per cent of the initial mortality. This phenomenon was not observed until mid-season 1958. However, eggs typical of those fed on were noted throughout the study in Michigan and Oregon, but it was earlier assumed to be the result of unaccountable predatory insects.

Eggs laid by certain females were immediately eaten by the ovipositing insect. In caged experiments, 4 females that had been noted by observation to eat their eggs, were confined in petri dishes, and they ate 34 out of the 43 eggs deposited in 24 hours. The fate of uneaten eggs, deposited by females that ate most of their eggs, was not determined, but in laboratory experiments the uneaten eggs did not hatch. There was no explanation for this activity, although some insects are known to require a protein feeding to develop their ovaries, and frequently eat their own eggs.

The 2,430 eggs that survived the above mortality factors (Table 10) hatched and the larvae entered through the valves into the interior of the pod. Only two pods were without larval entrances, and the majority of pods had many more entrances than seeds (average of 3.3 seeds per pod) as illustrated in histogram F (Figure 2).

The initial occurrence of larval mortality within the pod was due to failure of larvae to gain entrance into a seed. This accounted for a 21.7 per cent mortality of the initial population, and a 34.6 per cent mortality of the larval population (Table 10). It appeared, by observation of dissected material, that the principle cause of the mortality was failure of larvae to find a point of purchase in order to enter the seed. This type of mortality was confined to the early stadia of first instar larvae.

Failure to mature within the seed accounted for a 23.5

per cent mortality of the initial population, or a 41.9 per cent mortality of the total larval population.

Destruction of one individual by another (as mentioned by Pinckney 1937) was found in only one seed; and then both larvae (third instar) were dead in a common central cavity. However, in other dissections, larvae (second and third instar) were alive in a central cavity and apparently had not attacked one another. Until the tunnels or burrows in the seed opened into a central cavity, there was never an instance of tunnels contacting each other. In spite of this lack of physical contact by first and second instar larvae, many of them were dead in their isolated burrows. The cause of this mortality was not determined. By circumstantial evidence, it appeared that the presence of older larvae within the seed caused the death of younger individuals. Possibly they altered the micro-environment or secreted a toxin of some type. Late entry into a seed, when the seed was mature and quite hard, was not the cause of mortality. This was easily observed in seeds in which there were no early-season entries. And yet, in similar seeds, all late entering larvae soon died within their tunnels if a later and more mature instar larva or larvae (third instar for certain, and possibly late second instar) were feeding in a central cavity. This association might have accounted for some of the mortality within a seed, particularly of the early instars.

There was very little difference in success of larvae between those which entered the seed through the hilum, or those which entered along the side of the seed. Figure 3 is a series of histograms showing these relationships. It was significant that there was a 25 per cent mortality when a single larva entered a seed through the side of the seed (Figure 3, A), and was the only individual in the seed; and there was a 28 per cent mortality when a single individual entered the seed through the hilum (Figure 3, B), and was the only individual in the seed. Thus, quite surprisingly, there was an approximate 25 per cent mortality of single individuals within a seed, presumably developing free of larval competition. Although this observation, or the possibility of environmental toxicity, did not explain the cause of larval mortality within a seed, they did confirm the observation that the suspected cannibalism was not a significant factor.

There must have existed a large group of innately "weak" individuals in the larval populations. This was suggested because the higher the larval population within a seed, the greater the chances were for an adult to be produced from the seed (Figure 3, A, B, C, D, E).

The 155 seeds which did not produce an adult during the experiment were dissected. Six of the seeds contained a dead prepupa or late fourth instar larva, and four of the seeds contained a dead adult (Table 10). Combined, these

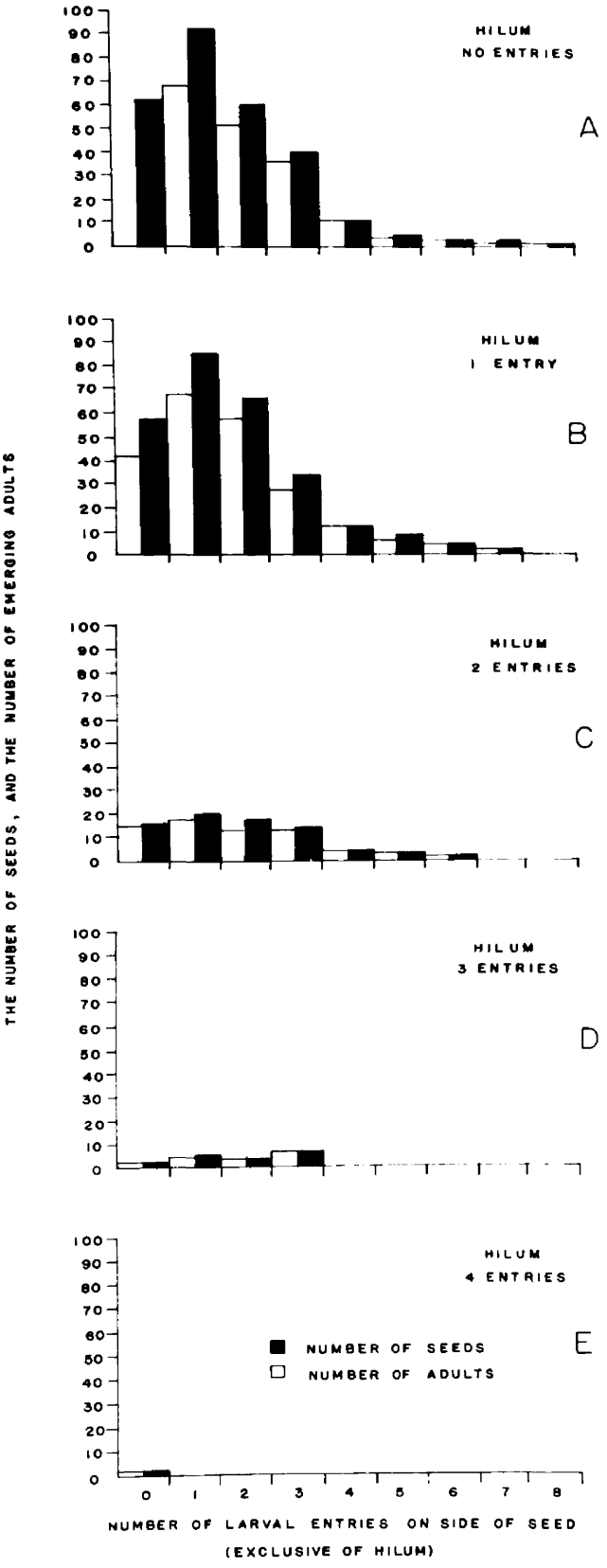

Figure 3, Histograms showing the number of adult vetch bruchids produced from hairy vetch seeds with various combinations of larval entrance positions and numbers.

two mortality factors accounted for less than 1.0 per cent of the total mortality.

None of the previously mentioned dissected seeds contained a dead pupa. It appeared that any larva that pupated successfully transformed into an adult.

The total mortality of 89.1 per cent (Table 10) was only slightly greater than a calculated mortality would have been for the conditions of the experiment. Based on the 4,333 eggs in the initial count, and a total of 620 seeds in the sample, a calculated mortality would have been 85.7 per cent. Thus, under the conditions of the experiment, approximately one adult was produced for each ten eggs deposited on the pods of hairy vetch.

The mortality rate of 89.1 per cent in 1958 (Table 10) was similar to the total mortality obtained in a preliminary study in 1957. At that time a 91 per cent mortality was obtained, but it was undoubtedly higher than that because a different (and not as sensitive) procedure was used in scoring eggs lost from the pod.

No parasitic insects were reared from any of the material collected in Oregon. However, had parasites been recovered, they would have comprised an additional immature mortality factor.

Parasites

Material collected in Michigan in 1956 was infested with a chalcid parasite, Bruchobius mayri (Masi.). Specimens were identified by Dr. R. D. Burk, Insect Identification Laboratories, U.S.D.A., Beltsville, Maryland.

Bridwell and Bottimer (1933) reared six species of chalcid parasites from vetch in New Jersey, and Pinckney (1937) reared five species from vetch in North Carolina, including Bruchobius mayri (Masi.).

In a shipment of hairy vetch pods and seeds from Michigan in 1957 many fungus-covered adults were found dead within the seeds. The adults had failed to open the lid or cap on the seed. Dr. C. G. Thompson, Insect Pathologist, Insect Pathology Laboratory, U.S.D.A., Beltsville, Maryland, identified the fungus as Entomopthorales, but could not identify it further because the specimens were so overrun with saprophytic fungi. No apparent fungus-killed bruchids were found in Michigan material examined in 1958.

SUMMARY

The results of field and laboratory studies in Michigan during 1956 and in Oregon during 1957 and 1958 with the vetch bruchid, Bruchus brachialis Fahraeus, on hairy vetch may be summarized as follows:

The insect was reared from infested seeds of Vicia villosa Roth and V. dasycarpa Ten., but it was not found to infest seeds of V. pannonica Crantz, V. atropurpurea Desf., or V. sativa L. A higher percentage of infested hairy vetch seeds produced adults than infested woolypod vetch seeds.

The vetch bruchid was found to overwinter as an adult in storage facilities in association with harvested seed, or in moss on oak trees adjacent to hairy vetch fields. Males left their overwintering habitats and appeared in vetch fields approximately one month prior to the formation of pods. A sex ratio of 1:1 was found immediately prior to the appearance of the first pods in hairy vetch fields.

Mating was observed in the field from the first appearance of florets until males were no longer present in the field. The insect never mated under caged (laboratory) conditions. The average number of developed eggs (or developed oocytes) dissected per gravid female was 10.9. Females confined in lamp chimney cages in the laboratory

laid an average of 10.2 eggs per 48 hours, but so much difficulty was encountered maintaining females in confinement, and the data were so varied, it was not possible to determine a valid egg-laying potential for the species.

The incubation period of the egg stage varied from 12 to 18 days, depending on the season, for the earliest deposited eggs. It was found that the developing embryo required approximately 3 days from eclosion until entry into the pod.

The first instar larva was found to spend from less than 12 hours to 3 days in order to gain a point of purchase and enter a seed. The seed was entered at any point, including the hilum. The first instar larval stadia lasted from 7 to 9 days.

The second and third instar (collectively) lasted approximately 25 days. The fourth instar larva had an average duration of 18 days. During these three stadia a large chamber was eaten out in the center of the seed, and the fourth instar larva cut a circular ring in the seed which afforded an escape lid for the adult.

The pupal stage lasted approximately 9 days. Thus, from egg to adult required a period ranging from 55 to 91 days, with an average duration of 72 days. The newly emerged adult either left the seed or remained quiescent within the seed. The size of the emerging adult of either sex was associated, up to a maximum size, with the size of the seed in which it developed.

A chalcid parasite, Bruchobius mayri (Masi.), was reared from Michigan material collected in 1956. No parasites were reared from Oregon collected material.

Life table data were collected on immature stages, from egg to emerging adult, with an initial population of 4,333 eggs producing 461 adults. Thus, in the 1958 studies approximately one adult was produced for each ten eggs laid. Mortality in the egg stage resulted from: loss of egg from pod (29.7 per cent), embryo dead in the egg (8.5 per cent), sterile, or non-viable eggs (4.0 per cent), and female bruchids eating their own eggs (1.7 per cent). 21.7 per cent of the larvae failed to find a point of purchase and enter a seed. 23.5 per cent of the larvae died within the seed. Mortality within a seed was expected because more than one larvae entered a seed, and only one adult was produced per seed. The factors responsible for mortality within a seed were not satisfactorily determined. There was no mortality in the pupal stage, and less than 1 per cent mortality in failure of prepupa to pupate or adults to escape from the seed.

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