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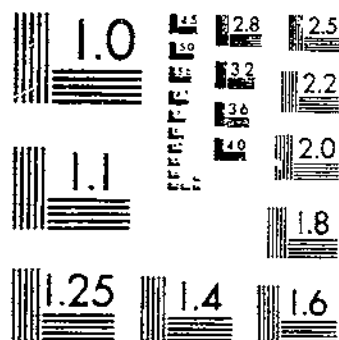
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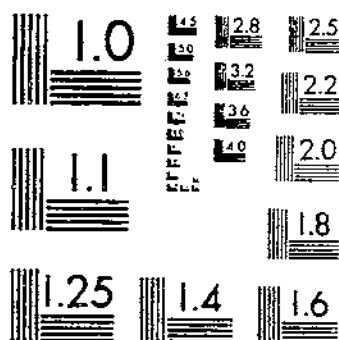
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BIOLOGY OF THE JAPANESE BEETLE
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BIOLOGY OF THE JAPANESE BEETLE

By Walter E. Fleming

Technical Bulletin No. 1449

Agricultural Research Service

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BIOLOGY OF THE JAPANESE BEETLE

BY WALTER E. FLEMING, *collaborator*,
Entomology Research Division, Agricultural Research Service

Little was known about the biology of the Japanese beetle (*Popillia japonica* Newman) when it was found in southern New Jersey in mid-August 1916, probably because it is a pest of minor importance in its native Japan. Prior to its discovery in the United States it was known to occur only on the main islands of the Japanese archipelago. The beetle is common but not abundant in Kyushu, Shikoku, and southern Honshu. It is the most abundant in northern Honshu and in all of Hokkaido where grasslands occur, but its population density never reaches that in the Eastern United States.

In New Jersey the beetle found a generally favorable climate, large areas of permanent turf for developing the immature stages, almost 300 species of plants to satisfy its voracious appetite, and at that time no important natural enemies. Fleming (1968)¹ has summarized the development of biological control of the beetle in the United States. The beetle spread rapidly in its new environment and it soon became a threat to American agriculture. The adult seriously damaged certain small fruits, tree fruits, truck and garden crops, ornamental herbaceous garden plants, ornamental shrubs and vines, shade and ornamental trees, and many noneconomic plants. The grub destroyed large areas of turf in lawns, golf courses, and pastures and damaged the roots of other plants.

Some phases of investigating the biology of the Japanese beetle in the United States were conducted by the U.S. Department of Agriculture in cooperation with other Federal agencies, State agricultural experiment stations, State departments of agriculture, and universities within the area infested by the insect. Reports on the progress of the investigation appeared from time to time in Federal and State publications and in various scientific journals, but much additional information is found in the unpublished progress reports by F. E. Baker, T. N. Dobbins, W. C. Ellis, W. E. Fleming, H. Fox, H. F. Goonewardene, C. H. Hadley, I. M. Hawley, M. G. Klein, T. A. Ladd, Jr., P. J. McCabe, J. T. McGuire, E. L. Plasket, L. B. Smith, C. A. Thomas, R. T. White, H. J. Willard, and D. B. Zepp on file

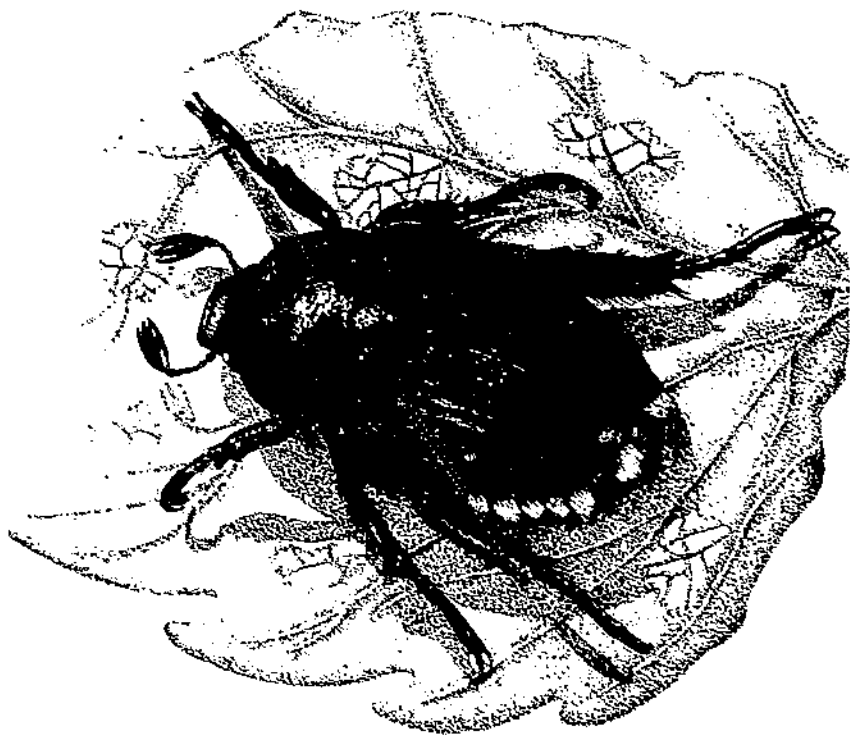
¹The year in italic after the author's name is the key to the reference in Literature Cited, p. 117.

at the Japanese Beetle Laboratory, Moorestown, N.J. This bulletin summarizes the results of published and unpublished studies conducted from 1917 to 1970 on the biology of the beetle.

EXTERNAL ANATOMY

The Adult Beetle

The adult beetle (fig. 1) is a beautiful brightly colored oval insect, varying in length from 8 to 11 mm. and in width from 5 to 7 mm. The female is usually larger than the male. The body is a brilliant metallic green. The three pairs of legs on the thorax are a dark coppery green, varying slightly in hue. The coppery brown elytra, which do not cover the abdomen completely, expose a row of five lateral spots of white hairs on each side of the abdomen and a pair of these spots on the dorsal surface of the last abdominal segment. These white spots on the green abdomen distinguish this beetle from all other beetles that resemble it. (Davis 1920a; Hadley 1922; Smith



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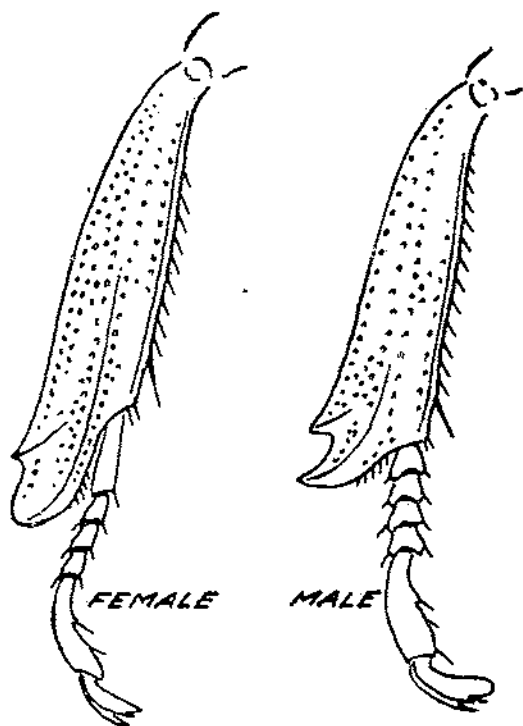
FIGURE 1.—Adult Japanese beetle. Five times natural size.

1925; Smith and Hadley 1926; Hadley and Hawley 1934; Fleming 1963a)

The dorsal surface of the body is slightly flattened and without pubescence or scales. The ventral surface is covered with short gray hairs. The head and thorax are thickly and coarsely punctated; the striae of the elytra are double punctured. The second stria is imperfect, terminating considerably below the apex of the elytron. (Smith and Hadley 1926)

There are seven well-developed parts in the mouth—the labium, hypopharynx, left and right maxillae, left and right mandibles, and labrum. When the beetle is feeding, the labium is pushed downward to regulate the space required by the grinding mouth parts. The maxillae and the mandibles swing laterally with a forward-and-back motion to rasp the plant tissue. (Swingle 1930a)

The sexes are most easily distinguished by slight differences in the shape of the tibia and tarsus of the first pair of legs. As shown in figure 2, the tarsus of the male is slightly shorter and stouter than



J-2056

FIGURE 2.—Foretibiae and foretarsi of Japanese beetle, showing difference in structure between male and female. Greatly enlarged.

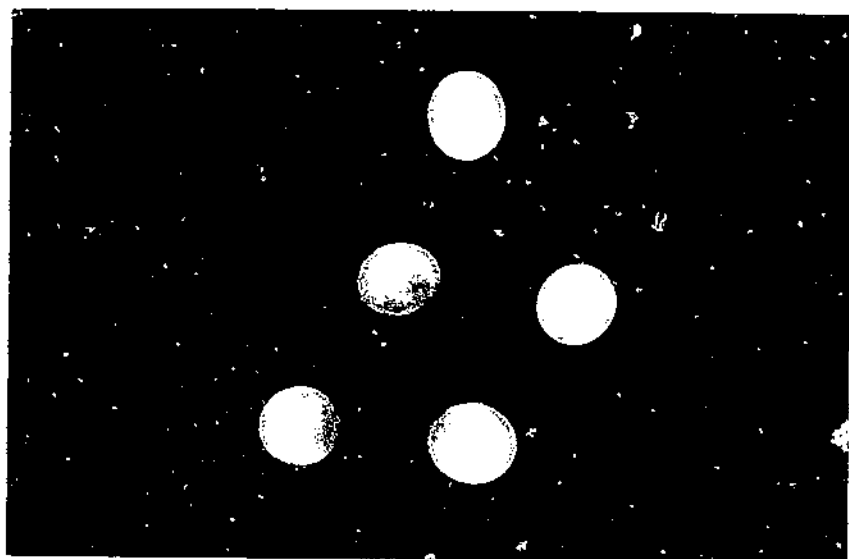
the tarsus of the female. The tibial spur of the male terminates in a sharp point, whereas this spur on the female is longer and rounded. (Smith and Hadley 1926; Hadley and Hawley 1934; Fleming 1963a)

The Egg

The size, shape, and color of newly deposited eggs vary considerably. Some are spheroides about 1.5 mm. in diameter, some are ellipsoides measuring 1.5 mm. in length and 1 mm. in width, and others tend to be slightly cylindrical. They range from a translucent white to creamy. The external surface of the protecting chorion is marked with small hexagonal areas. As the embryo develops, the egg enlarges until it is almost twice as large as the newly deposited egg and it becomes almost spherical in shape (fig. 3). The developing embryo is then visible through the chorion. (Davis 1920a; Smith and Hadley 1926; Hadley and Hawley 1934)

The Grub

A completely white grub about 1.5 mm. long emerges from the egg. Its head is equipped with biting mouth parts, each of the three thoracic segments bears a pair of legs, and there are 10 abdominal



J-722

FIGURE 3.—Mature eggs of Japanese beetle. Eight times natural size.

segments. It lies in its earthen cell curled in the general shape of a blunt-ended crescent in the same manner as the full-grown grub shown in figure 4. A few hours after the grub emerges, the head and the spiracles change to a yellowish brown. After feeding, the accumulation of fecal matter in the hindgut gives the posterior part of the abdomen a grayish to black appearance. The scutellum of the metathorax bears on each side a small hard mucronate process armed with sharp rigid points. Possibly these processes assist the hatching grub in breaking through the chorion. There is one pair of mesothoracic spiracles and there are eight pairs of abdominal spiracles. Each spiracle has a round disk-shaped respiratory plate, but there is no bulla or respiratory slit. (Boving 1921, 1939)

The entire grub is covered with rather long scattered brown hairs, which are interspersed with short blunt brown spines. On the ventral side of the last abdominal segment many rather long brown hooked spines are scattered, and there are many yellowish hairs at the sides and the end. Medially two conspicuous rows of six or seven shorter straight spines are arranged in the form of a V. This V-shaped



J-5123

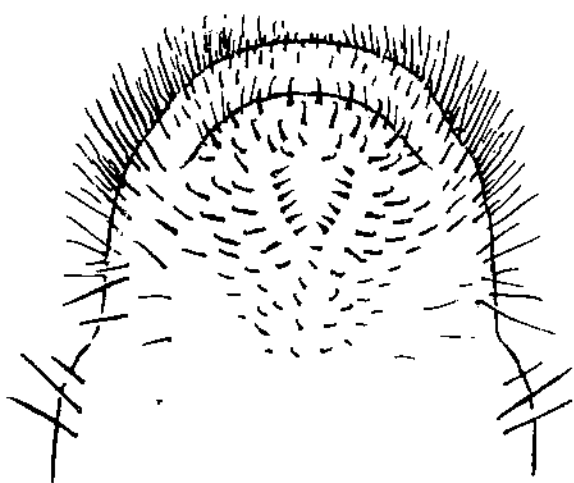
FIGURE 4.—Full-grown Japanese beetle grub. Six times natural size.

arrangement on the raster (fig. 5) distinguishes this grub from all other white grubs. Just prior to molting the middorsal length of the body averages 10.5 mm. The midventral length is slightly shorter. (Boving 1921, 1939; Sim 1934)

During the first molt the head is enlarged. The external characteristics of the second-instar grub are the same as those of the first instar with the following exceptions: The scutellum of the metathorax is not armed with a process on each side. Each spiracle has a concave respiratory plate surrounding a large bulla with a curved spiracle slit. The concavity of the respiratory plates of the thoracic spiracles faces posteriorly, whereas the concavity of the respiratory plates of the abdomen faces anteriorly. Just prior to the second molt the middorsal length of the body of the second-instar grub averages 18.5 mm. (Boving 1939)

During the second molt the head is again enlarged. The external characteristics of the third-instar grub are the same as those of the second instar. When the grub is mature, the middorsal length of the body averages 32 mm. (Boving 1939)

The difference in body length of the second and third larval instars is so marked that these instars can be distinguished by their size. The difference in size of the fully developed first instar and the newly molted second instar is less obvious, but the first instar is so well



J-3070

FIGURE 5.—Arrangement of hairs and spines on underside of last body segment of Japanese beetle grub. V-shaped arrangement of last two rows of spines distinguishes this grub from all others.

marked by the structure of the metathoracic scutellar process and the form of the spiracles that these two instars are easily separated.

Since the head does not grow during a stadium, its size is a most convenient measurement to separate the larval instars. The head of the first-instar grub averages 1.2 mm. wide and 0.7 mm. long, whereas the head of the second instar is 1.9 mm. wide and 1.2 mm. long and the head of the third instar 3.1 mm. wide and 2.1 mm. long. The head measurements of individuals in each instar are separate and distinct from those of another instar. The head of the smallest individual in an instar is distinctly larger than that of the largest individual of the preceding instar. Although the ratios for the increase in head width are different from those for the increase in length, the increase in width of the head is directly proportional to its increase in length. (Davis 1920a; Abercrombie 1936; Boving 1939; Ludwig and Abercrombie 1940)

The Prepupa

The existence of an instar between the last larval one and the pupal instar is usually not recognized, but such a form exists in the metamorphosis of a holometabolous insect such as the beetle. When the grub is mature, it ceases to feed, ejects the accumulated excrement, and becomes almost inactive. The body becomes pale and the cuticula shrunken. Eventually the developing appendages become everted from their sacs and lie for the first time outside the newly developed pupal cuticula, beneath the old larval cuticula. Internal changes also occur. The prepupa responds thigmotactically, but it does not feed.

The Pupa

During the transformation from prepupa into pupa the insect is inactive and helpless. The pupa (fig. 6) resembles somewhat the adult, except that the wings, legs, and antennae are folded closely to the body and functionless. The average pupa is 14 mm. long and 7 mm. wide. The movement of the developing pupa within the cast larval cuticula splits the skin on its dorsal side to expose a white or pale cream-colored pupa. The body gradually becomes a pronounced tan and finally the metallic green of the adult. The caudal abdominal segment is noticeably divaricated. The tergum, pleura, and sternum of most of the abdominal segments are elevated mesially into carinae-like ridges. (Ellis unpublished; Smith and Hadley 1926; Hadley and Hawley 1934; Fleming 1963a)

The male pupa is distinguished from the female pupa by a three-

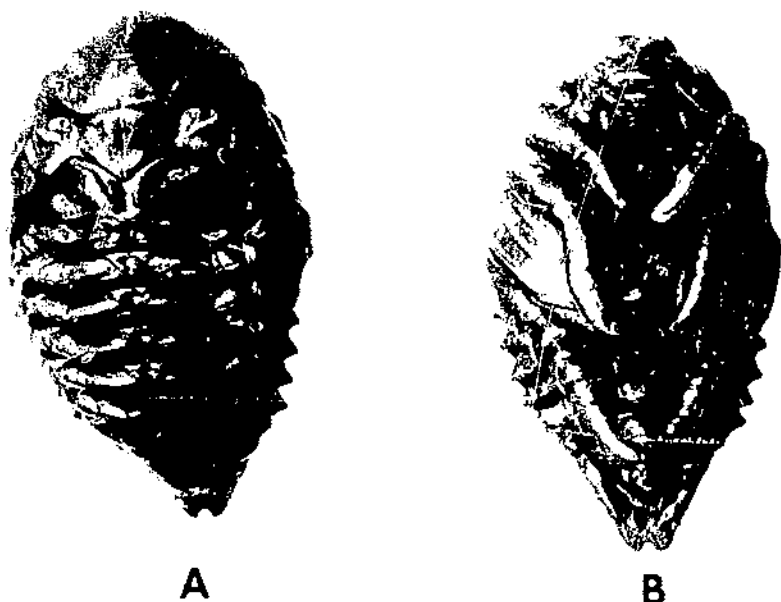


FIGURE 6.—Japanese beetle pupa: A, Dorsal view; B, ventral view.
Six times natural size.

J-5129

loba eruption covering the developing genitalia on the posterior ventral abdominal segments (Ladd and McCabe unpublished).

When the transformation to the adult is completed, the adult splits the pupal skin and withdraws its body and appendages. The newly emerged adult is soft and delicate. It remains in the earthen cell formed by the grub until the chitin of the cuticula hardens, the wings expand to normal size, and the sexual organs mature. (Ellis unpublished; Smith and Hadley 1926)

INTERNAL ANATOMY

The Adult Beetle

Alimentary Tract

Swingle (1930a) studied the alimentary tract of the adult beetle. It consists of the esophagus, the ventriculus, and the hindgut. The esophagus and the hindgut are invaginations of the ectoderm and resemble it in structure. The ventriculus developed from the endo-

derm of the embryo. The tract begins as a straight tube behind the mouth in the head and thorax, and after entering the abdomen it coils about itself, filling the major part of the cavity. The hindgut lies on the dorsal side of the body with the ventriculus beneath it. The alimentary tract is approximately twice as long as the body.

Esophagus.—The mouth opens into a short esophagus, which lies almost entirely within the head of the beetle. Two chitinous plates, one at the base of each mandible, fit into the anterior opening of the esophagus and serve to hold it open and to grind passing food. The anterior part is threadlike. The posterior half widens into a pear-shaped crop.

At the anterior end of the esophagus the intima is rather thick and forms spines extending into the tract. Beyond this the intima is thin and wavelike. The epithelium is uniform from the mouth to the esophageal valve and consists of pavement cells, which are about the same size throughout the esophagus. If a basement membrane is present, it is extremely thin and clings very closely to the base of the epithelial cells.

A thin layer of longitudinal muscles fits closely to the epithelium and forms almost a perfect sheath about the esophagus. The circular muscles are well defined but are present only in scattered strands.

The beetle apparently has no salivary glands. No glands were found in the head and thorax and no salivary enzyme was found in the alimentary tract or its contents.

Esophageal Valve.—The esophageal valve, a ring of epithelial cells that forms a constriction between the esophagus and the ventriculus, has no sphincter muscles. It is not efficient because the contents of the ventriculus are readily regurgitated into the esophagus.

Ventriculus.—The ventriculus is the major part of the alimentary tract. It ranges in length from 2 to 2½ cm. It goes back from the esophageal valve into the abdomen where it is coiled about itself. It narrows gradually toward the posterior end. The circular muscles are fairly well developed throughout the ventriculus and serve to force the food through the tract. The longitudinal muscles are thin and probably not important.

The anterior end of the ventriculus has a ring of modified epithelial cells, which forms a collar around the esophageal valve. These cells secrete a thin peritrophic membrane, which serves to protect the delicate epithelium from rough particles of food as they move through the ventriculus.

The epithelium of the ventriculus is composed of large columnar cells, which break and discharge a digestive secretion and are replaced by new cells developed in the nidi.

Pyloric Valve.—The posterior end of the ventriculus tapers into a conelike process, which enters the well-developed pyloric valve. The intima occurs in wavelike folds, which become thickened at the posterior end of the valve where they form large spines extending into the tract. The circular muscles are very well developed, forming the major part of the valve wall. A layer of longitudinal muscles covers the circular muscles.

Malpighian Tubes.—Four Malpighian tubes arise from the cone-like process as it enters the pyloric valve. Two of them open on either side; the other two have a common opening. The tubes are simple and straight as they leave the alimentary tract, but slightly beyond this they have a fine lacelike appearance. Two of the tubes cling to the wall of the tract and run anteriorly to the esophageal valve, where they turn and run posteriorly to the colon. The other two tubes are about one-half the length of the first pair.

Hindgut.—Beyond the pyloric valve the hindgut widens and has a very thick opaque yellow wall, which is usually wrinkled and pitted. In this part of the gut the intima is drawn out into long needlelike spines, which extend into the tract. When the beetle feeds, the finely ground particles of food become lodged among the spines until only a small passage remains through the center of the gut. The hindgut then narrows for a short distance, where it is relatively thin walled and translucent, and widens again to form a large rectum. It terminates at the anus.

The rectum, like the pyloric valve, is very muscular. The circular muscles are well developed throughout the hindgut; those in the forepart are much reduced in size, whereas those in the posterior part are greatly enlarged. Longitudinal muscles are present only in the forepart of the hindgut.

Respiratory System

Each of the spiracles is the opening of a trachea. The main tracheal trunk arising from a spiracle soon divides into several branches, and by repeated divisions an immense number of branches are formed. The ultimate branches of the tracheal system are connected with small tracheoles, which penetrate within living cells throughout the

body to supply oxygen and to remove carbon dioxide. The tracheoles are probably the essential organs of respiration and the tracheae serve as conduits.

Circulatory System

The beetle has an open circulatory system, the blood filling the cavities in the body and its appendages not occupied by the internal organs. The only blood vessel is a tube just beneath the dorsal body wall and above the alimentary tract, extending from the caudal end of the abdomen through the thorax into the head. The tube is divided into two sections—the heart, which lies in the abdomen, and the slender aorta, which traverses the thorax and terminates in the head. The heart is closed at the posterior end and is divided by constrictions into chambers, which are separated by valves. The muscular layer of the wall of the heart is composed chiefly of circular muscles. The rhythmic pulsations of the heart force the blood into the aorta, from which it flows in streams into the spaces between the internal organs. After bathing these organs, the blood returns to the heart and enters it through the ostia on its sides.

Reproductive Organs

Male.—Each of the two testes consists of six disklike divisions and are connected to the vas deferens by means of the vasa efferentia. The paired canals of the vas deferens expand near their junction with the ejaculatory duct to form the seminal vesicle in which the spermatozoa are assembled. There is one pair of accessory glands, which are about four times the length of the vas deferens. The ejaculatory duct is only 0.5 mm. long. The terminal section of the duct is enclosed in a fingerlike evagination of the ventral body wall to form the male intromittent organ, the aedeagus. The aedeagus enters the vagina of the female during coitus. (Williams 1945)

During spermatogenesis the testicular cyst cells form envelopes about groups of spermatocytes and continue to surround the developing gametes until they are mature. As the spermatozoa complete their development they attach themselves by their acrosomes to the cytoplasm of a cyst cell. The cyst cells contain cytoplasmic deposits of ribonucleoproteins, large amounts of glycogen, and lipid bodies. (Anderson 1950a)

The secretion of the accessory glands consists of a ground mass of mucouselike protein polysaccharide compound with large globules of mucus and many droplets of phospholipin and possibly other lipoidal substances. (Anderson 1950b)

Female.—The ovaries lie in the body cavity of the abdomen on either side of the alimentary tract. Each consists of six ovarioles, which open into the oviduct. The two oviducts combine to form the vagina. The duct of the spermatheca, the sac where the seminal fluid is stored, enters the vagina distad of the bursa copulatrix, or copulatory pouch. Two oval glandlike bodies are situated in the tissue surrounding the distal end of the vagina. (Williams 1945)

The seminal fluid of the male, which is deposited in the vagina of the female during coitus, contains spermatozoa in cyst cells and the secretion of the accessory glands. The cyst cells disintegrate in the lower part of the genital tract of the female, releasing the spermatozoa and the contents of the cells. The glycogen from the cyst cells and the mucopolysaccharides from the accessory glands may be an important source of nutrition for the spermatozoa stored in the spermatheca of the female. The egg becomes fully grown and the chorion is formed about it before it is fertilized. Small openings, the micropyle, in the chorion permit the entrance of the spermatozoa. (Anderson 1950b)

The Grub

Alimentary Tract

Beard (1945) and Rapp (1947) studied the alimentary tract of the grub. Many of its features are similar to those of the adult beetle.

Esophagus.—The mouth opens into a very short tube, the esophagus, which lies almost entirely within the head of the grub, and widens in its posterior half to form a simple crop.

Ventriculus.—The ventriculus is a straight tube extending posteriorly from the esophageal valve at the end of the esophagus. The well-developed muscles force the food through the tract. Three circles of cecal diverticula arise from the ventriculus. The first circle at the anterior end consists of short blunt irregularly furcated pouches. The ceca of the second circle, about one-third the distance between the first and third circles, are conical in shape. The ceca of the third circle arise near the posterior end of the ventriculus. They are conical in shape, directed anteriorly, and usually rather appressed to the gut. They are relatively short on the dorsal side and become progressively longer toward the ventral side.

Malpighian Tubes.—Two pairs of Malpighian tubes arise in the anterior part of the hindgut, not far back of the third circle of gas-

tric ceca. These tubes are long, extending anteriorly to the anterior part of the ventriculus and then posteriorly.

Hindgut.—The hindgut, which begins at the muscular pyloric valve, consists of three parts reflected upon each other in a Z-configuration. The anterior part, which is uppermost, tapers posteriorly to the greatly enlarged anteriorly directed rectal sac beneath it. The rectum beneath the rectal sac is directed posteriorly and terminates at the anus. The midpart of the rectum is expanded.

Respiratory System

Each of the nine pairs of spiracles is the opening of a trachea. The tracheal system extends to all parts of the body.

Circulatory System

The grub has an open circulatory system with the heart and the aorta on the dorsal side of the body.

EMBRYONIC DEVELOPMENT

Chromosomes

The male beetle has 18 somatic chromosomes—eight autosomal pairs and one pair of relatively small sex chromosomes (Smith 1953).

Cycle of Embryogenesis

Geise² studied the embryonic development of the beetle at 30° C. During the first 4 days embryogenesis consists of the formation and growth of the germ band and its associated structures, such as appendage buds and the rudiments of various internal organs. The germ band increases to such an extent that it is longer than the egg and grows dorsally to partly enclose the yolk. Blastokinesis occurs between the fourth and fifth days. It consists of a shortening of the germ band so that it is the same length as the egg and a buckling of the embryo so that the anterior and the posterior ends almost touch. Instead of growing around the yolk dorsally, as it did earlier, the posterior end twists under the middle part of the embryo and grows

²GEISE, E. C. EMBRYOGENY OF THE JAPANESE BEETLE, *POPILLIA JAPONICA* NEWMAN, AND A CORRELATION OF MORPHOLOGICAL EVENTS WITH KNOWN PHYSIOLOGICAL CHANGES. 1953. [Ph. D. thesis. Copy on file New York University.]

anteriorly. During this process the yolk, as viewed laterally, changes from an oval to a bean shape, a typical scarabaeoid shape. Beginning with the fifth day the formation of new structures becomes secondary to the growth and differentiation of structures already formed.

Increase in Weight

The newly laid egg weighs 0.83 to 0.86 mg. During incubation it increases to 2.3 to 2.4 mg. in 14 days at 20° C. (Ludwig 1932), in 8 days at 25° (Ludwig 1932), and in 4 days at 30° (Rothstein 1952). The weight remains practically constant during the remainder of the embryonic period.

The increase in egg weight is associated with the imbibition of water. The newly laid egg contains 49 to 50 percent of water. After the egg reaches its maximum weight, it contains 81.8 to 84 percent of water. The increase in water content is more than sufficient to account for the increase in weight, an indication that some loss of weight results from the metabolism of some of the egg substances. (Ludwig 1932; Rothstein 1952)

Importance of Water

The egg of the beetle, like those of other scarabaeid beetles, must absorb water as a prelude to and during embryonic development. Since it is adapted to develop in a moist soil, it apparently has no mechanism for retaining water. If there is not sufficient moisture in the soil, the eggs perish. (Ludwig 1932)

Effect of Temperature

Development at Constant Temperatures

No eggs hatched below 15° C., although Ludwig (1928a) observed some embryonic development at 13° and Fox (1939) at 12.5°. Ludwig (1928a) found that the average incubation period was as follows:

Days	° C.
61-----	15
33-----	17.5
21-----	20
15-----	22.5
11-----	25
9-----	27.5
8-----	30
0-----	34

Only 42 percent of the eggs hatched at 15° C., but 75 percent or more hatched at temperatures from 17.5° to 34°. The optimum for incubation appears to be about 30°. (Ludwig 1928a)

Effect of Alternating Temperatures on Development

The effect of alternating temperatures on the length of incubation as compared to the development at constant temperatures depended on the relationship of the temperatures to the threshold and the optimum temperatures for development. Eggs held at 10° C. one day, 20° the next day, 10° the following day, and so on hatched in 31 days, whereas those held at a constant temperature of 15° required 61 days to hatch. Eggs subjected to alternating temperatures of 15° and 25° hatched in 20 days; those held at 20° hatched in 21 days. Eggs subjected to alternating temperatures of 25° and 35° hatched in 12 days; those held at 30° required 8 days. These data show that embryogenesis is accelerated when the temperature fluctuates above and below the threshold temperature; it is not modified when the temperature fluctuates between the threshold and the optimum temperatures, and it is retarded when the temperature fluctuates above and below the optimum. (Ludwig 1928a)

Cold Hardiness

The eggs are not cold hardy. No eggs survived exposure for 1 week to 0° C. or for 1 day to -20°. At 3° to 5° the viability decreased to 90 percent in 6 days, 70 percent in 14 days, 50 percent in 21 days, and zero in 28 days. (Hall et al. 1968)

The viability of the eggs was decreased and their development retarded as the exposure to 10° C. was prolonged before incubating at 30°. Ninety-five percent of the eggs not exposed to the lower temperature hatched in 8.3 days. Exposure to 10° for 1 week reduced the hatch to 39 percent and increased the incubation period at 30° to 8.5 days. Two weeks' exposure reduced the hatch to 37 percent and increased the incubation period to 9.4 days; three weeks' exposure also reduced the hatch to 37 percent and increased the incubation period to 11.5 days. Many of the grubs hatching from eggs exposed to the lower temperature for 3 weeks were so weakened that they were unable to free themselves from the chorion. (Ludwig 1930)

Exposure to 10° C. for 1 week modified the vitality of the eggs during all stages of embryonic development at 30°. Newly laid eggs were the most susceptible to the cold; only 8 percent of them hatched. The hatch was 60 percent of the eggs 1 day old, 50 percent of those 3 days old, 39 percent of those 5 days old, and 50 percent of those 7 days old. (Ludwig 1930)

The eggs are not physiologically adapted to withstanding for long periods exposures below 15° C. It is not uncommon to find apparently normal eggs in the field in late fall or early spring, but none of them were viable. When brought to a warm laboratory, these eggs soon disintegrated. (Hawley 1944)

Biochemical Changes

pH

The contents of the egg are slightly alkaline; the pH is 7.1 during embryonic development (Fink 1925).

Nitrogen

The total nitrogen in the egg remained constant during embryogenesis. It ranged from 3.60 mg. (Rothstein 1952) to 3.95 mg. (Ludwig and Rothstein 1952) per 100 eggs. There was a slight loss of nitrogen during eclosion, which may be associated with the loss of the egg chorion. There were, however, changes in the distribution of nitrogen during the embryonic period.

In the newly laid egg 12.9 percent of the nitrogen was insoluble and 87.1 percent of it was soluble in water. The distribution of the water-soluble was 1.7 percent in phospholipids, 4.0 percent in amino, peptide, and other nonprotein nitrogenous compounds, and 81.4 percent in metaprotein, proteose, and peptone portions of the egg. The nitrogen in the insoluble nitrogenous portion increased to 71.8 percent just before hatching and then decreased to 66.4 percent in the newly hatched grub. (Ludwig and Rothstein 1952)

The phospholipid nitrogen increased to 11.2 percent in the 3-day-old egg and then decreased regularly to 7.2 percent in the newly hatched grub. The nonprotein nitrogen increased to 9.1 percent during the first 3 days of incubation, remained approximately constant during the remainder of the embryonic period, and increased to 15.3 percent in the newly hatched grub. The metaprotein, proteose, and peptone nitrogen decreased progressively to 10 percent just before hatching and then increased to 11.1 percent in the newly hatched grub. The shift of nitrogen from the metaproteins, proteoses, and peptones to insoluble nitrogen probably indicates the synthesis of structural proteins in the developing embryo. There was no evidence of the accumulation of waste nitrogen or that nitrogenous compounds were used as a source of energy in the egg. (Ludwig and Rothstein 1952)

Reducing Compounds

Reducing compounds, expressed as glucose, increased from 0.20 mg. per 100 eggs in the newly laid egg to 0.77 mg. in the 3-day-old egg, decreased to 0.50 mg. during the fourth and fifth days, and then slowly increased to 0.61 mg. at the end of the embryonic period (Rothstein 1952).

Glycogen

Glycogen decreased rapidly from 2.09 mg. per 100 eggs in the newly laid egg to 1.24 mg. during the first 4 days of incubation, remained constant during the next 2 days, and then decreased to 0.93 mg. at the time of hatching. It is possible that glycogen is the main source of energy during the early part of embryogenesis. (Rothstein 1952)

Phosphorus

The total phosphorus remained constant during embryonic development, averaging 0.422 mg. per 100 eggs, but there were changes in its distribution. In the newly laid egg 28.0 percent of the phosphorus was in the insoluble portion of the egg, 6.2 percent in the phospholipids, 41.2 percent in the acid-soluble portion, and 24.6 percent in the water-soluble portion precipitated by tungstic acid or trichloroacetic acid. The phosphorus in the insoluble portion increased to 41.1 percent in 3 days, remained at this level for the next 3 days, and decreased to 38.3 percent just before hatching and to 35.9 percent in the newly hatched grub. The phosphorus in the phospholipids increased steadily to 21.5 percent in the newly hatched grub. The phosphorus in the acid-soluble portion increased slightly to 42.8 percent during the first 3 days and then decreased steadily to 32.2 percent in the newly hatched grub. The phosphorus in the acid-precipitated portion decreased rapidly during the first 4 days to 3.7 percent and then during the last days of the embryonic period it increased slowly to 4.2 percent. (Ludwig 1958)

The change in the acid-precipitated portion was the reciprocal of that in the insoluble portion. The data indicate that the phosphorus in the acid-precipitated portion is transferred during embryogenesis to the other portions. The increase in the phosphorus in the insoluble portion may show the synthesis of protein tissue since phosphorus is an important constituent of protein. The increase in the phospholipids may also show the synthesis of tissue. (Ludwig 1958)

Fat

The bound lipid remained constant throughout the embryonic period. There was no change in the free fat (ether soluble) during the early part of embryogenesis, but beginning with the fourth day there was a marked decrease, which continued to the time of hatching. The total loss was approximately 58 percent. The indications are that free fat is the main source of energy during the last part of embryonic development. (Rothstein 1952)

Respiratory Metabolism

Corresponding to these changes in the concentration of the metabolites, the respiratory quotient decreased from 0.89 in the newly laid egg to 0.75 just before hatching. The rate of oxygen consumption increased rapidly during the first day of embryogenesis, remained constant during the next 2 days, and then increased steadily during the remainder of the embryonic period. (Ludwig and Wugmeister 1955)

Ludwig and Wugmeister (1955) studied the activities of the respiratory enzymes, cytochrome oxidase and succinic dehydrogenase, in egg homogenates at a dilution of 1:1,000. The oxygen consumption of each of these enzymes was high in the newly laid egg, but decreased rapidly during the first 4 days of embryogenesis because of the dilution of the enzymes by the imbibition of water. Beginning with the fifth day the activities of the enzymes increased rapidly until the end of the embryonic period. Ludwig and Barsa (1957) found that the oxygen consumption of 5-percent egg homogenates was enhanced during the embryonic period by adding sodium succinate or cytochrome c to the homogenates. When both substrates were added simultaneously, the increase in oxygen consumption was greater than with either substrate alone.

POSTEMBRYONIC DEVELOPMENT

Histological Changes

Abercrombie (1936) determined the number and the size of the cells in the epithelium of the ventriculus and in the brain during the development of the grub from hatching to maturity. At the end of the first stadium the average weight of the grubs was 5.73 times that of the newly hatched grubs, whereas the increase in the number of columnar cells in the ventriculus was only 1.67 times and in the brain cells 1.19 times. During the second stadium the average weight in-

creased 5.24 times, and the number of cells in the ventriculus increased 1.98 times and those in the brain 1.69 times. During the third stadium the weight increased 3.18 times, but there was practically no increase in the number of cells in the ventriculus or the brain. There was no increase in the number of cells in the ventriculus and the brain during molting, but the size of the head capsule increased only during this period. There was a close relationship between the increase in the weight of the grub and the increase in the volume of the cells. The mature third-instar grub was 96.2 times as heavy as the newly hatched grub. During this period the volume of the cells increased 99.8 times.

Ludwig and Abercrombie (1936) determined the time in the first and second stadia when cell divisions occurred and the mechanism by which the increase in the columnar cells in the ventriculus was attained. During the first 4 days of each instar at 25° C. there was no increase in the number of columnar cells; growth was due to the increase in the size of the cells already present. The number of columnar cells began to increase on the fifth day of each stadium and continued to increase until the grub prepared to molt. New columnar cells were produced by divisions of the basal or interstitial cells and their subsequent transformation into columnar cells. The new cells became elongated, pushed between adjacent columnar cells, and continued to grow until they reached the size of the columnar cells already present. Cell multiplication and differentiation occurred simultaneously and most rapidly near the end of each stadium.

Several investigators, including Przibram and Megusar (1912), Stjern (1914), Eidmann (1924a, 1924b), and Titschak (1924), claimed that molting in insects occurs when the weight has doubled. This doubling in weight was supposed to result from a single division of the body cells. When the weight was more than doubled before molting, Przibram and Megusar (1912), Bodenheimer (1927), and Alpatov (1929) claimed that the ratio of the weight to the number of cell divisions was some exponent of 2. Ludwig (1932) attempted to apply this principle to the growth of the grubs and concluded that his data did not substantiate the idea of a progression factor in their growth. This conclusion was questioned by Bodenheimer (1933).

Ludwig (1934a) made a more detailed analysis of his data, using the method advocated by Bodenheimer (1932, 1933) for calculating latent cell divisions in holometabolous insects. The observed and calculated weights of individual grubs were rarely in close agreement and wide discrepancies were common. He estimated that there were three probable cell divisions in the first instar, two in the second

instar, and three in the third instar. The estimated number of cell divisions during the development of the grub was not substantiated by determining the actual number of cell divisions. Abercrombie (1936) found that the number of columnar cells in the ventriculus increased 1.67 times during the first stadium and 1.98 times during the second stadium, but there was no significant increase in the number of cells during the third stadium.

Variation in Weight During Metamorphosis

Ludwig (1931) determined the weight of the different stages of the beetle during metamorphosis at a constant 25° C. These data are summarized in table 1.

There were great variations in the weight of the individuals at each stage of metamorphosis. The smallest female was not as heavy as the heaviest male. The average weight of the females, however, was consistently more than that of the males.

The grub reached its maximum weight upon maturity. The weight declined as the grub ceased feeding and began to prepare for transformation to a prepupa. Some grubs remained near maximum weight for several weeks. The decline in weight continued through the prepupal stage. There was a sharp loss of weight accompanying pupation. The emergence of the adult was accompanied by a loss of more than one-third of the pupal weight.

During metamorphosis the male lost 49.8 percent of its weight and the female 47.1 percent. Some of the loss was due to the elimination of matter from the alimentary tract as the grub changed to a prepupa, in the shedding of the larval skin as it changed to a pupa, and in the shedding of the pupal skin as it changed to an adult, but most of the loss was water. The water content was 78 percent in the mature grub, 74 percent in the prepupa and pupa, and 66.6 percent in the

TABLE 1.—*Variation in weight of Japanese beetle during metamorphosis at 25° C.*

Stage of development	Male			Female		
	Maxi- mum	Mini- mum	Aver- age	Maxi- mum	Mini- mum	Aver- age
	<i>Mg.</i>	<i>Mg.</i>	<i>Mg.</i>	<i>Mg.</i>	<i>Mg.</i>	<i>Mg.</i>
Mature grub -----	265	202	227	324	235	276
Early prepupa ----	245	190	206	310	230	254
Pupa -----	220	145	181	287	165	223
Adult -----	153	82	114	184	110	146

adult. During the transformation from grub to adult the male lost 56.8 percent of its water and the female 54.8 percent.

Effect of Temperature

Range for Development

The range of temperature for the development of the beetle is from 13° to 35° C., but all stages do not tolerate these extremes of temperature. No eggs hatched at 13° or above 34°. The range of temperature for embryonic development is from 15° to 34°. Grubs hatching at these extremes of temperature lived only a few days. Grubs developed at between 17.5° and 30°, but they did not pupate above 27.5°. Pupae developed at temperatures from 13° to 35°. Many of the adults emerging at these temperature extremes were abnormal. The optimum for development was 30° for the eggs, 27.5° for the grubs, and between 30° and 32° for the pupae. The beetle developed from egg to adult at between 17.5° and 27.5°. (Ludwig 1928a)

More recently Goonewardene (unpublished) and Ladd (unpublished) reared the beetle from egg to adult at 29°.

Although grubs hatched at 15° C. did not survive at this temperature, those hatched at 25° and transferred immediately to 15° were able to live, some of them developing to second instars (Ludwig 1928a).

Modification of Stadia at Constant Temperatures

Ludwig (1928a, 1932) determined the effect of temperature on the length of the stadia during the development of the beetle from newly hatched grub to adult at 20° and 25° C. These temperatures are well within the range for the development of all stages. The results are summarized in table 2.

TABLE 2.—*Effect of temperature on length of stadia of immature stages of Japanese beetle*

Temperature (° C.)	First-instar grub	Second-instar grub	Third-instar grub and prepupa	Pupa	Total
	Days	Days	Days	Days	Days
20 -----	30	56	105	17	208
25 -----	17	18	102	7	144

The average length of the development period from the newly hatched grub to the adult was 208 days at 20° and 144 days at 25° C. There were, however, great variations in the larval stadia at these temperatures. The variations in the pupal stadium were not given. The first larval stadium ranged from 29 to 30 days at 20° and from 16 to 28 days at 25°; the second larval stadium ranged from 33 to 70 days at 20° and from 17 to 35 days at 25°. The length of the third-instar grub-prepupal period ranged from 92 to 126 days at 20° and from 91 to 106 days at 25°. The length of this last period was modified by the past history of the individual; it was relatively long when the previous periods were short and relatively short when the previous periods were long. With this adjustment the period of development from first-instar grub to adult was practically constant at each temperature.

Since grubs are inactive during hibernation in the winter, Ludwig (1928a) suggested that the development of some grubs at favorable temperatures was due to a resting period during the first-, second-, or third-instar larval stages.

Modification of Stadia by Alternating Temperatures

The effect of alternating temperatures on the length of the grub and pupal periods as compared to constant temperatures depended on the relationship of the temperatures to the threshold and optimum temperatures (Ludwig 1928a).

The stadia were shortened when the temperature fluctuated daily above and below the threshold of development. First-instar grubs subjected to 10° C. one day, 30° the next, 10° the following day, and so forth, molted in 28 days; those held at a constant temperature of 20° molted in 30 days. Pupae subjected to alternating temperatures of 10° and 20° transformed to adults in 29 days, but those held at a constant temperature of 15° required 42 days to complete their development.

The stadia were not modified significantly when the fluctuation of the temperature was between the threshold and the optimum temperatures for development. Grubs subjected to alternating temperatures of 15° and 25° C. during the entire larval period pupated in 159 days; those held at a constant temperature of 20° pupated in 160 days. Pupae subjected to these alternating temperatures transformed to adults in 18 days; those held at a constant temperature of 20° transformed in 17 days.

The stadia were lengthened when the temperature fluctuated above and below the optimum temperature. First-instar grubs subjected to alternating temperatures of 25° and 35° C. molted in 23 days; those

held at a constant temperature of 30° molted in 17 days. Pupae subjected to these alternating temperatures transformed to adults in 9 days, but those held at a constant temperature of 30° transformed in 7 days.

Modification of Growth

Ludwig (1939) found that the temperature not only modified the length of the stadia but also affected the growth of the beetle. As shown in table 3, each stage reared at 25° C. was approximately 20 percent heavier than its counterpart reared at 20°.

This increase in weight at 25° C. could not be attributed to an increase in the number of cells in the body. Grubs reared at 20° had approximately the same number of cells as those reared at 25°. Ludwig (1939) counted the columnar cells in the ventriculus of the grubs between the second and third rings of gastric ceca. The cells in this area of grubs reared at 20° totaled 354 in the newly hatched grub, 561 in the freshly molted second instar, and 1,092 in the freshly molted third instar, whereas the corresponding cells in grubs reared at 25° were 355, 589, and 1,136, respectively. The small differences were not considered significant because the numbers for each stage did not differ by more than 5 percent.

In a further study Ludwig (1939) found that except in newly hatched grubs the cells in the ventriculus of grubs reared at 20° C. were smaller than those in grubs reared at 25°. The volume in cubic microns of cells in grubs reared at 20° was 455 in the newly hatched first instar, 1,172 in the freshly molted second instar, and 1,863 in the freshly molted third instar. The corresponding volumes in grubs

TABLE 3.—*Modification of weight of Japanese beetle during growth and metamorphosis at 2 temperatures*

Stage of development	Average weight at—	
	20° C.	25° C.
	Mg.	Mg.
First-instar grub (newly hatched) ----	2.3	2.3
Second-instar grub (just molted) ----	13.1	16.5
Third-instar grub:		
Just molted -----	60.0	86.1
Mature -----	223.4	270.8
Early prepupa -----	214.2	254.5
Early pupa -----	195.5	235.6
Adult -----	123.6	150.4

reared at 25° were 441, 1,584, and 2,404, respectively. The volume of the cells in the second-instar grubs reared at 25° was 35 percent greater than in those reared at 20°. It was 29 percent greater in third-instar grubs reared at 25°. The increase in weight of approximately 20 percent in grubs reared at the higher temperature can be attributed to the larger constituent cells.

Thermal Death Point

Adult Beetle.—The thermal death point at the higher temperatures is modified by the duration of the exposure. An exposure for 60 minutes in air at 43° C. killed 54 percent of the beetles. All beetles were killed by an exposure for 30 minutes at 50° and for 15 minutes at 55°. (Knipling and Sullivan 1958)

The beetle is not completely wetted by immersion in water. Air trapped among the body hairs encloses it in a bubble of air. It withstood immersion for 24 hours in water at 20° C. All beetles were killed by immersion for 30 minutes at 43°, 20 minutes at 44°, 10 minutes at 45°, and 1 minute at 50°. (Fleming and Baker 1932)

Grub.—Newly hatched grubs survived only a few days in soil at 35° C. (Ludwig 1928a). Third-instar grubs were more tolerant of heat but did not survive in soil at 40°.

Third-instar grubs survived immersion for 14 days in water at 20° C. (Fleming 1926), but in a cranberry bog flooded over the winter, where the water ranged from 0° to 10°, 23 percent of the grubs survived for 150 days (Baker unpublished). All first- and second-instar grubs were killed by immersion for 60 minutes in water at 43°, 40 minutes at 44°, 30 minutes at 45°, and 1 minute at 51°. Third-instar grubs were more resistant. Ninety-nine percent of the third instars were killed by immersion for 120 minutes at 43°, but none survived immersion for 70 minutes at 44°, 40 minutes at 45°, and 1 minute at 52°. (Fleming and Baker 1932)

Prepupa.—All prepupae were killed by immersion in water for 80 minutes at 43° C., 50 minutes at 44°, 30 minutes at 45°, and 1 minute at 52° (Fleming and Baker 1932).

Pupa.—Ninety-nine percent of the pupae were killed by immersion for 120 minutes in water at 43° C. None of them survived immersion for 70 minutes at 44°, 40 minutes at 45°, and 1 minute at 53°. (Fleming and Baker 1932)

Cold Hardiness

Grub.—Only a few first-instar grubs have been found in the field in early spring. In southern New Jersey and southeastern Pennsylvania the first instars were less than 0.1 percent of the overwintering population. (Hawley 1944)

The soil temperature at a depth of 7.5 cm. in southern New Jersey and southeastern Pennsylvania rarely falls below -3° C. during the winter. Usually during periods of cold weather the ground is covered with snow, which acts as an insulating blanket and keeps the soil at or near 0° , even when the air temperature falls to -15° (Fox 1935; Hawley and Dobbins 1941). The average winter mortality of the grubs during 1927-34 was only 3 percent, but a reduction of 12 percent occurred in the winter of 1928-29 and 13 percent in the winter of 1933-34 (Fox 1935, 1937).

Grubs hatched at 15° C. but did not survive, but grubs hatched at 25° and transferred before feeding to 10° lived for 17 days. The first instars became progressively more cold hardy the longer they fed at 25° . The longevity at 10° was 20 days after feeding 4 days, 31 days after feeding 8 days, and 50 days after feeding 12 days. When the grubs ceased feeding after the 12th day and eliminated the contents of the alimentary tract in preparation for molting, they became more susceptible to cold. Their longevity at 10° declined progressively with the prolongation of the time they were held at 25° . (Ludwig 1928b) Apparently only first-instar grubs that have fed sufficiently to accumulate a reserve of food and have not entered into the early stages of ecdysis are able to hibernate overwinter.

The second- and third-instar grubs, the overwintering stages, are well adapted to withstanding long periods of inactivity at temperatures below the developmental threshold, except when the alimentary tract is cleared in preparation for molting, during molting, and immediately after molting. Payne (1928) found that the survival of third-instars while inactive in moist sand at 10° C. was 88 percent after 2 months, 68 percent after 4 months, 45 percent after 6 months, 23 percent after 12 months, and 10 percent after 24 months. Goonewardene and Zepp (unpublished) found that the maturity of the third-instar grub was a factor in its survival at 4.5° .

The minimum temperature withstood by grubs is dependent on the intensity of the cold, the duration of the exposure, and their maturity and condition. The mortality of grubs held for 60 days at 0° C. was only 24 percent (Payne 1928). Alternating the temperature between 0° and 30° every 24 hours killed 70 percent of them in 60 days (Payne 1928). Grubs starved for 30 days at 20° did not withstand

exposure to -1.7° (Payne 1928). Grubs removed from soil did not survive exposure to -8.3° (Fox 1935). When the temperature of the soil was reduced from 10° to -8.3° in 11 hours and the soil was thawed gradually, the mortality was 92 percent (Smith unpublished). All grubs were killed by reducing the soil from 10° to -9.4° and holding it at this temperature for 3 or 4 hours or by reducing it to -11.1° and holding this temperature for 15 minutes (Smith unpublished). From a study of these data Fox (1935, 1939) concluded that -9.4° was the highest soil temperature likely to cause a mortality of the grubs approaching 100 percent under natural conditions in the field.

Prepupa.—Prepupae did not withstand prolonged exposure to 10° C. (Payne 1928). A short exposure to 4.4° killed them (Hawley 1944).

Pupa.—Pupae were killed by a prolonged exposure to 10° C. (Payne 1928) or a short exposure to 4.4° (Hawley 1944).

Adult Beetle.—Adult beetles were not affected by exposure for 60 minutes to 0° C., but an exposure of this duration killed 42 percent of them at -5° , 84 percent at -10° , and 100 percent at -15° (Knipling and Sullivan 1957). The disappearance of beetles in the fall is attributed to their having completed their lifespan rather than the low temperatures.

Effect of Relative Humidity

The immature stages of the beetle are adapted to living in a moist soil where the relative humidity is high. Ludwig and Landsman (1937) investigated the effect of the relative humidity of the air on their survival and metamorphosis.

The survival of the immature stages at 25° C. varied directly with the humidity. The survival of third-instar grubs increased progressively from 4 days at 5-percent relative humidity to 30 days at 96-percent humidity. The death of the grubs at the higher humidities was attributed to starvation. The survival of early prepupae increased progressively from 5 days at a humidity of 5 percent to 22 days at 96-percent humidity. The survival of early pupae increased from 2 days at 5-percent humidity to 10 days at 96-percent humidity.

Metamorphosis from grub to prepupa and from prepupa to pupa occurred only when the relative humidity was not less than 82 per-

cent. The transformation from pupa to adult occurred when the humidity was not less than 76 percent. With the exception of the grubs where starvation was a factor, more individuals metamorphosed at 96-percent humidity than at a lower humidity.

Fleming (1934) found the survival of adult beetles held without food at 32° C. increased progressively with the increment in the humidity. Beetles subjected to 5-percent humidity lived 48 hours, whereas those subjected to 35- to 40-percent humidity lived 96 hours, and those subjected to 90- to 95-percent humidity lived 140 hours.

The evaporation of water from a free surface is approximately proportional to the saturation deficiency of the atmosphere. With all these stages apparently lacking the ability to conserve body water, their longevity varied directly with the humidity of the air.

Effect of Desiccation

Ludwig (1936) studied the effect of desiccation on the immature stages of the beetle. When the immature stages were held at 25° C. in air with a relative humidity of 30 to 35 percent, 30 percent of the initial weight was lost by first-instar grubs in 20 hours, second-instar grubs in 48 hours, third-instar grubs in 55 hours, prepupae in 95 hours, and pupae in 160 hours. The fatal limit in the loss of weight by desiccation was 50 percent by the grubs, 44 percent by early prepupae, 34 percent by late prepupae, and 31 percent by pupae.

When grubs were not desiccated to the fatal limit, the lost water was restored before development proceeded. The time required for recovery depended on the extent and the rate of desiccation. Third-instar grubs required 9 days to regain a 30-percent loss of weight, 15 days to regain a 35-percent loss, 19 days to regain a 40-percent loss, and 23 days to regain a 45-percent loss. Recovery was attained in 14 days after desiccation for less than 72 hours, 15 days after desiccation for 72 to 100 hours, 21 days after desiccation for 100 to 150 hours, and 26 days after desiccation for more than 150 hours.

When prepupae were not desiccated to the fatal limit, the lost water was only partially recovered. Practically no lost water was recovered in the pupal stage. Desiccation of prepupae or early pupae tended to prolong the pupal period. The emergence of adults was normal when the loss of water by desiccation was no more than one-half of that normally lost during metamorphosis, but adults did not emerge when more water was lost. The desiccation of prepupae or pupae did not modify the water content of the adult beetle.

Biochemical Changes During Metamorphosis

In the Insect

No food is ingested during the transformation from grub to adult. The energy required during metamorphosis must be obtained from the substances stored in the grub before transformation into a prepupa.

Nitrogenous Substances.—Anderson (1948) found no significant loss of nitrogen, but its distribution changed during metamorphosis. The nitrogen in the water-soluble compounds increased sharply at pupation, followed by a gradual increase during the remainder of the pupal period. The amino acid nitrogen increased at pupation and then decreased during the remainder of the pupal period. The nitrogen in soluble protein—proteose and peptone—decreased sharply between the grub and the early prepupal stages, rose to a high level on the second or third day of the pupal period, and then returned to its former low level by the sixth or seventh day of the pupal period.

These complementary shifts in the distribution of nitrogen were believed to indicate the destruction of the larval tissues in the early pupa followed by the gradual construction of the adult structures during the remainder of the pupal stage. The breakdown of insoluble proteins did not coincide with the increase in oxygen consumption or the increase in the acidity of the blood but occurred later in metamorphosis.

Carbohydrates.—The glucose content of the third-instar grub was 0.52 percent. It decreased to 0.42 percent in the early prepupa and then increased to 0.79 percent in the newly molted pupa. The glucose dropped to 0.68 percent in the 1- and 2-day-old pupae and then increased slowly, reaching 0.86 percent on the last day of the pupal period. The emergence of the adult was accompanied by a loss of glucose. (Ludwig and Rothstein 1949)

The glycogen increased from 1.43 percent in the third-instar grub to 2.07 percent in the early pupa. Glycogen was lost rapidly during the first 4 days of the pupal period, increased on the fifth day, and then steadily decreased to 0.96 percent on the last day. There was no change in the glycogen upon emergence of the adult. (Ludwig and Rothstein 1949)

The increase in glucose and glycogen at the time of pupation might be the result of the breakdown of insoluble proteins in the larval tissue and of the degradation products being stored temporarily as carbohydrates. The decline of glycogen during the pupal period prob-

ably indicates the utilization of glycogen as a source of energy by the pupa. (Ludwig and Rothstein 1949)

Fats.—The fat content of the third-instar grub was 3.16 percent. It increased to 3.76 percent in the prepupa and remained at approximately this level until the fourth day of the pupal period. It decreased on the fifth and sixth days to 3.23 percent and remained relatively constant during the remainder of the pupal period. A loss of fat occurred on the emergence of the adult. (Ludwig and Rothstein 1949)

Respiratory Metabolism.—The respiratory metabolism of the third-instar grub varied directly with the temperature. The oxygen consumption increased from 1.53 cubic mm. per minute per gram of body weight at 10° C. to 13.53 cubic mm. at 34°. The carbon dioxide produced increased from 1.07 cubic mm. at 10° to 11.92 cubic mm. at 34°. The respiratory quotient, the ratio of the carbon dioxide produced to the oxygen consumed, varied from 0.68 at 10° to 0.88 at 34°. (Kleinman 1934)

The rate of oxygen consumption at 25° C. remained high during the grub stage, ranging from 7 to 10 cubic mm. per minute per gram of body weight. A slight decrease in the rate of consumption occurred a few days before the external characteristics of the prepupa appeared. The rate of consumption decreased rapidly during the prepupal stage and the first 2 or 3 days of the pupal period, reaching a low of 2 cubic mm. per minute. The consumption then increased rapidly until at the end of the pupal period it was 10 cubic mm. per minute. This high rate of oxygen consumption continued in the adult. (Ludwig 1931)

The respiratory quotient of the grub at 25° C. varied from 0.70 to 0.97. During metamorphosis it gradually decreased until it varied from 0.40 to 0.70 in the pupa. The emergence of the adult was followed by an increase in the respiratory quotient to 0.70 and 0.80. (Ludwig 1931)

The activity of the respiratory enzymes, succinic dehydrogenase and cytochrome oxidase, dropped rapidly on the transformation of the grub to a prepupa and continued to fall until it was at its lowest level 2 days after pupation. Then the activity of the enzymes increased during the remainder of the pupal period. No sex differences were observed in the activity of succinic dehydrogenase, but the activity of cytochrome oxidase was higher in the male than in the female. (Ludwig 1953; Ludwig and Barsa 1955)

The decrease in respiratory metabolism during the prepupal and

early pupal stages was indicative of the destruction of larval tissue during this period, whereas the increase in metabolism in the last pupal stage was indicative of the growth of adult structures (Ludwig 1931).

In the Blood

The blood of a normal grub contains 91.2 percent of water. It has a freezing point of -1.03° C. and an osmotic pressure at 0° of 12.4 atmospheres. (Ludwig 1951)

The oxygen dissolved in the blood of the grub at 25° C. was equivalent to 33.4 to 42.0 percent of the oxygen saturation of 0.25 molar potassium chloride. There was 0.078 to 0.100 micromole of dissolved oxygen in a milliliter of hemolymph. (Weiner 1965; Weiner et al. 1966)

One hundred ml. of the blood contained 46.5 mg. of sodium, 37.2 mg. of potassium, 31.6 mg. of calcium, 47.1 mg. of magnesium, 67.5 mg. of inorganic chlorides, and 15.2 mg. of inorganic phosphates. The sodium index (24.0) and the potassium index (11.3) were low, whereas the magnesium index (46.0) was very high. This amount of blood also contained 248 mg. of reducing compounds, of which 179 mg. were not fermentable, and 1,300 mg. of nitrogen, of which 800 mg. were in proteins, 500 mg. in nonproteins, and 240 mg. in amino acids. These observations are in agreement with the generalization that insect blood is characterized by high concentrations of amino acids and nonfermentable reducing compounds and by a high magnesium index. (Ludwig 1951)

Glutamine, arginine, histidine, proline, glycine, alanine, and valine were the principal amino acids occurring free in the hemolymph of the grub. Lysine, aspartic acid, threonine, serine, glutamic acid, isoleucine, leucine, tyrosine, beta-alanine, tryptophan, and asparagine were also detected. Sixteen amino acids were identified in the insoluble proteinaceous material in the blood. These were lysine, histidine, arginine, aspartic acid, threonine, serine, proline, glutamic acid, glycine, alanine, valine, methionine, isoleucine, leucine, tyrosine, and phenylalanine. (Shotwell et al. 1963)

Stubblefield et al. (1966) found volatile and nonvolatile organic acids in the blood of the grub. Of the volatile acids, 100 ml. of hemolymph contained 38.8 mg. of acetic acid, 3.8 mg. of propionic acid, 3.6 mg. of butyric acid, and 2.3 kg. of formic acid. This volume of blood contained the following milligrams of the nonvolatile acids: Lactic acid 57, succinic acid 50, citric acid 48, glycolic acid 35, malic acid 24, tartaric acid 19, glyoxylic acid 17.7, pyruvic acid 15.7, alpha-ketoglutaric acid 4.6, and traces of the oxaloacetic acids.

pH.—Payne (1928) found that the pH of the blood of the third-instar grub ranged from 6.35 to 7.16. Ludwig (1934b) determined that the pH ranged from 6.66 to 7.35 in the third-instar grub, 6.42 to 7.25 in the early prepupa, 6.33 to 7.13 in the late prepupa, and 6.23 to 7.23 in the pupa and adult. The range of pH with each stage was greater than the differences between them. The average pH of the blood was 7.07 in the grub, 7.00 in the early prepupa, 6.79 in the late prepupa, and 6.94 in the pupa and adult. The increase in acidity in the late prepupa was probably the result of autolysis of the larval tissue.

Nitrogen.—Ludwig (1954) studied the changes in the distribution of nitrogen in the blood during growth and metamorphosis. The protein nitrogen was low in the early second-instar grub, but it increased steadily during the stadium. Some protein nitrogen was lost during ecdysis. It remained low during the first 2 weeks of the third-instar grub and then increased progressively. The increase continued through the prepupal stage and for the first 5 days of the pupal stage, and then the protein nitrogen decreased rapidly to the end of the pupal period. The emergence of the adult was accompanied by the loss of a large amount of water and the blood became more concentrated. The decrease in fluidity was associated with the higher protein nitrogen in the blood of the newly emerged adult.

The nonprotein nitrogen increased in the blood of the second-instar grub until ecdysis. There was a slight loss during molting. It increased steadily in the third-instar grub until the approach of metamorphosis. The change to the prepupa was accompanied by a sharp decrease in nonprotein nitrogen. The protein nitrogen increased during the early part of the pupal period and then decreased rapidly during the remainder of the period. The emergence of the adult was accompanied by an increase in nonprotein nitrogen, which was associated with the loss of water that occurred at this time.

The amino acids remained relatively constant throughout the larval, prepupal, and pupal periods. Uric acid was low in the third-instar grubs, but it increased quickly in the prepupae. This increase was associated with the uric acid granules in the blood. Urea decreased during the prepupal stage, but it increased during pupation. It then decreased to a level where it remained during the last half of the pupal period.

In the Alimentary Tract

Grub.—The alimentary tract of the grub is distinctly alkaline. The pH was 8.0 to 8.4 in the foregut, 9.4 to 9.5 in the ventriculus, and

7.5 to 7.6 in the hindgut. The acidity of the soil had little effect on the pH of the alimentary tract. The alkalinity of the tract of grubs feeding in soil with a pH of 3.47 was the same as those feeding in soil with a pH of 6.45, showing that there was a strong buffering action in the digestive secretions. A qualitative analysis of the digestive secretions showed the presence of aluminum, ferrous iron, calcium, magnesium, potassium, sodium, and ammonium salts. The acidic ions were carbonate, chloride, nitrite, and phosphate. The enzymes in the tract were not determined. (Swingle 1930b, 1931a, 1931b)

Adult.—The alimentary tract of the adult was less alkaline than that of the grub. The pH of the foregut was 7.20, the ventriculus 7.36 to 7.53, and the hindgut 7.40 to 7.60. Digestion was by secretions of the cells in the epithelial layer. There were no specialized secretory cells. Maltose and sucrose were broken down to monosaccharides by the enzymes maltase and invertase, respectively, in the foregut and the ventriculus. Fats were broken down to fatty acids by the enzyme lipase in the ventriculus. Proteins were broken down to proteoses, peptones, peptides, and amino acids by the enzyme tryptase (probably trypsin) in the ventriculus. No starch digestion could be demonstrated. (Swingle 1930a, 1931a)

Biochemical Changes During Starvation of the Grub

In the Insect

Newton (1954) determined the various metabolic products in normal third-instar grubs and in grubs that had been starved for 4 weeks at 25° C. and a high relative humidity. During starvation the grubs lost 80 percent of their glycogen, 71 percent of their fat, and 25 percent of their reducing substances. There was only a slight loss of nitrogen during starvation, but there was a change in the distribution of nitrogen among the various nitrogenous substances. The insoluble protein nitrogen decreased from 68.4 to 56.7 percent, and there was a corresponding increase in the lipid nitrogen and the nonprotein nitrogen.

The respiratory metabolism of the grubs decreased rapidly during the first 2 days of starvation and then decreased slowly until death. The oxygen consumption decreased during the first 2 days from 6.55 cubic mm. per minute per gram of body weight to 3.18 cubic mm. and then decreased slowly to 1.92 cubic mm. just before death. The respiratory quotient decreased from 0.82 to 0.70. The rapid decrease in the metabolic rate to a low point, barely sustaining life, probably

is the factor that enabled the grubs to live as long as a month at 25° C. and a relative humidity of 96 percent. (Bellucci 1939)

In the Blood

The water content and the osmotic pressure of the blood remained constant throughout starvation. The blood did not appear to be a reservoir of materials to be used as a source of energy during starvation. The changes in its composition probably reflect metabolic changes occurring elsewhere in the grub. The amino nitrogen and the nonprotein nitrogen increased steadily. Urea nitrogen increased during the first week and then remained relatively constant at the higher level. Uric acid nitrogen decreased during the first week and then remained approximately constant. Allantoin nitrogen did not change during inanition. Free fat increased during the first 2 weeks and then decreased during the final 2 weeks to about the normal level. The reducing compounds increased steadily during starvation. (Ludwig and Wugmeister 1953; Ludwig and Cullen 1956)

SEASONAL LIFE HISTORY

The development of the beetle from egg to adult, shown diagrammatically in figure 7, is completed in 1 year in most of the areas where the insect is established. In certain northern areas some individuals require 2 years to complete their development.

Japan

Clausen et al. (1927) studied the life history of the beetle in its native Japan. There is one generation a year in most of Japan, but in the northern part of the archipelago the beetle usually has a 2-year life cycle, with 75 percent of the adults emerging in alternate years.

Beetles appear the last week of May at Yokohama (lat. 35.5° N.), about the same latitude as Raleigh, N.C., reach maximum abundance about the third week of June, and then decline gradually until only a few stragglers are found the last week of July.

Beetles begin to emerge the first week of July at Koiwai near Morioka (lat. 39.5° N., altitude 1,500 feet), about the same latitude as Philadelphia, Pa., reach maximum abundance the fourth week of July, and then decline until by the second week of September only a few are found in the field.

Beetles appear the first week of July at Sapporo (lat. 43° N.),

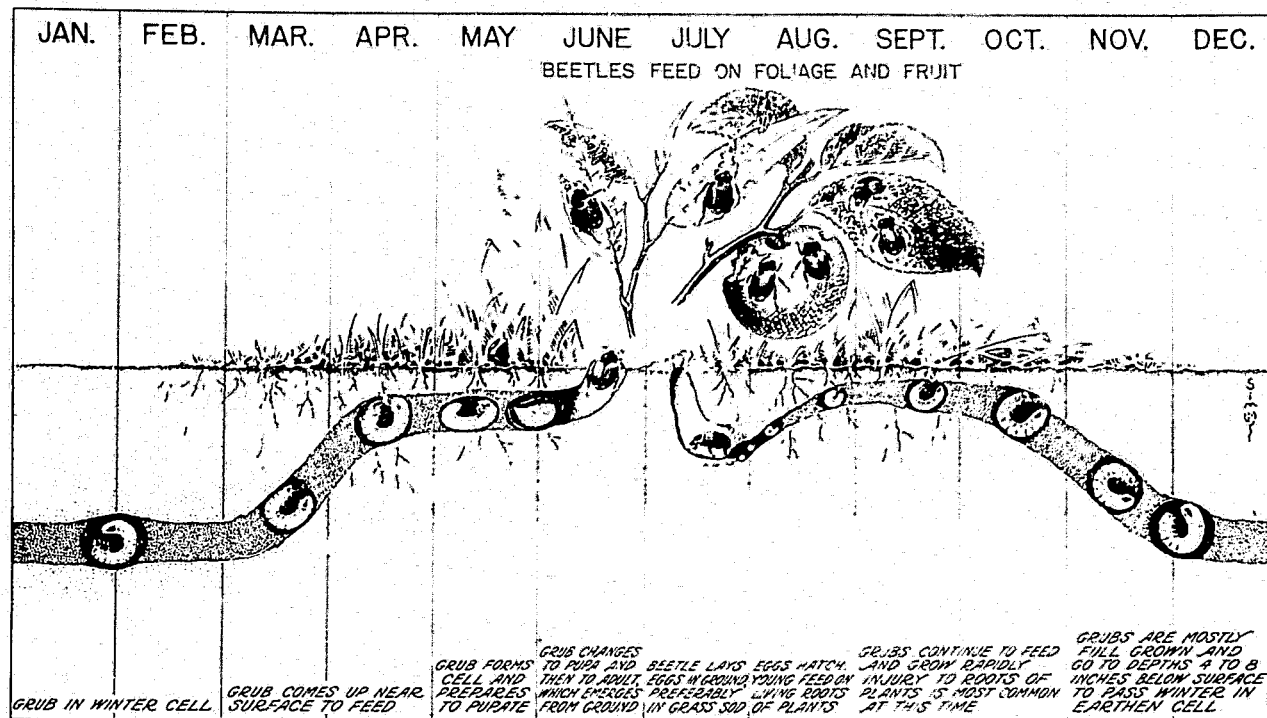


FIGURE 7.—Seasonal life cycle of Japanese beetle in southern New Jersey.

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about the same latitude as Keene, N.H., and reach maximum abundance the last week of July. In the years when 25 percent of the beetle fauna appear, only a few beetles are found by the first week of August, but in other years beetles are found until early September.

United States

The beetle has one generation a year in the areas where it is established in the United States. At Keene, N.H., the most northern area studied by Hawley (1944), about 1 percent of the soil population just before hibernation consisted of third-instar grubs of the previous annual brood, indicating that a few of the eggs deposited late in August might require 2 years to complete their development to adults. Eggs laid in September usually did not hatch because the soil temperature is too low for embryonic development.

Emergence and Persistence of Adult Beetles

Along the Atlantic seaboard beetles begin to emerge from the soil the third week of May in central North Carolina, reach maximum abundance the second week of June, and then decline until only a few are found after the middle of July. In the mountainous western part of the State beetles appear the last week of June, the peak of abundance occurs about the middle of August, and beetles are still numerous in September. (Fleming and Hawley 1950; Fleming 1963a)

In mountainous eastern Tennessee beetles appear the first week of June and reach maximum abundance the third week of June. Only a few beetles are found early in September. (Ladd unpublished)

In central Virginia beetles appear the last week of May or the first week of June, reach maximum abundance the second week of July, and then decline until only a few are found in August (French et al. 1949; Fleming 1963a).

In central Maryland and in Delaware emergence begins the middle of June. The population peak is reached about the middle of July. The population then declines. A few beetles are found late in September. (Cory and Langford 1944; Fleming 1963a)

In southern New Jersey and southeastern Pennsylvania beetles appear the third week of June and reach the peak of abundance the last week of July. The population usually remains at a high level for about 2 weeks and then declines. A few beetles are found during September. The emergence is 1 or 2 weeks later in the mountainous parts of Pennsylvania and New Jersey and along the coast of New

Jersey. (Hadley 1924; Smith and Hadley 1926; Guyton 1929; Hawley 1944; Fleming 1963a)

In southeastern New York, Connecticut, Rhode Island, and southern Massachusetts emergence begins the last week of June and the population peak is reached the last week of July. The population usually remains at a high level for 1 or 2 weeks and then declines. A few beetles are found in September. (Stene 1929; Britton and Johnson 1938; Johnson 1939; Hawley 1944; Carruth et al. 1946; Schread 1947, 1953; Adams and Matthysse 1949; Fleming 1963a)

In southern New Hampshire and southern Vermont beetles begin to emerge the first week of July and the population peak is reached the last week of July or the first week of August. Some years the population declines gradually until late in September, but in other years a second emergence occurs early in September and the population continues at a high level during the month. (Hawley 1944)

In the Midwestern States between latitude 39° N. and latitude 40.5° N. the emergence and buildup of the beetle population are similar to those in southern New Jersey. Farther north along the shores of the Great Lakes the emergence of the beetle is 1 or 2 weeks later. (Denning and Goff 1944; Hawley 1944; Polivka 1950, 1959; Gould 1963)

In central California, the only area on the west coast where the beetles became established, they begin to emerge the first week of June and reach their maximum abundance about the first week of July (Gammon 1961).

Development of the Soil Population

During 1926-36 Fox (*in* Hawley 1944) made systematic surveys at about weekly intervals in southern New Jersey and southeastern Pennsylvania to determine the different stages of the beetle in the soil throughout the year. Some surveys were made when the beetle was emerging; adults found in the soil were considered to be a part of the soil population. Surveys usually extending over fewer years and not always throughout the year were made by W. E. Fleming, C. H. Hadley, I. M. Hawley, and R. T. White in North Carolina, Virginia, West Virginia, Washington, D.C., Maryland, Delaware, northern New Jersey, northeastern, central, and western Pennsylvania, New York, Connecticut, Rhode Island, Massachusetts, New Hampshire, and Vermont, and by Gould (1963) in northwestern Indiana. The results of these surveys are summarized in table 4, commencing in July and ending the following June to coincide approximately with the development of the beetle from egg to adult.

TABLE 4.—*Development of soil populations of Japanese beetle in different areas in Eastern United States*

Month	Eggs	First-instar grubs	Second-instar grubs	Third-instar grubs	Pre-pupas	Pupae	Adults
	Percent	Percent	Percent	Percent	Percent	Percent	Percent
WESTERN NORTH CAROLINA							
July	—	—	—	25	25	22	28
August	10	20	40	21	(1)	—	—
October	1	8	47	49	—	—	—
May	—	(1)	1	57	34	8	—
June	—	—	—	44	12	44	(1)
EASTERN VIRGINIA							
July	14	53	33	—	—	—	—
August	—	(1)	34	66	—	—	—
May	—	—	—	34	60	6	—
June	—	—	—	17	59	24	—
NORTHERN VIRGINIA							
August	4	62	34	—	—	—	—
June	—	—	—	89	11	—	—
NORTH-CENTRAL WEST VIRGINIA							
June	—	—	—	60	2	38	—
WASHINGTON, D.C.							
July	14	85	1	—	—	—	—
August	—	4	75	21	—	—	—
September	—	3	33	64	—	—	—
October	—	—	14	86	—	—	—
May	—	—	(1)	71	24	5	—
June	—	—	—	51	29	20	—
EASTERN MARYLAND							
July	34	66	—	—	—	—	—
August	4	49	43	4	—	—	—
September	(1)	22	46	32	—	—	—
October	—	—	17	83	—	—	—
April	—	—	10	90	—	—	—
May	—	—	(1)	80	20	—	—
June	—	—	—	56	8	34	—
NORTHWESTERN MARYLAND							
September	1	41	58	—	—	—	—
CENTRAL DELAWARE							
June	—	—	—	50	19	31	—

See footnote at end of table.

TABLE 4.—*Development of soil populations of Japanese beetle in different areas in Eastern United States—Continued*

Month	Eggs	First-instar grubs	Second-instar grubs	Third-instar grubs	Pre-pupae	Pupae	Adults
	Percent	Percent	Percent	Percent	Percent	Percent	Percent
SOUTHERN NEW JERSEY AND SOUTHEASTERN PENNSYLVANIA							
July	55	15	1	3	2	9	15
August	8	31	55	6	--	(¹)	(¹)
September	(¹)	2	29	69	--	--	--
October	(¹)	(¹)	7	93	--	--	--
May	--	(¹)	5	95	--	--	--
June	1	--	(¹)	40	25	28	6
NORTHEASTERN NEW JERSEY							
July	--	--	--	43	23	20	8
August	19	75	6	--	--	--	--
September	(¹)	10	31	59	--	--	--
June	--	(¹)	5	74	8	10	3
NORTHWESTERN NEW JERSEY							
July	--	--	--	17	15	49	19
August	38	19	43	(¹)	--	--	--
September	1	14	42	43	--	--	--
May	--	2	44	54	--	--	--
June	--	--	(¹)	59	30	11	--
NORTHEASTERN PENNSYLVANIA							
August	25	27	47	1	--	--	--
September	13	53	21	13	--	--	--
October	7	19	66	8	--	--	--
May	--	1	16	60	18	5	--
June	--	--	(¹)	53	37	10	--
CENTRAL PENNSYLVANIA							
June	--	--	--	36	54	10	--
WESTERN PENNSYLVANIA							
June	--	--	(¹)	39	7	42	12
SOUTHEASTERN NEW YORK							
September	6	4	43	47	--	--	--
June	--	--	--	34	28	38	(¹)
NORTH-CENTRAL NEW YORK							
September	55	25	16	4	--	--	--
June	--	--	10	85	5	--	--
SOUTH-CENTRAL NEW YORK							
August	27	42	29	2	--	--	--
June	--	--	3	68	18	11	--

See footnote at end of table.

TABLE 4.—*Development of soil populations of Japanese beetle in different areas in Eastern United States—Continued*

Month	Eggs	First-instar grubs	Second-instar grubs	Third-instar grubs	Pre. pupas	Pupae	Adults
	Percent	Percent	Percent	Percent	Percent	Percent	Percent
SOUTHERN CONNECTICUT							
July	--	--	1	48	11	40	(¹)
August	16	56	22	6	--	--	--
September	8	23	36	33	--	--	--
May	--	7	53	40	--	--	--
June	--	--	1	70	15	14	--
CENTRAL CONNECTICUT							
September	40	20	34	6	--	--	--
October	--	8	40	52	--	--	--
June	--	--	--	87	13	--	--
RHODE ISLAND							
October	--	5	33	62	--	--	--
May	--	--	29	71	--	--	--
EASTERN MASSACHUSETTS							
May	--	--	14	86	--	--	--
CENTRAL MASSACHUSETTS							
October	--	--	34	66	--	--	--
June	--	--	--	99	1	--	--
CONNECTICUT RIVER VALLEY IN MASSACHUSETTS							
August	3	7	53	37	--	--	--
September	(¹)	1	19	80	--	--	--
October	--	--	12	88	--	--	--
June	--	--	3	38	5	51	3
WESTERN MASSACHUSETTS							
August	21	36	43	--	--	--	--
May	--	--	9	91	--	--	--
June	--	--	--	95	5	--	--
SOUTHERN NEW HAMPSHIRE							
July	--	--	--	58	36	5	1
August	23	66	7	4	--	--	--
September	19	20	50	11	--	--	--
October	13	15	58	14	--	--	--
April	7	18	59	16	--	--	--
May	(¹)	8	59	33	--	--	--
June	--	--	3	88	9	--	--

See footnote at end of table.

TABLE 4.—*Development of soil populations of Japanese beetle in different areas in Eastern United States—Continued*

Month	Eggs	First- instar grubs	Second- instar grubs	Third- instar grubs	Pre- pupas	Pupas	Adults
	Percent	Percent	Percent	Percent	Percent	Percent	Percent
SOUTHERN VERMONT							
September	15	20	37	28	--	--	--
May	--	1	34	65	--	--	--
NORTHWESTERN INDIANA							
August	50	41	--	--	--	--	--
September	0	82	9	--	--	--	--
October	(¹)	27	45	28	--	--	--
November	--	12	58	30	--	--	--
April	--	4	47	49	--	--	--
May	--	--	44	50	--	--	--
June	--	--	6	42	39	13	(¹)

¹ Few individuals found; number less than 1 percent of population and not considered in computing percentages.

Development of the beetle differed greatly throughout the area covered by these surveys as shown by the following data:

Area	Proportion of population metamorphosing in June (percent)
Coastal plain:	
Eastern Virginia	83
Washington, D.C.	40
Eastern Maryland	42
Central Delaware	50
Southern New Jersey	50
Virginia:	
Eastern	83
Northern	11
New Jersey:	
Southern	50
Northeastern	21
Northwestern	41
Pennsylvania:	
Southeastern	50
Northeastern	47
Central	64
Western	61

<i>Area</i>	<i>Proportion of population metamorphosing in June (percent)</i>
New York:	
Southeastern -----	88
North central -----	5
South central -----	29
Connecticut:	
Southern -----	29
Central -----	13
Massachusetts:	
Central -----	1
Western -----	5
Connecticut River Valley -----	50

The development of the beetle was the most retarded in central and western Massachusetts and in southern New Hampshire and Vermont.

The development of the beetle in western North Carolina was similar to its development in southern New Jersey and in the Connecticut River Valley, whereas its development in north-central West Virginia was similar to that in eastern Maryland, and its development in northwestern Indiana similar to that in central Delaware.

HABITS OF ADULTS

Emergence

Ellis (unpublished) studied the habits of the adult beetle during its emergence from the pupal skin and its movement to the surface of the ground. When the beetle is fully transformed, it ruptures the delicate pupal skin surrounding it and withdraws its body. The discarded pupal skin is passed posteriorly over the body. The adult at this time is practically helpless and very vulnerable in its earthen cell. The body wall is flexible and soft. The true wings are smoke-colored sacs filled with fluid. The sexual organs are not fully matured.

The adult remains in its earthen cell from 2 to 14 days depending on the temperature and other environmental conditions. During this time the chitin of the cuticula hardens and the body becomes fully pigmented. The fluid in the wings is absorbed, the wings expand to normal size, and they are neatly folded beneath the abbreviated elytra. The maturation of the sexual organs is completed. The adult is now ready to leave its subterranean home.

The beetle uses its mandibles and the tibiae of its forelegs, which are adapted for fossorial work, to dig to the surface of the ground. As it advances upward, the soil is pushed posteriorly, filling the earthen cell and the tunnel behind it. A beetle may work for 1 or more days to complete the tunnel depending on the nature of the soil. The exit hole is spherical in shape. In a heavily infested field the surface of the ground is riddled by thousands of these holes, which remain visible until obliterated by wind and rain.

Most of the beetles leave their tunnels in the morning of clear days when the air becomes warm, but some may delay until the afternoon. After emerging from the ground they usually climb on various low-growing plants and rest before flying. The beetles remain in their tunnels on cool rainy days.

Length of Life

The length of life of the individual beetle varies considerably depending on its environment. Its life is relatively short at high temperatures and relatively long at low temperatures. In captivity male beetles lived from 9 to 74 days and female beetles from 17 to 105 days; the average was 39 days for the males and 52 days for the females. (Ellis unpublished) Davis (1920a) reported that beetles lived from 7 to 70 days. Smith and Hadley (1926) found that the average life of male beetles supplied daily with fresh sassafras leaves was 34 days and the female beetles 38 days. When the beetles were not fed, the average survival of the males was 7 days and the females 9 days. It is generally accepted that the normal life of the beetle is usually from 30 to 45 days (Hadley and Hawley 1934; Fleming 1963a).

Protective Reactions

Extension of Legs

In common with other Scarabaeidae the adult beetle has the peculiar habit of extending its metathoracic legs obliquely from the body at the approach of a potential enemy. This reaction is not induced by the normal movement of plants in the wind.

When beetles are feeding on a row of plants at between 21° and 29° C., the legs are extended upward and forward not only in the immediate vicinity of but for 8 to 10 feet down the row from the potential enemy. The stimulus created by potential danger is appar-

ently relayed from beetle to beetle. The males and feeding females extend their legs at the slightest threat, but mating females react only when continuously threatened. The legs remain taut until the threat of danger passes. If an attempt is made to capture an alerted beetle, it will fly or drop to the ground.

When the temperature is above 29° C. and the relative humidity is low, the beetles are very nervous and fly at the slightest threat of danger in lieu of extending their legs.

Feigning Death

When beetles on plants are threatened at temperatures below 21° C., they draw their legs compactly to the body and drop to the ground feigning death. It is well known that predatory insects, birds, and other animals rarely attack apparently lifeless beetles. In falling, the beetles usually land on their backs. When the air is cool, they may remain in this position for several minutes. It is a struggle for a beetle to right itself. This is accomplished by using the mesothoracic legs as the fulera and pushing with the metathoracic legs and the elytra. When it is on its feet, it usually makes a frantic effort to conceal itself under litter or in the ground.

Mating

Mating usually takes place on plants, but it may be on the ground. It occurs most frequently in the early morning or in the evening, but it may take place at any time during the day. Coitus may be brief or prolonged for several hours. It is repeated at frequent intervals during the life of the individual. Ellis (unpublished) observed a male mating with seven females during an evening; another male mated twice in the evening on 5 consecutive days. Other males mated only two to nine times during a 13-day period. The female usually mates between each oviposition period. There is no apparent uniformity in the number of times a beetle may mate. However, it is common for a male to mount a female or even another male and remain in this position for several hours without mating. The male does not eat while riding a female, but the female invariably continues to feed on plants regardless of the actions of its mate, frequently feeding during coitus.

The promiscuousness of the beetle undoubtedly is of importance in maintaining the racial characteristics. During her life a female may mate with males that are abnormally large and diminutive, excellent

and poor fliers, and with a long and a short span of life. Ladd (1966) in studying chemosterilants demonstrated that the sperms introduced in the last mating before oviposition are those most likely to fertilize the ova.

Virgin females emerging from the soil are very attractive to males, particularly early in the summer. Smith (1923) and Smith and Hadley (1926) observed many male beetles flying low over turf in the early morning of clear warm days, searching for emerging females. As a virgin female emerged from the ground many males alighted 4 to 6 inches on her leeward side and crawled toward her. They always approached a female against the wind. As the direction of the wind shifted the trail of beetles shifted accordingly, indicating that the unmated female has a powerful volatile sex pheromone. The congregated mass of males about a female resembled an animated ball; each mass was composed of a single female and from 25 to 200 male beetles. Within an area of 25 square yards 78 "balls" of beetles were seen at one time. Coitus rarely occurred when so many males were competing for a female. In examining several hundred "balls" only one female was found copulating. The "balling" usually ceased about midday and did not occur again until another favorable morning. It rarely occurred later than 2 or 3 weeks after the initial emergence of the beetle.

Ladd (1970) demonstrated that newly emerged unmated females removed from "balls" of beetles were more attractive to males than the best chemical lure, a 9:1 mixture of phenylethyl butyrate and eugenol. A trap baited with nine freshly collected virgin females caught within 1 hour 2,975 males and 23 females, whereas a trap with nine unmated females collected the previous day captured 2,498 males and 30 females and the chemically baited trap 497 males and 879 females. Traps baited with mated females or with males caught only a few beetles.

Goonewardene et al. (1970) found that virgin females reared in the laboratory were attractive to males as long as they remained alive and unmated. In the laboratory at 28° C. the females emerged from the soil 9 days after transforming to adults. Virgin females 6 to 15 days old were the most attractive as lures in traps. Their attractiveness then tended to decline with the increment in their age.

Ladd (1970) exposed isolated abdomens and heads plus thoraces of unmated females and found that the attractive substance was produced in the abdomen. The attempts by Richmond (1931), Fleming

(1969), and Ladd (1970) to extract the sex pheromone with various solvents were not successful.

Oviposition

Selection of Oviposition Site

Many factors influence the female beetle in selecting a site for oviposition. The most obvious are the proximity of a suitable site to the plant upon which she is feeding, the nature of the ground cover, and the condition of the soil. However, when beetles are flying in all directions on warm summer days, the females may select all kinds of fields to deposit their eggs.

Proximity to Favored Plants.—The female beetle tends to deposit her eggs in a suitable site in the vicinity of the plant upon which she is feeding. Beetles feeding in a cornfield usually deposit their eggs in the field. In suburban areas where turf is abundant, most beetles feeding on trees, shrubs, and vines tend to deposit their eggs in nearby grass. The effect of favored plants on the local distribution of the beetle population was demonstrated by Whittington et al. (1942). Traps 5 to 10 feet from preferred plants caught from 2 to $2\frac{1}{2}$ times as many beetles as traps 100 feet away. Schwartz (1968) also found that the number of beetles captured by traps decreased with the increment in the distance from a favored food plant.

Effect of Ground Cover.—Clausen et al. (1927) found that the beetle was the most abundant in parts of Japan where grasslands occur. Davis (1920a) found that in southern New Jersey most of the eggs were laid in pastures and other grassy areas. Smith and Hadley (1926) found that although most of the eggs were deposited in pastures, lawns, and golf courses, the beetle laid eggs in fields of rye, clover, corn, beans, tomatoes, and nursery stock.

Langford et al. (1940, 1941) made extensive surveys in Maryland and Hawley (1944) in southern New Jersey to determine the soil population in land growing crops common to these areas. The soil populations reflected the preferences of the female beetle in selecting sites for oviposition in rural areas. From these data the following estimates were made:

<i>Soil population (percent)</i>	<i>Oviposition site</i>
19.5 -----	Pastures.
11.7 -----	Asparagusfields.
11.2 -----	Fields of timothy and clover.
10.6 -----	Alfalfafields.
10.3 -----	Cornfields.
6.0 -----	Fallow land.
6.5 -----	Potatofields.
5.9 -----	Pepperfields.
5.8 -----	Soybeanfields.
4.9 -----	Tomatofields.
4.2 -----	Orchards.
1.2 -----	Fields of wheat or rye.
1.0 -----	Barleyfields.
.3 -----	Nonagricultural land.
.3 -----	Woodlots.

For each time a female beetle selected nonagricultural land or a woodlot for oviposition, she selected the following sites:

<i>Oviposition site</i>	<i>Number of times selected</i>
Barleyfields -----	3
Fields of wheat or rye -----	4
Orchards -----	12
Tomatofields -----	16
Soybeanfields -----	19
Pepperfields -----	20
Potatofields -----	21
Fallow land -----	22
Cornfields -----	34
Alfalfafields -----	35
Fields of timothy and clover -----	37
Asparagusfields -----	39
Pastures -----	65

The abundance of the soil population varies widely throughout a field and in different fields with the same crop. The population is usually higher near the edge than at the center of a cropped field.

The development of the crop also modifies the number of eggs deposited. More eggs are deposited in a cornfield in silk when beetles are abundant than in fields where silking is past or delayed. Beetles lay more eggs in asparagusfields with an abundance of tall brush than in fields with low brush. When feeding on the flowers and foliage of alfalfa or clover, they lay few eggs in the field, but after the crop is harvested, they may deposit many eggs in the field. Beetles feeding on soybeans with a dense growth lay few eggs in the field.

The presence of such favored weeds as smartweed (*Polygonum pensylvanicum*) throughout a field tends to increase the number of eggs deposited in the field.

Effect of Drought.—During summers of deficient rainfall when pastures become hard and dry, the beetle seeks more suitable sites for oviposition. She usually selects low poorly drained ground, fields and turf under irrigation, and cultivated and fallow fields where the soil is loose and moist. Under these conditions more eggs may be deposited in a tomatofield than in a pasture.

Egg Laying

The female beetle usually leaves the plant upon which she is feeding in the afternoon and digs into the soil at a selected site to deposit eggs. After burrowing to a depth of 2 to 4 inches she deposits an egg in a depression in the soil made by her ovipositor. This depression becomes a small cell surrounding the egg when the beetle digs laterally, pushing the loosened soil behind her. There apparently is no excretion to strengthen the walls of this cell. She may deposit an egg at three or more places in the vicinity. The beetle may emerge from the soil in the morning, or she may remain there for 3 or 4 days. After emerging and spending 1 or more days feeding and mating, the female returns to the soil to deposit another complement of eggs. During her life a female may enter the soil 16 or more times, depositing up to 133 eggs. Usually she lays 40 to 60 eggs during her life. (Ellis unpublished; Smith and Hadley 1926; Hadley and Hawley 1934)

In southern New Jersey 27 percent of the eggs are deposited in July, 52 percent in August, 20 percent in September, and 1 percent in October (Ellis unpublished). The peak of the oviposition period occurs in July in central Virginia and late in August in southern New Hampshire.

Flight

Factors Affecting Flight

Early in the morning beetles are usually resting quietly on plants. On clear summer days when the temperature reaches about 21° C. and the relative humidity is below 60 percent, beetles begin to fly in all directions. They leave the plants with a strong buzzing, which becomes a higher pitch and more refined in tone as full flight is attained. There is no audible sound when a beetle reaches full flight

or is hovering about a plant before alighting. The flight is swaying and undulating. The speed of flight increases with the temperature up to about 35°. Flight usually ceases above this temperature and beetles often seek shade by crawling to the underside of leaves or burrowing into the ground. Flight is also retarded when the relative humidity rises above 60 percent. Late in the afternoon flying slackens and the beetles tend to remain on the plants. There is little flying on cool windy days or on cloudy days and no flying on rainy days. The beetle is very responsive to a change in the weather; a passing cloud causes a beetle in flight to seek a suitable resting place immediately. (Fleming 1933; Hawley and Metzger 1940)

Smith and Hadley (1926) asserted that beetles normally fly against the wind. It is an impressive phenomenon to see swarms of beetles flying against the wind to an orchard with ripening fruit. Fox (1927) questioned the accuracy of their statement because in the absence of chemotropic stimuli the flight of the beetle is essentially aimless and the insect tends to drift with the wind.

Distance of Flight

Most of the flights of the beetle are for short distances. It is a restless insect. Beetles fly constantly from one spot to another on a large plant and from plant to plant. Van Leeuwen (1932) estimated that about one-third of the beetles alighting on a tree left the tree during the day. Marked beetles have been recovered 1 to 2¾ miles from where they were released. (Smith and Hadley 1926; Metzger and Maines unpublished)

Smith and Hadley (1926) estimated that the average outward spread of the beetle from the point of introduction in New Jersey was at the rate of 10 to 15 miles per year, indicating that in short flights the beetle was capable of flying this distance during the summer. Fox (1932), however, estimated the outward movement of the periphery of the infestation varied from 2 to 10 miles per year, generally averaging 5 miles annually.

The beetle is capable of flying 5 miles in sustained flight. With an offshore wind millions of beetles flew in 1933 from New Jersey over the Atlantic Ocean and some of them alighted on fishing boats 5 miles off the coast (Fleming 1958). Beetles alighted on ships plying between New York City and Bermuda while proceeding down the New Jersey coast (Waterston 1938).

Massive Flights

Beginning in 1923 and continuing for several years massive flights of millions of beetles developed in the heavily infested areas in New

Jersey. The stimulus that induced these flights is not known. Probably the defoliation of favored plants stimulated the beetles to seek new areas.

Beginning in 1923 and continuing for 10 years millions of beetles flew during late July and early August from the rural areas in New Jersey across the Delaware River (about a mile wide) into the downtown shopping and marketing districts of Philadelphia, Pa. (Fox 1927; Hoyt 1934; Fleming 1958). Swarms of beetles flew from New Jersey across upper Delaware Bay into Delaware in 1933. Many of them dropped into the bay and were washed up dead and alive on the Delaware shore (Fox 1934). With an offshore wind millions of beetles flew from New Jersey over the Atlantic Ocean and later were washed up dead and alive in windrows on the beaches of New Jersey and Long Island (Fox 1934; Fleming 1958).

Feeding

The beetle is a polyphytophagous insect. It is particularly attracted to certain species of Aceraceae, Anacardiaceae, Betulaceae, Clethraceae, Ericaceae, Fagaceae, Gramineae, Hippocastanaceae, Juglandaceae, Lauraceae, Leguminosae, Liliaceae, Lythraceae, Malvaceae, Onagraceae, Platanaceae, Polygonaceae, Rosaceae, Salicaceae, Tiliaceae, Ulmaceae, and Vitaceae.

Attraction to Plants

Odor is probably the most important factor in the beetle's selection of a plant, but little information is available on the odoriferous constituents of various plants. Smith (1924) and Smith and Hadley (1926) reported that a series of plants preferred by the beetle had been analyzed and all of them contained geraniol in varying quantities. Langford et al. (1943) reported that the following odoriferous chemicals, which most often occur in combination with each other and with other plant constituents, had been isolated from the ripe fruits of apple and peach, the foliage of sassafras, and the flowers of rose:

Chemical	Isolated from—
Acetic acid	Apple, peach, rose, sassafras.
Benzaldehyde	Apple, peach.
Caproic acid	Apple.
Citral	Apple, rose.
Citronellol	Rose.
Eugenol	Rose, sassafras.
Geraniol	Apple, rose, sassafras.

Chemical	Isolated from—
Linalool -----	Peach, rose, sassafras.
Phenyl ethyl alcohol ----	Rose.
Valeric acid -----	Apple, peach, sassafras.

Eugenol and geraniol were especially attractive to the beetle. Mixtures of odoriferous chemicals were almost invariably more attractive than would be expected from the attractiveness of their components (Fleming 1969).

In an effort to explain the beetle's preference for certain plants, Metzger et al. (1934) determined the odor of the clarified alcoholic extracts and the reducing sugar as glucose in the foliage and sometimes the fruit of 97 species and varieties of plants that differed in their susceptibility to attack by the beetle. Thirty-nine of the extracts had an ethereal or fruity odor, 22 were fragrant, five aromatic, and three empyreumatic; 10 had various odors and 18 no distinctive odor. Of the plants with extracts having a fruity odor, the feeding was moderate to severe on 47 percent of those with a sugar content up to 15 mg. per gram of plant material and on 71 percent of those with a sugar content of 15 to 30 mg. Of the plants without the fruity odor the corresponding percentages were 18 and 22, respectively. Unfortunately the substances causing the fruity odor were not identified. The plants attacked by the beetle ranged from 19 percent of those having less than 5 mg. of sugar to 85 percent of those having 25 to 30 mg. of sugar. It appears that the odor of a plant modifies its attractiveness to the beetle and the sugar content the extent of feeding.

Major and Tietz (1962) demonstrated the importance of odor in the beetle's preference for certain plants. Maidenhair tree (*Ginkgo biloba*) is rarely attacked by the beetle. When the leaves were coated with juice pressed from cherry leaves (*Prunus* sp.), a preferred plant, the beetles ate the coated *Ginkgo* leaves readily without any harmful effect. Cherry leaves coated with juice from *Ginkgo* leaves were eaten about as readily as uncoated cherry leaves. It was evident that *Ginkgo* is not repellent or poisonous to the beetles but lacked odoriferous substances attractive to them.

Development of Infestation on Plants

Either sex may climb or alight on an uninfested plant and begin to feed. The males fly in the early morning before most of the females emerge from the soil. The males feed erratically for short periods on several plants or may continue to feed on the first plant selected.

Early in the morning two-thirds of the initial infestations of plants are by males. Later in the day when about the same number of each sex is flying, either sex is likely to begin an infestation on a plant. (Smith 1923; Smith and Hadley 1926)

The beetle is a gregarious insect. When one or more beetles are feeding on a plant, other beetles in the vicinity tend to alight on the plant. A female attracts many males to a plant (Smith and Hadley 1926). Fifty percent more beetles alight on a plant on which beetles are feeding than on an uninfested plant of the same species in the vicinity (Van Leeuwen et al. 1928; Van Leeuwen 1932). Enormous populations may build up on certain plants, whereas other plants of the same species in the vicinity are only lightly populated.

The number of beetles on a plant usually increases in the morning and declines in the afternoon. Smith (1923) found that the proportion of the sexes on a plant varied throughout the day. The population on apple trees (*Malus sylvestris*) was about 15-percent female until 8 a.m. standard time. During the forenoon the proportion of females increased progressively to 47 percent at 1 p.m. and then declined progressively to 20 percent by 4 p.m. and to 15 percent by 6 p.m. The change in the sex ratio on corn (*Zea mays*), grapes (*Vitis vinifera*), and shrub-althea (*Hibiscus syriacus*) followed this pattern. The population on smartweed (*Polygonum pennsylvanicum*), marshmallow (*Althaea officinalis*), and evening-primrose (*Oenothera biennis*) was about 25-percent female until 8 a.m. The proportion of females gradually increased to 40 percent by 1 p.m. and gradually decreased to 25 percent by 8 p.m.

Factors Affecting Feeding

Beetles prefer to feed on plants exposed to the direct rays of the sun. Plants in shade are never fed on as heavily as those in the sun. Plants in dense woods are rarely attacked. Usually beetles begin to feed on foliage at the top of a plant, regardless of its height, and work downward. It is immaterial whether the plant is a tree 50 feet high or a succulent plant 6 inches high. By the time one-half to two-thirds of the foliage on a tree has been consumed, the beetles may leave the tree and attack other plants in the vicinity, or they may continue feeding until the tree is completely defoliated. (Smith 1923; Fleming et al. 1934; Hawley and Metzger 1940)

Moore and Cole (1921) demonstrated in the laboratory that the beetle is positively phototropic. In 1918, before much information was available on the habits of the insect, it was assumed that light traps might be of value in catching beetles. Goodwin (1919) caught only an occasional beetle in light traps operated at night during the

summer; these beetles were probably captured at dawn or at dusk. This result would be expected with an insect that does not fly at night.

Beetles are most active and feed most extensively on clear summer days between 9 a.m. and 3 p.m. standard time when the temperature is between 29° and 35° C. and the relative humidity is above 60 percent. There is little feeding below 21° or above 35°. A relative humidity below 60 percent inhibits feeding and induces the beetle to fly. Late in the afternoon feeding slackens. There is little feeding on cool windy days or on cloudy days and no feeding on rainy days. (Fleming 1934; Hawley and Metzger 1940)

Diseased plants and those injured by other insects are more susceptible to attack by the beetle than healthy plants. Elm trees (*Ulmus americana*, *U. procera*) injured by the elm leaf beetle (*Pyrrhalta luteola* (Muller)) or infected by Dutch elm disease (*Cerastomella ulmi* Buis.) were usually attacked before healthy trees. Norway maples (*Acer platanoides*) heavily infested by the Norway maple aphid (*Periphyllus lyropictus* (Kessler)) were more attractive to the beetle than uninfested trees. Mann (1942) observed that peach trees (*Prunus persica*) infected by the peach yellows virus (*Chlorogenus persicae* Holmes) or the little peach virus (*C. persicae* var. *micropersica* Holmes) were almost defoliated, whereas adjacent healthy trees were hardly touched by the beetle.

The fruits of late-ripening varieties of apples (*Malus sylvestris*), peaches, and grapes (*Vitis vinifera*) are usually not injured by the beetle. However, immature apples infested by the codling moth (*Laspeyresia pomonella* (Linnaeus)) and infected by black rot (*Botryosphaeria ribis* Gross & Dug.), immature peaches infected by brown rot (*Monilinia fructicola* (Wint.)), and immature grapes infested by the grape berry moth (*Paralobesia viteana* (Clemens)) and infected by black rot (*Guignardia bidwellii* (Ell.) Viala & Ravaz) were attacked readily by the beetle. When this fruit was consumed, the beetles fed on the healthy immature fruit. (Smith and Hadley 1926; Fleming and Metzger 1936; Fleming and Maines 1947)

Seasonal Changes in Preferred Plants

Hawley and Metzger (1940) studied the change in the beetle's choice of plants during the summer. During the first week or 10 days after beetles begin to emerge from the ground, feeding is confined largely to low-growing plants such as smartweed (*Polygonum orientale*, *P. pennsylvanicum*), evening-primrose (*Oenothera biennis*), rhubarb (*Rheum raphaniticum*), and rose (*Rosa* spp.). There is also feeding on grape (*Vitis aestivalis*, *V. labrusca*), sweet cherry (*Prunus*

avium), and sassafras (*Sassafras albidum*). Feeding on the favored plants often continues until the plants are defoliated.

Early in July in southern New Jersey the beetles move from the low-growing plants to fruit and shade trees. Feeding on the trees may continue for several weeks. During this period in densely populated areas such favored trees as apple (*Malus sylvestris*), cherry (*Prunus avium*, *P. cerasus*, *P. serotina*), plum (*Prunus domestica*), elm (*Ulmus americana*, *U. procera*), horsechestnut (*Aesculus hippocastanum*), linden (*Tilia americana*), poplar (*Populus nigra italica*), and willow (*Salix discolor*) may lose most of their foliage.

As the leaves on the trees become older, tougher, and less attractive to the beetles, there is a movement from the trees to lower growing plants. Beetles become abundant on flowers then in bloom, such as roses (*Rosa* spp.), marshmallow (*Althaea officinalis*), hollyhock (*A. rosea*), shrub-althea (*Hibiscus syriacus*), and mallow (*Malva rotundifolia*), and they move into fields of corn (*Zea mays*), asparagus (*Asparagus officinalis*), soybeans (*Glycine max*), clover (*Trifolium hybridum*, *T. pratense*), and alfalfa (*Medicago sativa*). Feeding is more extensive on poison-ivy (*Rhus toxicodendron*), ragweed (*Ambrosia artemisiifolia*, *A. trifida*), and other weeds.

Types of Feeding

The beetles feed on the upper surface of the foliage of most plants, chewing out the tissue between the veins and leaving a lacelike skeleton (figs. 8 and 9, *a-d*). The skeletonized foliage is the most common type of feeding by the beetle. The injured leaves eventually turn brown and most of them fall from the plants. This injury is conspicuous, particularly when the foliage of orchard and shade trees is skeletonized. (Smith 1923; Smith and Hadley 1926; Hawley and Metzger 1940; Fleming 1963a)

Other types of feeding occur on certain plants. Beetles consume large irregularly shaped parts of rose petals (fig. 9, *e*) and other flowers where the delicate veins are not unpalatable to them. Plants with thick tough leaves are usually not attacked by the beetle, but when such leaves are eaten, the feeding is restricted to nibbling on the upper surface and does not penetrate to the lower surface. The freshly eaten leaves have an uneven pitted appearance. (Hawley and Metzger 1940)

The beetles do much damage to the young leaflets and to the epidermis of the branches and stalks of asparagus. Several hundred beetles sometimes collect on a single plant and bend it over by their weight (fig. 9, *f*). Extensive feeding weakens a plant and reduces the



J-1103b

FIGURE 8.—Leaves of Norway maple destroyed by feeding of Japanese beetle. Soft tissue has been eaten, leaving network of veins.

yield the following spring. (Hawley and Metzger 1940; Fleming 1963a)

Masses of beetles collect on the maturing silk of corn and cut it off as it grows (fig. 9, *g*). This prevents the pollination of many embryonic kernels and results in malformed kernels and reduced yield. They also burrow into the tip of pollinated ears and feed on the developing kernels. (Smith and Hadley 1926)

The beetles rarely attack peach leaves borne on new wood. They feed on the underside of mature leaves on old wood, making many small holes, but the leaves are rarely skeletonized (Smith and Hadley 1926). Beetles often gather in large numbers on the fruit of early ripening varieties of apples and peaches (fig. 10) and continue to feed until only the core or stone remains. As many as 296 beetles have been found on a single apple, although only a few of those in the inner layer were actually feeding on the fruit. When beetles are abundant, "balling" may occur on every fruit on a tree. (Hawley and Metzger 1940; Fleming 1963a)



A



B

J-3718, J-3443, J-2721, J-2566, J-2726, J-2822, J-728

FIGURE 9.—Japanese beetles feeding on (A) soybeans, (B) grapevine, (C) smartweed, (D) rhubarb, (E) rose bush, (F) asparagus plants, and (G) corn silk.

*C**D*

FIGURE 9.—Continued.



E



F

FIGURE 9.—Continued.



G

FIGURE 9.—Continued.

Rate of Feeding

The beetle feeds intermittently. The time spent in feeding on various plants and the rate of food consumption are affected by the weather. It was estimated from the data of Smith (1923) that during a 6-hour period the male beetle fed for 48 minutes on apple foliage and 34 minutes on grape foliage, whereas the female fed for 93 minutes on apple and 64 minutes on grape foliage.

For each hour of feeding the male consumed 40.2 square mm. of apple foliage and 30.0 square mm. of smartweed foliage and the female 43.5 square mm. of apple and 40.5 square mm. of smartweed foliage (Smith 1923). Although the quantity consumed by the individual beetle is small, the feeding is very destructive when several thousand beetles are on a tree. Smith and Hadley (1926) collected 2,745,600 beetles from 156 10-year-old peach trees, an average of 17,600 beetles per tree, early in the morning while it was cool and the beetles were inactive, but 24 hours later the population on the trees was about the same as it had been the previous day.



B

J-7601, J-3049

FIGURE 10.—Japanese beetles feeding on fruit and foliage of (A) apple and (B) peach.

Plants Toxic to the Beetle

Many plants have been reported from time to time by the public to be toxic to the beetle. The usual evidence was the presence of a large number of dead beetles on the ground beneath the canopy of a plant on which they had been feeding. These reports almost invariably came after the peak of the beetle population, when many beetles had completed their normal lifespan. It is common to find dead beetles beneath the canopy of all kinds of plants late in the summer. Usually it was not possible to demonstrate experimentally that these plants contained constituents toxic to the beetle, but some of them contained substances that caused paralysis and even death of the beetles.

The geranium (*Pelargonium domesticum*) was reported frequently as being toxic to the beetle. Davis (1920a) found that beetles lying apparently dead on the ground beneath geraniums almost invariably became active within 24 hours. Ballou (1929) studied the effect of geraniums on the beetle more extensively. He found that beetles feeding on the foliage and flowers of this plant often became paralyzed and dropped from the plants. The flowers were more toxic than the foliage. The effect was enhanced when the feeding was on plants exposed to sunlight. The paralysis began with the metathoracic legs and progressed cephalad. Most of the beetles recovered within 24 hours after becoming paralyzed, but 35 percent of them died within 4 days. The ventriculus of beetles dying from eating geraniums disintegrated within 24 hours and the muscles and soft contents of the body cavity within 48 hours. The disintegration was accompanied by a strong fetid odor. The toxic substance in geranium has not been identified.

On several occasions it was reported that beetles had been killed by feeding on the silverbell (*Halesia carolina*). Hawley and Metzger (1940), however, were not able to demonstrate that the foliage or seed capsules had any toxic action on the beetle.

The beetles feed readily on the flowers of the bottlebrush buckeye (*Aesculus parviflora*), and if feeding continues long enough, they become paralyzed and eventually die. The first symptom of poisoning is paralysis of the legs. The foliage is much less toxic than the flowers. (Hawley and Metzger 1940) This plant is in bloom when the beetle population is at its peak, whereas the horsechestnut (*Aesculus hippocastanum*) produces flowers before beetles appear. The toxic substance in the bottlebrush buckeye has not been identified.

Landreth (1932a, 1932b) reported that large numbers of beetles were killed by feeding on castorbean (*Ricinus communis*). The use of this plant as a killing agent for the beetle was advertised widely,

and many people grow it for this purpose. Metzger (1933) found that the beetle fed lightly on the varieties *sanguineus* and *zanzibarensis* but scarcely touched the varieties *cambodgensis*, *gibsoni*, *panormitans*, and Red Spire. Most of the feeding occurred after the seed pods had developed and after more favored food plants had been severely injured. The foliage of these varieties was nontoxic to the beetle. The castorbean had no value as a trap crop for the beetle. Since a toxic substance in castorbean was not demonstrated, the high mortality reported late in the summer was probably due to old age rather than to toxicity.

Food Plants in Japan

Japanese entomologists had little information on the food plants of the beetle, probably because it is not a serious pest in Japan. Clausen et al. (1927) found the beetle feeding on several trees, shrubs, and herbaceous plants. The following plants marked with an asterisk (*) are preferred by the beetle:

Scientific name	Common name
<i>Alnus japonica</i>	Japanese alder
* <i>Ampelopsis japonica</i>	Japanese ampelopsis
* <i>Asparagus officinalis</i>	Garden asparagus
<i>Berchemia racemosa</i>	Japanese supplejack
* <i>Castanea crenata</i>	Japanese chestnut
<i>Dioscorea esculenta</i>	Chinese yam
<i>Filipendula camtschatica</i>	Kamchutka meadowsweet
<i>Glycine max</i>	Soybean
<i>Hibiscus syriacus</i>	Shrub-althea
<i>Hypericum japonicum</i>	Japanese St. Johnswort
* <i>Melia azedarach</i>	Chinaberry
<i>Oenothera biennis</i>	Evening-primrose
<i>Phaseolus vulgaris</i>	Garden bean
<i>Platanus orientalis</i>	Oriental planetree
<i>Polygonum convolvulus</i>	Corn bindweed
<i>Polygonum cuspidatum</i>	Japanese fleecetflower
<i>Polygonum nodosum</i>	Cinutade
* <i>Polygonum Reynoutria</i>	Itadori
<i>Populus maximowiczii</i>	Japanese poplar
* <i>Populus nigra italica</i>	Lombardy poplar
<i>Prunus japonica</i>	Chinese bushcherry
<i>Prunus serrulata</i>	Oriental cherry
* <i>Pteridium aquilinum</i>	Bracken
<i>Quercus acutissima</i>	Sawtooth oak
<i>Quercus variabilis</i>	Oriental oak
<i>Rosa multiflora</i>	Japanese rose
* <i>Rubus crataegifolius</i>	Hawthorn raspberry
<i>Rumex</i> sp.	Dock
<i>Salix viminalis</i>	Basketwillow

Scientific name	Common name
<i>Smilax china</i>	Chinaroot greenbrier
<i>Tilia japonica</i>	Japanese linden
<i>Tilia miqueliana</i>	Linden
<i>Trifolium pratense</i>	Red clover
<i>Ulmus parvifolia</i>	Chinese elm
* <i>Vitis thunbergii</i>	Thunberg grape
* <i>Vitis vinifera</i>	European wine grape
* <i>Wistaria floribunda</i>	Japanese wisteria
<i>Zelkova serrata</i>	Japanese zelkova

Clausen et al. (1927) observed that the density of the beetle population throughout Japan never reaches that in the United States, probably because of the agricultural conditions in certain areas and the presence of its natural enemies, which keep it under control. With these lighter populations plant injury is sporadic and less extensive.

The preference of the beetle for certain weeds, particularly for *Polygonum Reynoutria*, growing along the roadsides usually prevented serious injury to crops and to ornamental plants. Clausen et al. (1927) found this weed almost skeletonized at Koiwai, whereas only an occasional beetle was found in a large adjacent field of soybeans. In addition, plants preferred by the beetle in some districts were hardly touched in other districts.

Food Plants in the United States

In contrast to Japan, the beetle has a wide range of food plants in the United States. It attacks certain small fruits, tree fruits, truck and garden crops, field crops, ornamental herbaceous garden plants, ornamental shrubs and vines, shade and ornamental trees, and many noneconomic plants. Plants attacked or immune to injury by the beetle are listed by Davis (1920a), Smith and Hadley (1926), Safo (1928a, 1928b, 1928c), Metzger and Grant (1932), Hadley and Hawley (1934), Metzger et al. (1934), Hawley and Metzger (1940), Hadley (1940), and Fleming (1955, 1960, 1963a, 1963b). Hawley and Metzger (1940) made the most complete listing of the food plants of the beetle.

There are some discrepancies in these lists. Some plants listed prior to 1940 as being immune to injury were attacked in more recent years in heavily infested areas. Other plants listed in the earlier publications as being injured by the beetle were eliminated in the later publications because the early reports of injury were not substantiated.

Plants Injured Most Severely.—The following plants are always attacked by the beetle and in areas of dense population may be defoliated:

Scientific name	Common name
<i>Acer palmatum</i>	Japanese maple
<i>Acer platanoides</i>	Norway maple
<i>Aesculus hippocastanum</i>	Horsechestnut
<i>Althaea officinalis</i>	Marshmallow
<i>Althaea rosea</i>	Hollyhock
<i>Asparagus officinalis</i>	Asparagus
<i>Betula populifolia</i>	Gruy birch
<i>Castanea dentata</i>	American chestnut
<i>Clethra alnifolia</i>	Sweet pepperbush
<i>Glycine max</i>	Soybean
<i>Hibiscus palustris</i>	Common rosemallow
<i>Hibiscus syriacus</i>	Shrub-althea
<i>Juglans nigra</i>	Black walnut
<i>Kerria japonica</i>	Globeflower
<i>Lagerstroemia indica</i>	Crape-myrtle
<i>Malus baccata</i>	Crabapple
<i>Malus floribunda</i>	Japanese flowering crabapple
<i>Malus sylvestris</i>	Apple
<i>Malva rotundifolia</i>	Mallow
<i>Oenothera biennis</i>	Evening-primrose
<i>Parthenocissus quinquefolia</i> ..	Virginia-creeper
<i>Platanus acerifolia</i>	London planetree
<i>Polygonum orientale</i>	Princesplume smartweed
<i>Polygonum pennsylvanicum</i>	Pennsylvania smartweed
<i>Populus nigra italica</i>	Lombardy poplar
<i>Prunus armeniaca</i>	Apricot
<i>Prunus avium</i>	Sweet cherry
<i>Prunus cerasus</i>	Sour cherry
<i>Prunus domestica</i>	Garden plum
<i>Prunus persica</i>	Peach
<i>Prunus persica nectarina</i>	Nectarine
<i>Prunus salicina</i>	Japanese plum
<i>Prunus serotina</i>	Black cherry
<i>Rheum rhabarbarum</i>	Garden rhubarb
<i>Rhus toxicodendron</i>	Poison-ivy
<i>Rosa</i> spp.	Rose
<i>Salix discolor</i>	Pussy willow
<i>Sassafras albidum</i>	Sassafras
<i>Sorbus americana</i>	American mountain-ash
<i>Tilia americana</i>	American linden
<i>Ulmus americana</i>	American elm
<i>Ulmus procera</i>	English elm
<i>Vaccinium corymbosum</i>	Highbush blueberry
<i>Vitis aestivalis</i>	Summer grape
<i>Vitis labrusca</i>	Foxgrape
<i>Vitis vinifera</i>	European wine grape
<i>Zea mays</i>	Corn

Susceptibility of Various Plants to Attack.—Records are available on the susceptibility of 435 species of plants in 95 families to

attack by the beetle. The beetle has not been observed feeding on 140 species, but this is an incomplete listing of the plants apparently immune to attack. It occasionally feeds lightly on 122 species only in areas where it is very abundant. It generally feeds lightly on 67 species, moderately on 59 species, and extensively on 47 species, but under certain conditions more than the usual amount of feeding may occur. Light feeding generally causes little injury to a plant; moderate feeding is sufficient to cause damage of economic importance.

The preference of the beetle for various plants, grouped in families, is summarized in table 5.

TABLE 5.—*Extent of feeding by Japanese beetle on various plants in United States*

Extent of feeding ¹	Family and species	Common name	Part attacked
ACERACEAE			
x	<i>Acer negundo</i>	Boxelder	Foliage.
xxxx	<i>Acer palmatum</i>	Japanese maple	Do.
xxxx	<i>Acer platanoides</i>	Norway maple	Do.
xx	<i>Acer pseudoplatanus</i>	Sycamore maple	Do.
0	<i>Acer rubrum</i>	Red maple	None.
0	<i>Acer saccharinum</i>	Silver maple	Do.
xx	<i>Acer saccharophorum</i>	Sugar maple	Foliage.
ALISMACEAE			
xx	<i>Sagittaria latifolia</i>	Common arrowhead	Do.
AMARANTHACEAE			
x	<i>Amaranthus retroflexus</i>	Rough pigweed	Do.
0	<i>Celosia argentea cristata</i>	Cockscomb	None.
ANACARDIACEAE			
x	<i>Cotinus coggygria</i>	Common smoketree	Foliage.
xx	<i>Rhus copallina</i>	Flame-leaf sumac	Do.
xxxx	<i>Rhus toxicodendron</i>	Poison-ivy	Do.
x	<i>Rhus typhina</i>	Staghorn sumac	Do.
APOCYNACEAE			
xx	<i>Apocynum androsaemifolium</i>	Spreading dogbane	Do.
0	<i>Visca minor</i>	Ground-myrtle	None.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
AQUIFOLIACEAE			
0	<i>Ilex aquifolium</i>	English holly	Do.
0	<i>Ilex cornuta</i>	Chinese holly	Do.
0	<i>Ilex crenata</i>	Japanese holly	Do.
0	<i>Ilex opaca</i>	American holly	Do.
x	<i>Ilex verticillata</i>	Winterberry	Foliage.
ARACEAE			
xxx	<i>Peltandra virginica</i>	Virginia arrow-arum	Do.
ARALIACEAE			
xxx	<i>Aralia hispida</i>	Bristly sarsaparilla	Do.
x	<i>Hedera helix</i>	English ivy	Do.
ASCLEPLADACEAE			
x	<i>Asclepias incarnata</i>	Swamp milkweed	Foliage, flower.
x	<i>Asclepias purpurascens</i>	Purple milkweed	Do.
x	<i>Asclepias syriaca</i>	Common milkweed	Do.
BALSAMINACEAE			
0	<i>Impatiens balsamina</i>	Garden balsam	None.
xx	<i>Impatiens biflora</i>	Spotted snapweed	Foliage.
BEGONIACEAE			
0	<i>Begonia rex-cultorum</i>	Begonia	None.
BERBERIDACEAE			
xx	<i>Berberis thunbergii</i>	Japanese barberry	Foliage.
xx	<i>Berberis vulgaris</i>	European barberry	Do.
BETULACEAE			
xxx	<i>Alnus glutinosa</i>	European black alder	Do.
xxx	<i>Betula pendula</i>	European white birch	Do.
xxxx	<i>Betula populifolia</i>	Gray birch	Do.
x	<i>Corylus americana</i>	American hazelnut	Do.

See footnote at end of table.

TABLE 5.—*Extent of feeding by Japanese beetle on various plants in United States—Continued*

Extent of feeding ¹	Family and species	Common name	Part attacked
BIGNONIACEAE			
xx	<i>Campsis radicans</i>	Trumpet creeper	Do.
xxx	<i>Catalpa bignonioides</i>	Southern catalpa	Do.
BORAGINACEAE			
0	<i>Myosotis sylvatica</i>	Forget-me-not	None.
BUXACEAE			
0	<i>Buxus sempervirens</i>	Box	Do.
0	<i>Pachysandra terminalis</i>	Japanese spurge	Do.
CALYCANTHACEAE			
0	<i>Calycanthus floridus</i>	Carolina allspice	Do.
CANNACEAE			
xxx	<i>Canna generalis</i>	Garden canna	Foliage, flower.
xxx	<i>Canna indica</i>	India canna	Do.
CAPRIFOLIACEAE			
0	<i>Lonicera fragrantissima</i>	Winter honeysuckle	None.
x	<i>Lonicera japonica</i>	Japanese honeysuckle	Foliage.
x	<i>Sambucus canadensis</i>	American elder	Do.
0	<i>Symphoricarpos albus</i>	Snowberry	None.
0	<i>Symphoricarpos orbiculatus</i>	Coralberry	Do.
xxx	<i>Viburnum dentatum</i>	Arrowwood	Foliage.
x	<i>Viburnum opulus</i>	European cranberry bush	Do.
xx	<i>Weigela florida</i>	Weigela	Do.
CARYOPHYLLACEAE			
xx	<i>Agrostemma githago</i>	Corncockle	Do.
0	<i>Dianthus barbatus</i>	Sweet-william	None.
0	<i>Dianthus caryophyllus</i>	Carnation	Do.
0	<i>Gypsophila paniculata</i>	Babybreath	Do.
0	<i>Gypsophila repens</i>	Creeping gypsophila	Do.
0	<i>Stellaria media</i>	Common chickweed	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
CELASTRACEAE			
0	<i>Celastrus scandens</i>	American bittersweet	Do.
0	<i>Euonymus alatus</i>	Winged euonymus	Do.
0	<i>Euonymus fortunei</i>	Climbing euonymus	Do.
CHENOPODIACEAE			
XX	<i>Beta vulgaris</i>	Beet	Foliage.
X	<i>Chenopodium album</i>	Lambsquarters	Do.
X	<i>Chenopodium ambrosioides</i>		
	<i>anthelminticum</i>	American wormseed	Do.
X	<i>Chenopodium paganum</i>	Pigweed	Do.
0	<i>Spinacia oleracea</i>	Spinach	None.
CLETHRACEAE			
XXXX	<i>Clethra alnifolia</i>	Sweet pepperbush	Foliage, flower.
COMMELINACEAE			
X	<i>Commelina virginica</i>	Virginia dayflower	Foliage.
0	<i>Tradescantia fluminensis</i>	Wandering-Jew	None.
X	<i>Tradescantis virginiana</i>	Spiderwort	Foliage.
COMPOSITAE			
X	<i>Achillea millefolium</i>	Common yarrow	Foliage, flower.
0	<i>Ageratum conyzoides</i>	Ageratum	None.
XXX	<i>Ambrosia artemisiifolia</i>	Common ragweed	Foliage.
XXX	<i>Ambrosia trifida</i>	Giant ragweed	Do.
X	<i>Aster noxae-anglicae</i>	New England aster	Do.
X	<i>Aster patens</i>	Skydrop aster	Do.
X	<i>Aster undulatus</i>	Wave aster	Do.
X	<i>Aster vimineus</i>	Small white aster	Do.
X	<i>Baccharis halimifolia</i>	Groundsel-bush	Do.
0	<i>Caladium bicolor</i>	Caladium	None.
XX	<i>Calendula officinalis</i>	Pot marigold	Foliage.
0	<i>Centaurea cineraria</i>	Dusty-miller	None.
0	<i>Centaurea cyanus</i>	Cornflower	Do.
0	<i>Centaurea montana</i>	Mountain-bluet	Do.
X	<i>Chrysanthemum coccineum</i>	Pyrethrum	Foliage.

See footnote at end of table.

TABLE 5.—*Extent of feeding by Japanese beetle on various plants in United States—Continued*

Extent of feeding ¹	Family and species	Common name	Part attacked
COMPOSITAE—continued			
x	<i>Chrysanthemum leucanthemum</i>	Oxeye daisy	Do.
x	<i>Cichorium endivia</i>	Endive	Do.
xx	<i>Cichorium intybus</i>	Chicory	Do.
x	<i>Cirsium arvense</i>	Canada thistle	Flower.
0	<i>Coreopsis lanceolata</i>	Lance coreopsis	None.
x	<i>Cosmos bipinnatus</i>	Common cosmos	Foliage.
x	<i>Cynara scolymus</i>	Artichoke	Do.
xxx	<i>Dahlia variabilis</i>	Dahlia	Foliage, flower.
x	<i>Erigeron annuus</i>	Daisy fleabane	Foliage.
x	<i>Erigeron canadensis</i>	Horseweed	Do.
x	<i>Erigeron strigosus</i>	White-top	Do.
xx	<i>Eupatorium album</i>	White thoroughwort	Do.
x	<i>Eupatorium purpureum</i>	Joe-pye-weed	Do.
x	<i>Gaillardia aristata</i>	Gaillardia	Do.
x	<i>Galinsoga parviflora</i>	Quickweed	Do.
xx	<i>Helianthus annuus</i>	Common sunflower	Foliage, flower.
x	<i>Helichrysum bracteatum</i>	Strawflower	Foliage.
0	<i>Lactuca sativa</i>	Lettuce	None.
0	<i>Rudbeckia hirta</i>	Brown-eyed-susan	Do.
0	<i>Rudbeckia laciniata</i>	Coneflower	Do.
0	<i>Rudbeckia laciniata hortensis</i>	Goldenglow	Do.
xx	<i>Solidago juncea</i>	Plume goldenrod	Foliage.
xx	<i>Tagetes erecta</i>	Aztec marigold	Do.
xxx	<i>Tagetes patula</i>	French marigold	Do.
0	<i>Taraxacum officinale</i>	Common dandelion	None.
x	<i>Tragopogon porrifolius</i>	Salsify	Foliage.
xx	<i>Vernonia noveboracensis</i>	Common Ironweed	Do.
xxx	<i>Zinnia elegans</i>	Common zinnia	Foliage, flower.
CONVOLVULACEAE			
x	<i>Ipomoea batatas</i>	Sweetpotato	Foliage.
xx	<i>Ipomoea purpurea</i>	Common morning-glory	Do.
CORNACEAE			
0	<i>Cornus florida</i>	Flowering dogwood	None.
xx	<i>Nyssa sylvatica</i>	Black tupelo	Foliage.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
CRASSULACEAE			
0	<i>Sedum spectabile</i>	Showy sedum	None.
CRUCIFERAE			
0	<i>Brassica campestris</i>	Bird rape	Do.
xx	<i>Brassica hirta</i>	White mustard	Foliage.
0	<i>Brassica napobrassica</i>	Rutabaga	None.
xxx	<i>Brassica oleracea botrytis</i>	Broccoli	Foliage.
0	<i>Brassica oleracea botrytis</i>	Cauliflower	None.
x	<i>Brassica oleracea capitata</i>	Cabbage	Foliage.
x	<i>Brassica oleracea gemmifera</i>	Brussels sprouts	Do.
0	<i>Brassica oleracea viridis</i>	Kale	None.
x	<i>Brassica rapa</i>	Turnip	Foliage.
0	<i>Iberis sempervirens</i>	Evergreen candytuft	None.
0	<i>Raphanus sativus</i>	Garden radish	Do.
CUCURBITACEAE			
x	<i>Citrullus vulgaris</i>	Watermelon	Foliage.
x	<i>Cucumis melo</i>	Muskmelon	Do.
x	<i>Cucumis melo reticulatus</i>	Cantaloup	Do.
x	<i>Cucumis sativus</i>	Cucumber	Do.
x	<i>Cucurbita pepo</i>	Pumpkin	Do.
x	<i>Cucurbita pepo melopepo</i>	Summer squash	Do.
x	<i>Sicyos angulatus</i>	Bar-cucumber	Do.
CUPRESSACEAE			
0	<i>Chamaecyparis lawsoniana</i>	Lawson white-cedar	None.
0	<i>Chamaecyparis obtusa</i>	Hinoki-cypress	Do.
0	<i>Chamaecyparis pisifera</i>	Sawara-cypress	Do.
0	<i>Chamaecyparis thyoides</i>	Atlantic white-cedar	Do.
x	<i>Juniperus chinensis</i>	Chinese juniper	Foliage.
x	<i>Juniperus communis</i>	Common juniper	Do.
x	<i>Thuja occidentalis</i>	American arborvitae	Do.
x	<i>Thuja orientalis</i>	Oriental arborvitae	Do.
CYPERACEAE			
x	<i>Cyperus esculentus</i>	Chufa	Do.
DIPSACEAE			
0	<i>Scabiosa atropurpurea</i>	Sweet scabious	None.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
EBENACEAE			
x	<i>Diospyros virginiana</i>	Common persimmon	Foliage.
ERICACEAE			
x	<i>Gaylussacia baccata</i>	Black huckleberry	Foliage, fruit.
0	<i>Kalmia latifolia</i>	Mountain-laurel	None.
x	<i>Rhododendron catawbiense</i>	Catawba rhododendron	Foliage.
x	<i>Rhododendron maximum</i>	Rosebay rhododendron	Do.
x	<i>Rhododendron molle</i>	Chinese azalea	Do.
0	<i>Rhododendron nudiflorum</i>	Pinksterbloom azalea	None.
xxx	<i>Rhododendron obtusum japonicum</i>	Kurume azalea	Foliage.
x	<i>Rhododendron obtusum kumpferi</i>	Torch azalea	Do.
x	<i>Rhododendron viscosum</i>	Swamp azalea	Do.
xx	<i>Vaccinium angustifolium</i>	Lowbush blueberry	Foliage, fruit.
xxxx	<i>Vaccinium corymbosum</i>	Highbush blueberry	Do.
x	<i>Vaccinium macrocarpon</i>	American cranberry	Foliage.
EUPHORBACEAE			
xx	<i>Acalypha virginica</i>	Virginia copperleaf	Do.
xx	<i>Ricinus communis</i>	Castorbean	Do.
FAGACEAE			
xx	<i>Castanea crenata</i>	Japanese chestnut	Do.
xxxx	<i>Castanea dentata</i>	American chestnut	Do.
xx	<i>Fagus grandifolia</i>	American beech	Do.
xx	<i>Fagus sylvatica</i>	European beech	Do.
x	<i>Quercus alba</i>	White oak	Do.
x	<i>Quercus borealis</i>	Northern red oak	Do.
x	<i>Quercus coccinea</i>	Scarlet oak	Do.
x	<i>Quercus falcata</i>	Southern red oak	Do.
xxx	<i>Quercus ilicifolia</i>	Scrub oak	Do.
xx	<i>Quercus montana</i>	Chestnut oak	Do.
xxx	<i>Quercus palustris</i>	Pin oak	Do.
x	<i>Quercus stellata</i>	Post oak	Do.
x	<i>Quercus velutina</i>	Black oak	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
FUMARIACEAE			
0	<i>Dicentra formosa</i>	Pacific bleedingheart	None.
GERANIACEAE			
xx	<i>Pelargonium domesticum</i>	Lady Washington geranium	Foliage, flower.
GINKGOACEAE			
x	<i>Ginkgo biloba</i>	Maidenhair tree	Foliage.
GRAMINEAE			
0	<i>Avena sativa</i>	Oats	None.
0	<i>Bambusa vulgaris</i>	Common bamboo	Do.
x	<i>Cortaderia selloana</i>	Pampasgrass	Foliage.
0	<i>Dactylis glomerata</i>	Orchardgrass	None.
xx	<i>Digitaria sanguinalis</i>	Hairy crabgrass	Foliage.
0	<i>Hordeum vulgare</i>	Barley	None.
x	<i>Phleum pratense</i>	Timothy	Foliage.
0	<i>Secale cereale</i>	Rye	None.
x	<i>Setaria italica</i>	Millet	Foliage.
0	<i>Triticum aestivum</i>	Wheat	None.
xxxx	<i>Zea mays</i>	Corn	Foliage, ear, tassel.
HAMAMELIDACEAE			
x	<i>Hamamelis virginiana</i>	Witch-hazel	Foliage.
x	<i>Liquidambar styraciflua</i>	American sweetgum	Do.
HIPPOCASTANACEAE			
xxxx	<i>Aesculus hippocastanum</i>	Horsechestnut	Do.
xxx	<i>Aesculus parviflora</i>	Bottlebrush buckeye	Foliage, flower.
HYPERICACEAE			
xxx	<i>Hypericum perforatum</i>	St. John's-wort	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
IRIDACEAE			
xx	<i>Gladiolus hortulanus</i>	Gladiolus	Do.
x	<i>Iris germanica</i>	Bearded iris	Do.
x	<i>Iris japonica</i>	Fringed iris	Do.
x	<i>Iris kaempferi</i>	Japanese iris	Do.
JUGLANDACEAE			
x	<i>Carya glabra</i>	Pignut hickory	Foliage.
x	<i>Carya ovata</i>	Shagbark hickory	Do.
xx	<i>Carya tomentosa</i>	Mockernut hickory	Do.
x	<i>Juglans cinerea</i>	Butternut	Do.
xxxx	<i>Juglans nigra</i>	Black walnut	Do.
xx	<i>Juglans sicboldiana</i>	Siebold walnut	Do.
LABIATAE			
0	<i>Hedeoma pulegioides</i>	American pennyroyal	None.
0	<i>Hyssopus officinalis</i>	Hyssop	Do.
x	<i>Leonurus cardiaca</i>	Motherwort	Foliage.
0	<i>Mentha spicata</i>	Spearmint	None.
x	<i>Monarda didyma</i>	Oswego-tea	Foliage.
x	<i>Monarda fistulosa</i>	Wildbergamot	Do.
x	<i>Nepeta cataria</i>	Catnip	Do.
0	<i>Physostegia virginiana</i>	False-dragonhead	None.
xx	<i>Salvia splendens</i>	Scarlet sage	Foliage.
x	<i>Teucrium canadense</i>	American germander	Do.
LAURACEAE			
xxx	<i>Lindera benzoin</i>	Common spicebush	Foliage, flower.
xxxx	<i>Sassafras albidum</i>	Common sassafras	Foliage.
LEGUMINOSAE			
0	<i>Albizia julibrissin</i>	Mimosa	None.
0	<i>Arachis hypogaea</i>	Peanut	Do.
0	<i>Baptisia australis</i>	Blue false-indigo	Do.
xx	<i>Cassia fasciculata</i>	Partridgepea	Foliage.
0	<i>Cercis chinensis</i>	Chinese redbud	None.
x	<i>Desmodium canadense</i>	Hoary tickclover	Foliage.
xxxx	<i>Glycine max</i>	Soybean	Do.
0	<i>Lathyrus latifolius</i>	Perennial pea	None.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
0	<i>Lathyrus odoratus</i>	Sweetpea	Do.
xx	<i>Lespedeza striata</i>	Lespedeza	Foliage.
xxx	<i>Medicago sativa</i>	Alfalfa	Foliage, flower.
xx	<i>Phaseolus limensis</i>	Lima bean	Foliage.
xxx	<i>Phaseolus vulgaris</i>	Garden bean	Do.
x	<i>Pisum sativum</i>	Garden pea	Do.
xx	<i>Pisum sativum arvense</i>	Field pea	Do.
x	<i>Robinia pseudoacacia</i>	Black locust	Do.
x	<i>Sophora japonica</i>	Japanese pagoda tree	Do.
xxx	<i>Trifolium hybridum</i>	Alsike clover	Foliage, flower.
xxx	<i>Trifolium pratense</i>	Red clover	Do.
xx	<i>Trifolium repens</i>	White clover	Do.
x	<i>Vicia sativa</i>	Common vetch	Do.
xxx	<i>Wisteria sinensis</i>	Chinese wisteria	Foliage.
LILIACEAE			
0	<i>Allium cepa</i>	Common onion	None.
0	<i>Allium porrum</i>	Leek	Do.
xxxx	<i>Asparagus officinalis</i>	Asparagus	Foliage.
0	<i>Convallaria majalis</i>	Lily-of-the-valley	None.
0	<i>Erythronium albidum</i>	Dogtooth violet	Do.
x	<i>Hemerocallis fulva</i>	Tawny daylily	Foliage.
0	<i>Lilium longiflorum</i>	Easter lily	None.
0	<i>Lilium speciosum</i>	Showy lily	Do.
0	<i>Lilium tigrinum</i>	Tiger lily	Do.
x	<i>Smilax rotundifolia</i>	Horse brier	Foliage.
0	<i>Yucca filamentosa</i>	Adam's needle yucca	None.
LOBELIACEAE			
xx	<i>Lobelia cardinalis</i>	Cardinalflower	Foliage.
LOGANIACEAE			
xxx	<i>Buddleia davidii</i>	Orange-eye butterflybush	Foliage, flower.
LYTHRACEAE			
xxxx	<i>Lagerstroemia indica</i>	Crape myrtle	Do.
x	<i>Lythrum salicaria</i>	Purple loosestrife	Foliage.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
MAGNOLIACEAE			
0	<i>Liriodendron tulipifera</i>	Tuliptree	None.
0	<i>Magnolia grandiflora</i>	Southern magnolia	Do.
0	<i>Magnolia soulangeana</i>	Saucer magnolia	Do.
0	<i>Magnolia virginiana</i>	Laurel magnolia	Do.
MALVACEAE			
xxx	<i>Abutilon theophrasti</i>	Velvetleaf	Foliage.
xxxx	<i>Althaea officinalis</i>	Marshmallow	Flower.
xxxx	<i>Althaea rosea</i>	Hollyhock	Foliage, flower.
xx	<i>Gossypium hirsutum</i>	Upland cotton	Do.
x	<i>Hibiscus esculentus</i>	Okra	Foliage.
xxxx	<i>Hibiscus palustris</i>	Common rosemallow	Flower.
xxxx	<i>Hibiscus syriacus</i>	Shrub-althea	Do.
xxx	<i>Hibiscus trionum</i>	Flower-of-an-hour	Foliage, flower.
xxxx	<i>Malva rotundifolia</i>	Mallow	Flower.
MELASTOMACEAE			
xxx	<i>Rhexia virginica</i>	Common meadowbeauty	Foliage, flower.
MORACEAE			
0	<i>Ficus carica</i>	Fig	None.
x	<i>Ficus elastica</i>	India rubber tree	Foliage.
x	<i>Humulus lupulus</i>	Common hop	Do.
0	<i>Morus rubra</i>	Red mulberry	None.
MUSACEAE			
x	<i>Musa paradisiaca sapientum</i>	Common banana	Foliage.
MYRICACEAE			
xx	<i>Myrica pensylvanica</i>	Northern bayberry	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
NYCTAGINACEAE			
xxx	<i>Mirabilis jalapa</i>	Common four-o'clock	Foliage, flower.
NYMPHAEACEAE			
xxx	<i>Nelumbo lutea</i>	American lotus	Do.
xxx	<i>Nuphar advena</i>	Common spatterdock	Foliage.
0	<i>Nymphaea odorata</i>	American waterlily	None.
OLEACEAE			
0	<i>Forsythia intermedia</i>	Border forsythia	Do.
0	<i>Forsythia suspensa</i>	Weeping forsythia	Do.
0	<i>Fraxinus americana</i>	White ash	Do.
0	<i>Fraxinus pennsylvanica</i>	Red ash	Do.
xx	<i>Ligustrum ovalifolium</i>	California privet	Foliage.
x	<i>Ligustrum vulgare</i>	Common privet	Do.
0	<i>Syringa persica</i>	Persian lilac	None.
0	<i>Syringa vulgaris</i>	Common lilac	Do.
ONAGRACEAE			
xxxx	<i>Oenothera biennis</i>	Common evening-primrose	Foliage, flower.
OSMUNDACEAE			
xxx	<i>Osmunda cinnamomea</i>	Cinnamonfern	Foliage.
OXALIDACEAE			
xx	<i>Oxalis stricta</i>	Common yellow oxalis	Do.
PAPAVERACEAE			
0	<i>Papaver nudicaule</i>	Iceland poppy	None.
0	<i>Papaver orientale</i>	Oriental poppy	Do.
PHYTOLACCACEAE			
0	<i>Phytolacca americana</i>	Common pokeberry	Do.

See footnote at end of table.

TABLE 5.—*Extent of feeding by Japanese beetle on various plants in United States—Continued*

Extent of feeding ¹	Family and species	Common name	Part attacked
PINACEAE			
0	<i>Abies concolor</i>	Balsam fir	Do.
x	<i>Cryptomeria japonica</i>	Cryptomeria	Foliage.
xxx	<i>Larix decidua</i>	European larch	Do.
0	<i>Picea abies</i>	Norway spruce	None.
0	<i>Picea orientalis</i>	Oriental spruce	Do.
0	<i>Pinus sylvestris</i>	Scotch pine	Do.
x	<i>Pinus virginiana</i>	Virginia pine	Foliage.
0	<i>Pseudotsuga taxifolia</i>	Douglas fir	None.
xxx	<i>Taxodium distichum</i>	Baldcypress	Foliage.
0	<i>Tsuga canadensis</i>	Hemlock	None.
PLANTAGINACEAE			
x	<i>Plantago lanceolata</i>	Buckhorn	Foliage.
x	<i>Plantago major</i>	Plantain	Do.
PLATANACEAE			
xxxx	<i>Platanus acerifolia</i>	London planetree	Do.
xxx	<i>Platanus occidentalis</i>	American planetree	Do.
POLEMONIACEAE			
x	<i>Phlox paniculata</i>	Perennial phlox	Do.
POLYGONACEAE			
x	<i>Fagopyrum esculentum</i>	Buckwheat	Do.
xxx	<i>Polygonum arifolium</i>	Broadleaf tearthumb	Do.
xxx	<i>Polygonum convolvulus</i>	Corn bindweed	Do.
xxx	<i>Polygonum cuspidatum</i>	Japanese fleecedower	Do.
xxx	<i>Polygonum dumetorum</i>	Hedge knotweed	Do.
xxx	<i>Polygonum hydropiper</i>	Common smartweed	Do.
xxxx	<i>Polygonum orientale</i>	Princesplume smartweed	Foliage, flower.
xxxx	<i>Polygonum pensylvanicum</i>	Pennsylvania smartweed	Foliage.
xxx	<i>Polygonum persicaria</i>	Ladysthumb smartweed	Do.
xxx	<i>Polygonum scandens</i>	Climbing false- buckwheat	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
xxxx	<i>Rheum raphaniticum</i>	Garden rhubarb	Do.
xx	<i>Rumex crispus</i>	Yellow dock	Do.
xx	<i>Rumex obtusifolius</i>	Bitter dock	Do.
POLYPODIACEAE			
x	<i>Adiantum capillus-veneris</i>	Southern maidenhair fern	Do.
xx	<i>Onclea sensibilis</i>	Sensitive fern	Do.
xxx	<i>Pteridium latiusculum</i>	Eastern bracken	Do.
PONTEDERIACEAE			
xxx	<i>Pontederia cordata</i>	Pickersweet	Do.
PORTULACACEAE			
0	<i>Portulaca grandiflora</i>	Common portulaca	None.
RANUNCULACEAE			
0	<i>Aquilegia canadensis</i>	American columbine	Do.
0	<i>Aquilegia vulgaris</i>	European columbine	Do.
0	<i>Clematis heracleaefolia</i>	Tubeclematis	Do.
x	<i>Clematis paniculata</i>	Sweet autumn clematis	Foliage.
0	<i>Delphinium formosum</i>	Hardy larkspur	None.
0	<i>Helleborus niger</i>	Christmas-rose	Do.
xx	<i>Paeonia officinalis</i>	Common peony	Foliage.
0	<i>Ranunculus acris</i>	Meadow buttercup	None.
0	<i>Ranunculus sceleratus</i>	Bitter buttercup	Do.
RESEDACEAE			
0	<i>Reseda odorata</i>	Common mignonette	Do.
ROSACEAE			
xxx	<i>Chaenomeles lagenaria</i>	Japanese flowering quince	Foliage.
xx	<i>Crataegus monogyna</i>	Singleseed hawthorn	Do.
xx	<i>Crataegus oxyacantha</i>	English hawthorn	Do.
xxx	<i>Cydonia oblonga</i>	Common quince	Foliage, fruit.
xx	<i>Erochorda racemosa</i>	Pearlbush	Foliage.
xx	<i>Fragaria chiloensis</i>	Chilone strawberry	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
ROSACEAE—continued			
xx	<i>Fragaria chiloensis ananassa</i>	Garden strawberry	Do.
0	<i>Geum chiloense</i>	Chile avens	None.
xxxx	<i>Kerria japonica</i>	Globeflower	Foliage.
xxxx	<i>Malus baccata</i>	Crabapple	Foliage, fruit.
xxxx	<i>Malus floribunda</i>	Japanese flowering crabapple	Do.
xxxx	<i>Malus sylvestris</i>	Apple	Do.
xxxx	<i>Prunus armeniaca</i>	Apricot	Do.
xxxx	<i>Prunus avium</i>	Sweet cherry	Do.
xxxx	<i>Prunus cerasus</i>	Sour cherry	Foliage.
xxxx	<i>Prunus domestica</i>	Garden plum	Foliage, fruit.
xxxx	<i>Prunus persica</i>	Peach	Do.
xxxx	<i>Prunus persica nectarina</i>	Nectarine	Do.
xxxx	<i>Prunus salicina</i>	Japanese plum	Do.
xxxx	<i>Prunus scrotina</i>	Black cherry	Foliage.
xxx	<i>Prunus serrulata</i>	Oriental cherry	Do.
xx	<i>Prunus virginiana</i>	Common chokeberry	Do.
x	<i>Pyracantha coccinea</i>	Firethorn	Do.
x	<i>Pyrus communis</i>	Pear	Do.
xxxx	<i>Rosa</i> spp	Rose	Foliage, flower.
xx	<i>Rubus argutus</i>	Highbush blackberry	Foliage.
xx	<i>Rubus cuneifolius</i>	Sand blackberry	Do.
x	<i>Rubus flagellaris</i>	Northern dewberry	Do.
xxx	<i>Rubus idaeus</i>	Red raspberry	Foliage, fruit.
xxx	<i>Rubus occidentalis</i>	Blackcap raspberry	Do.
xxxx	<i>Sorbus americana</i>	American mountain-ash	Foliage.
xx	<i>Spiraea tomentosa</i>	Hardhack spirea	Do.
xx	<i>Spiraea trilobata</i>	Three-lobed spirea	Do.
xx	<i>Spiraea vanhouttei</i>	Vanhoutte spirea	Do.
RUBIACEAE			
xxx	<i>Cephalanthus occidentalis</i>	Buttonbush	Foliage, flower.
xx	<i>Galium pilosum</i>	Hairy bedstraw	Foliage.
xx	<i>Galium triflorum</i>	Sweet-scented bedstraw	Do.
x	<i>Gardenia jasminoides</i>	Gardenia	Do.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
RUTACEAE			
xxx	<i>Citrus sinensis</i>	Sweet orange	Foliage, flower.
SALICACEAE			
0	<i>Populus alba</i>	White poplar	None.
0	<i>Populus alba pyramidalis</i>	Boiteau poplar	Do.
xxxx	<i>Populus nigra italica</i>	Lombardy poplar	Foliage.
xxx	<i>Salix babylonica</i>	Babylon weeping willow	Do.
xxx	<i>Salix cordata</i>	Heartleaf willow	Do.
xxxx	<i>Salix discolor</i>	Pussy willow	Do.
SAXIFRAGACEAE			
xx	<i>Deutzia grandiflora</i>	Deutzia	Foliage, flower.
0	<i>Heuchera sanguinea</i>	Coralbells	None.
0	<i>Hydrangea arborescens</i>	Smooth hydrangea	Do.
0	<i>Hydrangea paniculata</i>	Panicle hydrangea	Do.
x	<i>Hydrangea petiolaris</i>	Climbing hydrangea	Foliage.
0	<i>Philadelphus coronarius</i>	Mockorange	None.
0	<i>Ribes prossularia</i>	European gooseberry	Do.
0	<i>Ribes oxycanthoides</i>	Northern gooseberry	Do.
xxx	<i>Ribes sativum</i>	Garden red currant	Foliage.
SCROPHULARIACEAE			
0	<i>Antirrhinum majus</i>	Snapdragon	None.
0	<i>Chelone glabra</i>	White turtlehead	Do.
0	<i>Digitalis purpurea</i>	Foxglove	Do.
xx	<i>Linaria vulgaris</i>	Butter-and-eggs toadflax	Foliage.
0	<i>Verbascum thapsus</i>	Mullein	None.
0	<i>Veronica officinalis</i>	Speedwell	Do.
SIMARUBACEAE			
x	<i>Ailanthus altissima</i>	Ailanthus	Foliage.

See footnote at end of table.

TABLE 5.—*Extent of feeding by Japanese beetle on various plants in United States—Continued*

Extent of feeding ¹	Family and species	Common name	Part attacked
SOLANACEAE			
0	<i>Capsicum frutescens</i>	Red pepper	None.
x	<i>Lycium halimifolium</i>	Matrimony-vine	Foliage.
0	<i>Lycopersicon esculentum</i>	Tomato	None.
0	<i>Nicotiana glauca</i>	Flowering tobacco	Do.
x	<i>Nicotiana tabacum</i>	Common tobacco	Foliage.
x	<i>Petunia hybrida</i>	Garden petunia	Do.
0	<i>Physalis alkekengi</i>	Chinese lanternplant	None.
x	<i>Solanum melongena</i>	Eggplant	Foliage.
x	<i>Solanum tuberosum</i>	Potato	Do.
STAPHYLEACEAE			
0	<i>Staphylea trifolia</i>	American bladdernut	None.
STYRACACEAE			
xxx	<i>Halesia carolina</i>	Silverbell	Foliage, fruit.
TAXACEAE			
0	<i>Taxus baccata</i>	English yew	None.
0	<i>Taxus brevifolia</i>	Western yew	Do.
0	<i>Taxus canadensis</i>	Canada yew	Do.
0	<i>Taxus cuspidata</i>	Japanese yew	Do.
TILIACEAE			
xxxx	<i>Tilia americana</i>	American linden	Foliage.
xxx	<i>Tilia cordata</i>	European linden	Do.
xxx	<i>Tilia petiolaris</i>	Silverpendent linden	Do.
xx	<i>Tilia tomentosa</i>	Silver linden	Do.
TROPAEOLACEAE			
0	<i>Tropaeolum majus</i>	Garden nasturtium	None.
TYPHACEAE			
xxx	<i>Typha latifolia</i>	Cattail	Foliage.

See footnote at end of table.

TABLE 5.—Extent of feeding by Japanese beetle on various plants in United States—Continued

Extent of feeding ¹	Family and species	Common name	Part attacked
ULMACEAE			
xxxx	<i>Ulmus americana</i>	American elm	Do.
xxxx	<i>Ulmus procera</i>	English elm	Do.
xx	<i>Ulmus rubra</i>	Slippery elm	Do.
UMBELLIFERAE			
x	<i>Apium graveolens dulce</i>	Celery	Do.
x	<i>Daucus carota</i>	Wild carrot	Do.
x	<i>Daucus carota sativa</i>	Garden carrot	Do.
x	<i>Pastinaca sativa</i>	Parsnip	Do.
0	<i>Petroselinum crispum</i>	Parsley	None.
0	<i>Pimpinella anisum</i>	Anise	Do.
VERBENACEAE			
0	<i>Callicarpa dichotoma</i>	Beautyberry	Do.
0	<i>Lantana camara</i>	Lantana	Do.
x	<i>Verbena hybrida</i>	Garden verbenae	Foliage.
VIOLACEAE			
0	<i>Viola odorata</i>	Sweet violet	None.
0	<i>Viola papilionacea</i>	Butterfly violet	Do.
0	<i>Viola tricolor</i>	Pansy	Do.
VITACEAE			
xxxx	<i>Parthenocissus quinquefolia</i>	Virginia-creeper	Foliage.
xx	<i>Parthenocissus tricuspidata</i>	Boston ivy	Do.
xxxx	<i>Vitis aestivalis</i>	Summer grape	Foliage, fruit.
xxxx	<i>Vitis labrusca</i>	Foxgrape	Do.
xxxx	<i>Vitis vinifera</i>	European wine grape	Do.

¹0=no record of beetle feeding on plant; x=occasional light feeding; xx=generally light feeding; xxx=moderate feeding; xxxx=extensive feeding.

HABITS OF GRUBS

Earthen Cell

When a grub hatches, it makes a cell in the soil slightly larger than its body. The cell is formed by the movements of the grub compressing the surrounding particles of soil. The grub lies in this cell curled in the general shape of a blunt-ended crescent. It feeds on the fine rootlets projecting into the cell. When these are consumed, the grub follows the course of a rootlet by enlarging the cell in that direction. This is accomplished by digging with its mandibles, rotating the body, and depositing the particles of soil behind it. When a rootlet has been consumed, the grub burrows horizontally through the soil in search of another rootlet. The grubs are positively thigmotactic to living roots and to stones and other objects in the soil if the roots are not available. The cell is enlarged as the grub grows to permit free movement of the body. When a grub is mature, it ceases to feed and enlarges its cell in preparation for metamorphosis. (Smith 1922)

Vertical Movement

The vertical movement of grubs is in response to changes in the moisture and temperature of the soil. Grubs are always somewhat deeper in dry than in moist soil, but the temperature is the dominant factor regulating the seasonal vertical movement. Fox (*in* Hawley 1944) determined the depth of the immature stages in permanent turf each month of the year during an 11-year period at eight sites in southern New Jersey and southeastern Pennsylvania. The depths at which 213,037 individuals were found in turf are summarized in table 6.

During the summer practically all the eggs and grubs are within the upper 4 inches of soil in turf; most of them are not more than 2 inches below the surface. As the surface layer of soil cools to about 15° C. in September, the grubs begin to move downward. The downward movement continues until the soil reaches 10°, when the grubs become inactive. Most of them hibernate 2 to 6 inches below the surface, but an occasional grub may be 8 to 10 inches deep. During the 11-year period only 0.10 percent of the grubs were as deep as 8 to 10 inches during the winter. In March when the soil goes above 10°, the grubs begin to migrate toward the surface. By May practically all of them are within the upper 2 inches of soil. During June some of the grubs go a little deeper into the soil to prepare for pupation, but they rarely go more than 4 inches.

TABLE 6.—Immature Japanese beetles found at various depths in turf in southern New Jersey and southeastern Pennsylvania during year

Month	Population at indicated depths (inches)				
	0-2	2-4	4-6	6-8	8-10
	Percent	Percent	Percent	Percent	Percent
July -----	84	16	(¹)	--	--
August -----	94	6	(¹)	--	--
September -----	93	7	(¹)	--	--
October -----	63	30	7	(¹)	(¹)
November -----	10	65	24	1	(¹)
December-February	5	62	31	2	(¹)
March -----	11	64	23	2	(¹)
April -----	63	28	9	(¹)	(¹)
May -----	95	5	(¹)	--	--
June -----	70	24	(¹)	--	--

¹ Less than 1 percent of population found at this depth.

The depths at which grubs hibernate in turf in the northern and southern ranges of the insect are not substantially different from those in southern New Jersey and southeastern Pennsylvania (Hawley 1944).

Hartzell and McKenna (1939) studied the vertical migration of grubs of mixed populations of *Popillia japonica* Newman and *Maladera castanea* (Arrow), but they did not differentiate between the species in recording the data. Grubs were found 2 to 12 inches below the surface of turf in January. Possibly most of the grubs found deeper than 6 inches were those of *Maladera*. Hallock (1932) found that this species normally hibernates 8 to 17 inches below the soil surface.

Grubs are usually somewhat deeper in cultivated soil than in turf, probably because the soil is looser and easier to dig through and the roots of plants penetrate deeper into the soil. Most of the grubs in cultivated soil hibernate within the upper 8 inches, but occasionally a grub may hibernate 10 to 12 inches below the surface. (Fleming et al. 1958)

Horizontal Movement

It was known for several years that grubs move horizontally in soil during the active feeding period, but no information was available on the distance a grub could travel. Grubs are often present in large

numbers among the roots of plants in cultivated fields and are scarce in the fallow ground between the rows of plants. When the grass in a part of a heavily infested lawn is killed by the grubs feeding on the roots, the grubs become less abundant there and increase in numbers beyond the edge of the killed-out area.

In a preliminary study of the movement of third-instar grubs through soil, grubs were introduced into fallow soil and into soil in which wheat or grass was growing in glass-sided cages, $\frac{3}{4}$ inch wide and 17 inches long, and were held in the dark at 20° C. In moving through this $\frac{3}{4}$ -inch mass of soil a grub so modified the structure of the soil that its trail was always visible. Under these conditions the grubs moved both vertically and horizontally and frequently changed their direction, particularly in the fallow soil. During a 29-day period they traveled an average distance of 195 inches in fallow soil, 109 inches in soil with growing wheat, and 30 inches in soil with growing grass. The grubs in fallow soil moved continuously in search of food, whereas those in turf often did not change their position for several days, and then they moved only a short distance.

Hawley (1935) introduced third-instar grubs in September into a circular area 3 feet in diameter in the center of turf and fallow plots, each 24 feet square, and in October, May, and June determined the distance the grubs had moved laterally beyond this area. Most of the grubs remained in the circular area. The average distance grubs were found beyond the circular area in turf was 7.2 inches by mid-October, 11.0 inches by May, and 17.4 inches by June, whereas in fallow land these distances were 12.0, 26.1, and 51.0 inches, respectively. However, each grub because of its zigzag movement actually traveled much farther through the soil.

Feeding

Grubs feed on the roots of a wide variety of garden and truck crops, ornamental plants, and grasses, but they do not thrive in plantings of red clover (*Trifolium pratense*), white clover (*T. repens*), sweetclover (*Melilotus indica*), alsike clover (*Trifolium hybridum*), soybeans (*Glycine max*), buckwheat (*Fagopyrum esculentum*), or orchardgrass (*Dactylis glomerata*). The feeding of the grubs on the underground stems and roots may not be suspected until the plants are badly damaged (Fleming 1963a). Davis (1920a) considered the grub to be of little economic importance, probably because at that time the grubs were not sufficiently numerous to seriously injure the roots of plants.

Analyses of the material eaten by the grubs showed that 67 percent of it was fresh and partially decomposed plant tissue and 33 percent soil particles. All the particles in the gut were fairly uniform in size. (Smith 1922; Smith and Hadley 1926)

Injury to well-kept turf usually is not apparent when there are less than 10 grubs per square foot. When the grubs are more numerous and the grass is retarded by low fertility or lack of adequate moisture, there may be several areas of dead grass in the sward by September or early October (fig. 11). There are many records where the aerial part of the grass was completely severed from the roots so that the turf over large areas could be rolled back with the fingers (fig. 12). (Smith and Hadley 1926; Fleming and Osburn 1932; Fleming 1936)

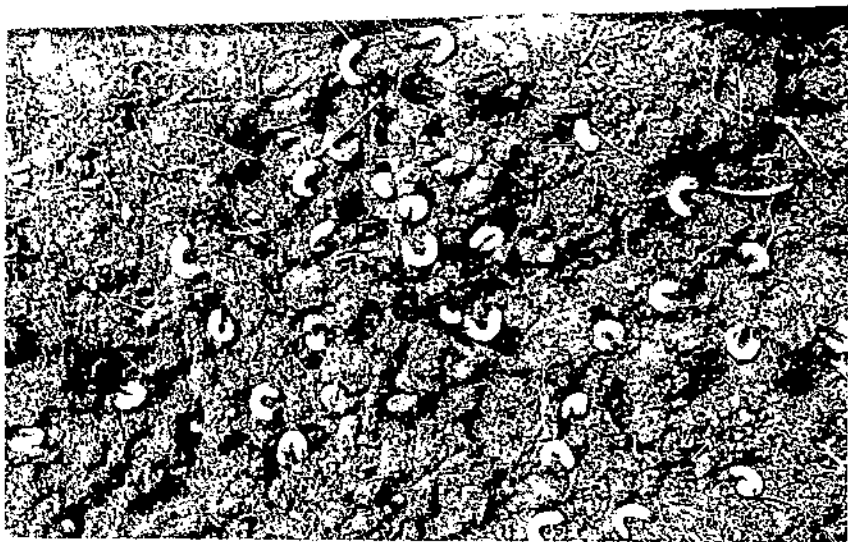
The grubs feed on the roots of garden and truck crops. Extensive feeding on the roots of corn, beans, tomatoes, and other crops reduces their vitality and sometimes kills the plants. (Smith and Hadley 1926; Fleming 1936a)

Grubs have destroyed many plants in nursery seedbeds and young plants in the field (fig. 13) and have killed 50 percent of the plants in strawberry beds. Usually the plants were killed by girdling the main roots at depths of $1\frac{1}{2}$ to $1\frac{3}{4}$ inches below the surface of the ground. (Fleming et al. 1937; Fleming 1936a)



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FIGURE 11.—Lawn damaged by feeding of Japanese beetle grubs on grass roots.



J-2010

FIGURE 12.—Japanese beetle grubs exposed when injured turf is rolled back.



J-341

FIGURE 13.—Plants killed by feeding of Japanese beetle grubs on their roots.

REARING BEETLES

Many thousand adult beetles and third-instar grubs have been collected annually in areas where abundant for laboratory experimentation. There was no problem in capturing beetles in well-aerated traps or in shaking them while inactive at dawn from heavily infested trees. However, each year it was necessary to travel farther from the laboratory to obtain an adequate supply of grubs free of infection by entomogenous pathogens until by the 1950's it was necessary to go more than 200 miles. This insect material was not entirely satisfactory because both the grubs and the adults were of unknown age and varied in their vigor and longevity.

Field Plots

Attempts were made as early as 1928 to rear the grubs in field plots. When the age of the grubs was not important, large numbers of beetles were attracted throughout the summer to the plots by chemical lures. Usually a substantial number of eggs was deposited in the soil. When grubs of known age were needed, beetles were caged over plots for a definite period and then excluded from the plots during the remainder of the summer. Caging beetles in the field was a failure because regardless of the size of the cage the beetles clung to the sides and the top trying to escape and only occasionally fed on the plants in the cage or dug into the soil to deposit eggs.

Although the summer surveys in the open field plots usually indicated a population of at least 10 to 25 eggs and young grubs per square foot, most of this population had disappeared by October, when the plots were dug to harvest the third-instar grubs. A third-instar population averaging only one or two per square foot was not economically practical to harvest. Since these plots were within the area where both *Bacillus popilliae* Dutky and *B. lentimorbus* Dutky, important pathogens of the grub, were established, the finding of infected grubs in the fall was not unexpected. No doubt these pathogens decimated the grub population. It was evident that this method of obtaining a supply of grubs could be used only in an area where the adult beetle was abundant and the pathogens had not become established. Such an area was not found within a practical distance from the laboratory.

Laboratory Rearing

A laboratory method for rearing the insect was needed so that all stages of known age and history could be available throughout the

year. Since Ludwig (1928a) reared the insect in small numbers from egg to adult in about 170 days at 25° C., there was a possibility of two overlapping generations a year in the laboratory.

The essential requirements for embryogenesis and metamorphosis are a moist soil or other suitable medium and a temperature within the range at which the insect develops normally; for the development of grubs, adequate food is also required.

Production of Eggs

Eggs were obtained at any time of the year by confining beetles in open-bottom cages over moist sterile sieved soil at between 25° and 30° C. in a lighted chamber and feeding them slices of apple or foliage of a favored plant, such as Pennsylvania smartweed (*Polygonum pennsylvanicum*) or sassafras (*Sassafras albidum*). Goonewardene and McKay (1969) developed an artificial diet for feeding adult beetles. It consisted of applesauce, alpacel, sugar sirup, wheat germ, pectin, protein, ascorbic acid and other vitamins, water, and preservatives. The eggs were harvested by passing the soil through a 12-mesh screen to remove beetles and then through a 20-mesh screen to separate the eggs from the soil. Eggs were also harvested by spreading the soil in a thin layer and picking up the eggs with a moist camel's hair brush.

Rearing Grubs

Fox and Ludwig (1937) and Ludwig and Fox (1937, 1941) used a modification of the method described by Davis (1915) for rearing Scarabaeidae. They placed each newly hatched grub in a sterile moist medium in a 1-ounce metal box and incubated it at 25° C. The development and metamorphosis of the grubs varied greatly in the different media. All the grubs in soil died before molting, showing that soil alone does not contain sufficient food for the development of the grubs. Sixty percent of the grubs pupated in a mixture of soil and *Andropogon* mold. When wheat was growing in the medium, the pupation was 42 percent in soil, 36 percent in a mixture of soil and *Andropogon* mold, and 44 percent in a mixture of soil and *Carex* mold. The *Andropogon* mold was collected beneath the tussocks of *Andropogon glomeratus* and *A. scoparius*, and the *Carex* mold beneath the tussocks of *Carex stricta*.

In tests with other substrata they found that 34 percent of the grubs pupated in *Andropogon* mold, but only 12 percent of them completed their development to the second molt in *Carex* mold before dying. All the grubs died before their first molt in peat and in sphagnum moss. When wheat was growing in the medium, 12 per-

cent of the grubs pupated in *Andropogon* mold and 8 percent in *Carex* mold.

In the propagation of the milky disease bacteria (*Bacillus popilliae* Dutky and *B. lentimorbus* Dutky), Dutky (1942) incubated inoculated third-instar grubs in cross sectional trays at 30° C. in soil containing sprouting seeds of redtop (*Agrostis alba*) and white clover (*Trifolium repens*) until macroscopic symptoms of infection developed. The incubation period was usually 10 to 12 days. Schwartz et al. (1970) using this medium to rear the beetle from egg to adult in 3-ounce cans at 27° had no emergence of adults in soil heated for 48 hours at 94° before mixing it with the seed, and only 4-percent emergence in unheated soil.

Schwartz et al. (1970) added redtop and white clover seed to dry sand, vermiculite, sphagnum peat, and Michigan peat, alone and mixed with soil, and after moistening with water determined the development of the insect from egg to adult in the substrata in 3-ounce cans at 27° C. The soil, sphagnum peat, and Michigan peat were dried for 48 hours at 94°; the sand and vermiculite were dry. No eggs hatched in sand, vermiculite, or in 2:1 mixtures of sand and soil and of vermiculite and soil. The hatch ranged from 6 to 50 percent in the other substrata. The adult emergence was 12 percent in a 2:1 mixture of sphagnum peat and soil and 2 to 6 percent in sphagnum peat, Michigan peat, a 1:1 mixture of sphagnum peat and soil, and 2:1 to 1:2 mixtures of Michigan peat and soil, but no adults emerged in the 1:1 and 1:2 mixtures of sand and soil and of vermiculite and soil or in the 1:2 mixture of sphagnum peat and soil.

The grubs seem to require some organic matter for growth. Schwartz et al. (1970) introduced third-instar grubs into sand and mixtures of sand and Michigan peat, which were seeded with redtop and white Dutch clover, and determined their survival and transformation into adults. Even though the supply of roots in the sand was ample, only 1 percent of the grubs survived in this medium for 43 days; these grubs were stiff and sluggish. Thirty-five to 49 percent of the grubs, apparently normal, survived at this time in the mixtures of sand and peat and also in peat. No adults emerged in the sand. The emergence in mixtures containing 10 percent or more of peat ranged from 10 to 25 percent. Since the emergence in sand-peat mixtures was better than in the soil-peat mixtures discussed in the previous paragraph, sand can be substituted for the soil in the mixtures and thus avoid the possibility of using soil contaminated with the milky disease bacteria, which in the laboratory can build up to high levels and decimate the grub population.

Goonewardene and Zepp (1969, 1970) improved the rearing technique by rearing the grubs at 29° C. in plastic pans containing 3 kg. of substratum. A mixture of equal parts of soil and Michigan peat, seeded with redtop (*Agrostis alba*), was used to hatch the eggs. Sixty-six to 70 percent of the eggs hatched. The first-instar grubs were transferred to a substratum composed of equal parts of soil, sand, peat, and vermiculite in which redtop was growing; 100 grubs were put in each pan. Twenty days after introducing the first-instar grubs, when 59 to 66 percent of the grubs survived, the second-instar grubs were transferred to this substratum in which redtop and ryegrass (*Lolium perenne*) were growing; 50 grubs were placed in each pan. After another 20 days, when the survival was 32 to 60 percent, the third-instar grubs were transferred to a fresh batch of the medium used for the second instars; 30 grubs were put in each pan. The transfer of third-instar grubs at 20-day intervals was repeated until pupation. The transfer of grubs to fresh medium was facilitated by growing the grass in the medium on a plastic screen to form a food pad, and after the grubs had been transferred, the food pan was placed over the medium. The roots soon penetrated through the screen into the medium containing the grubs.

In small-scale tests including a few hundred newly hatched grubs, about 22 percent of them completed their development and emerged as adults, but in large-scale tests including 1,000 or more newly hatched grubs, the emergence was only 6 to 8 percent.

Schwartz and Jurimas (1970) determined the effect of adding various foods to a 2:1 mixture of soil and Michigan peat on the development of third-instar grubs at 30° C. No adults emerged in the substratum to which no food was added. The emergence was 15 percent in the substratum containing sprouts of redtop and white clover, 12 percent by adding 1 gram of chopped raw carrots to 100 grams of substratum, and 3 percent by adding 1 gram of wheat germ. No adults emerged in the substratum containing 1 gram of skim milk, soybean protein, or brewer's yeast, or 0.1 gram of wheat germ.

Goonewardene et al. (unpublished) investigated the possibility of rearing the grubs on an artificial diet. A grass-clover powder was prepared by macerating seedlings of ryegrass (*Lolium perenne*), redtop (*Agrostis alba*), and white clover (*Trifolium repens*), extracting with acetone, drying, and pulverizing. The powder was spread evenly over moist filter paper, which was inverted and placed on the surface of a 1:1 mixture of sphagnum peat and soil containing third-instar grubs, and then the filter paper was covered with the sphagnum peat-soil mixture. The filter paper and the peat-soil mixture were replaced at 7-day intervals. At 25° C. no grubs fed the

grass-clover powder emerged as adults, but when linoleic acid, linolenic acid, and choline chloride were added to the grass-clover powder, the emergence ranged from 33 to 45 percent. Adding vitamins and Wesson's salts to the fortified powder did not increase the emergence.

ABUNDANCE OF BEETLES

Methods of Estimating Populations

Extent of Feeding

For many years the density of beetle populations over large areas was estimated empirically by determining the extent of feeding on the most favored food plants in midsummer, when the beetles are the most numerous and the injury to foliage the most conspicuous. The boundary of densely populated areas and the spread of the beetle were determined by this method each year until 1952. The six categories used in this evaluation are as follows:

<i>Estimate of population density</i>	<i>Extent of feeding</i>
Very dense -----	Over 50 percent of favored trees with brown or no foliage and all low-growing plants and vines defoliated.
Dense -----	25 to 50 percent of favored trees with brown or no foliage and nearly all low-growing plants and vines defoliated.
Moderate -----	10 to 25 percent of favored trees with brown foliage and extensive feeding on low-growing plants and vines.
Light -----	Less than 10 percent of favored trees with brown foliage and moderate feeding on low-growing plants and vines.
Very light -----	Favored trees not brown, although there may be some light feeding, and light feeding on low-growing plants and vines.
Trace -----	No feeding on favored trees and only occasional feeding on low-growing plants and vines.

Soil Survey

A more accurate estimate of the abundance of the beetle is obtained by determining the density of the soil population before the emer-

gence of the insect. Since the density of the soil population varies with the nature of the cover crop, it is necessary to determine the population in turf, uncultivated fields, fields with various crops, orchards, and so forth, to estimate the beetle population on a farm or in a township or county. Usually the average density of the soil population was determined for each type of ground cover by surveying a representative section of each one. With information on the average soil population and the acreage of each type of ground cover, an estimate is made of the beetle population expected in the summer in the area being surveyed.

Fleming and Baker (1936) developed a survey method by determining the natural grub population in each square foot of four 2,500-square foot plots, two of which were in pastures and the other two in cornfields, and then calculating the size and number of samples needed to adequately estimate the mean density of the heterogeneous populations. It was concluded that 1 square foot was the most satisfactory sampling unit. When 10 1-square foot samples were taken at random over a 1,000-square foot area selected for survey, the standard error of the mean population density was estimated at 8 percent with an average population of 19 per square foot, 15 percent with average populations of five or nine per square foot, and 18 percent with an average population of three per square foot. When the number of samples was increased to 20, the standard errors were 6, 11, 11, and 13 percent, respectively.

Polivka (1959) used a sampler cutting a $\frac{1}{2}$ -square foot plug in the random sampling of soil.

The timing of a survey is important because of the natural decimation of the soil population. Fox (1937) determined the abundance of the soil population throughout the year in surveys made during a 7-year period in southern New Jersey and southeastern Pennsylvania. The peak of the grub population occurred during the first half of September. When the grubs began hibernation in November, the population had decreased 21 percent. An additional 3 percent was lost during hibernation in the winter. When metamorphosis began late in May, the population had decreased 32 percent. By mid-June, when 63 percent of the grubs had transformed to prepupae and pupae, the population had decreased 43 percent. It was estimated that for each 1,000 grubs that completed their development to adult beetles, a survey during the first half of June would indicate the emergence of about 1,000 beetles, whereas the expected emergence would be about 1,200 beetles with a survey in the last half of May, and about 1,300 with a survey in March, April, or the first half of May. The survey should not be made in the fall because one in

September would indicate the emergence of about 1,700 beetles and in October about 1,500 beetles. The most accurate estimate of the emerging beetle population is by a soil survey just before the pupae begin to transform to adults.

This method of estimating the beetle population was used by Langford et al. (1940, 1941) and the Japanese Beetle Laboratory.

Traps

Fleming et al. (1940) estimated that a properly constructed trap with a good lure caught about 75 percent of the beetles attracted to it. The zone of attraction by a trap varies with the environment. It may be small in suburban areas where trees, houses, and other structures deflect and impede air movement. In rural areas with open fields the limit of the zone of attraction may be 1,320 feet (Mehrhof and Van Leeuwen 1930) or 900 to 1,500 feet (Metzger 1934, 1936), but most of the beetles are attracted from the general vicinity of a trap. Polivka (1949) caught 58 percent of the marked beetles in traps within 200 feet of the liberation point, 28 percent in traps from 200 to 300 feet away, 13 percent in traps from 300 to 400 feet away, and 1 percent in traps 400 feet away.

Traps were used for many years to determine the relative abundance of the beetle throughout the summer and from summer to summer. The same type of trap with the same lure was placed at the same sites each year to avoid variations in the capture introduced by these factors. Only the relative abundance of the insect was determined because the relationship between the number of beetles captured and the population in an area had not been established.

Langford et al. (1940) determined the relationship between the number of beetles captured by traps and the population in an area by making a soil survey before the emergence of the beetle to estimate the density of the beetle population. The 5,338 traps on 6,750 acres of farmland in Cecil County, Md., caught 30 percent of the estimated population, but on individual farms the capture ranged from 24 to over 100 percent. The high captures on certain farms were attributed to the migration of beetles to these farms from adjacent untrapped areas.

Langford et al. (1941) continued the study, using 1,941 traps on 3,231 acres of farmland. The captures were high on 261 acres where migration of beetles occurred and usually low on 1,679 acres where less than one trap was used per acre. On the 1,291 acres where traps were placed at approximately one per acre, the traps caught 32 percent of the estimated population, but on the individual farms the capture ranged from 8 to 97 percent.

Ladd (unpublished) released marked beetles in open rural country in eastern Tennessee. Two thousand traps on 188 acres caught 30 percent of the marked beetles in 1969 and 740 traps on 55 acres caught 30 percent of them in 1970. Whether the population was estimated by soil survey or a population of marked beetles was used, traps over a large area caught approximately one-third of the population. The marked beetle method is the more practical for establishing the relationship between the number of beetles captured by traps and the total population. Further tests with marked beetles are needed to determine this relationship in other rural areas with different flora and in suburban areas.

Pattern of Distribution

During 1920-29 the area occupied by the beetle was almost spherical in shape with a very densely populated core surrounded by a zone where the population decreased progressively until it was very light at the periphery. The size of the infested area increased each year. Beginning in 1930 the population in the central core began to decrease and by 1931 the very dense population occurred in a slightly broken band surrounding the core. As the beetle continued to move outward, this band disappeared and dense populations developed at the most favorable sites. The outline of the area occupied by the beetle became slightly arcuate in 1935, and by 1941 it was very irregular with prominent arms extending up the river valleys. (Fox 1927, 1932, 1934; Hadley 1932; Hawley and Dobbins 1945)

A study was made of the rise and the decline of the beetle population within a radius of 5 miles of the site in New Jersey where the insect was discovered in 1916. Based on the soil surveys of Davis (1920b), Smith (1925, 1928), Smith and Hadley (1926), and Hawley (1944, 1949), the average density of the beetle population in this area from 1920 through 1945 was estimated as follows:

<i>Year</i>	<i>Population per acre</i>	<i>Year</i>	<i>Population per acre</i>
1920.....	90,500	1931.....	300,600
1921.....	186,800	1933.....	339,900
1922.....	302,000	1934.....	257,000
1924.....	747,000	1935.....	383,000
1927.....	622,900	1936.....	122,000
1928.....	405,100	1937.....	74,000
1929.....	744,900	1945.....	43,000
1930.....	87,120		

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UPDATA
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The rise and decline of the beetle population in this area have been repeated with modifications as the beetle invaded new areas and became well established at favorable sites.

Only about a dozen beetles were found in this area in the summer of 1916 (Dickerson and Weiss 1918; Smith and Hadley 1926). From a few beetles the population increased rapidly, reaching 90,500 per acre in 1920 and 747,000 per acre in 1924. Smith (1925) reported that in 1924 populations up to 3,470,000 per acre occurred in pastures and up to 7,410,000 per acre in the turf on golf courses. Hawley (1949) suggested that the population might have increased more rapidly if the rainfall during the summers of 1916 and 1918 had not been somewhat deficient. The population remained high through the summer of 1929. The marked decline in the summer of 1930 was attributed to the drought during the previous summer (Fox 1939; Hawley 1949). With adequate rainfall during the summer of 1930 the beetle partially overcame this setback and reached about one-half of its peak density in 1931. It remained at approximately this level of density until 1936, when there was another abrupt drop in population. This decline was attributed to the unusually high mortality of the hibernating grubs during the winter of 1935-36 (Hawley and Dobbins 1941). Since 1937 the population has remained at a relatively low level, with some increase and decrease following summers of adequate and inadequate rainfall, respectively.

During the 1920's and early 1930's the summer rainfall was the most important factor modifying the density of the beetle population. The insect-feeding birds, small terrestrial mammals, and the few predaceous and parasitic insects indigenous to the area were unable to cope with the reproductive potential of the beetle. Diseased grubs were found only occasionally in the field. In the 1930's the imported insect parasites, particularly *Tiphia vernalis* Rohwer, were becoming established in the area and the incidence of disease among the grubs greatly increased, caused mostly by the milky disease bacteria *Bacillus popilliae* Dutky and *B. lentimorbus* Dutky. The establishment and buildup of the imported insect parasites and the entomogenous diseases were facilitated by the dense beetle populations. These biotic factors are principally responsible for keeping the beetle population at a relatively low level.

NATURAL SPREAD

Factors Affecting Spread

When favored food plants and suitable sites for oviposition are available, the natural spread of the beetle is affected largely by the

topography of the land, the direction of the wind, and the temperature and rainfall.

Topography

The effect of topography on the spread of the beetle is discussed by Fox (1927, 1932, 1934) and Hawley and Dobbins (1945). The spread of the beetle is facilitated in a farming area where there are extensive tracts of nearly level or gently rolling country. These features are found in the coastal plain section of the lower Delaware River Valley and other parts of southern New Jersey.

There was no physiographic feature to impede the southern movement of the beetle on the coastal plain until it reached Delaware Bay. When the population became very dense on the New Jersey side of the bay, the beetles flew across the bay into Delaware.

The heavily wooded area east of the Delaware River Valley, known as the New Jersey Pine Barrens, had little food and few favorable oviposition sites, factors that tended to retard the eastward movement, but it was not a formidable barrier. The easterly movement of the beetle was stopped by the Atlantic Ocean.

The Delaware River was not a barrier in the westerly movement of the beetle from New Jersey into Pennsylvania. Westward in Pennsylvania and northward in New Jersey the beetle had only a few miles to travel to reach the fall line, marking the boundary between the coastal plain and the Piedmont plateau, where the topography is more rugged. The eastern foothills of the Appalachian Mountains extend in a northeasterly-southwesterly direction across Pennsylvania, northwestern New Jersey, and southeastern New York. The mountains impeded the westerly movement of the beetle, but by 1943 the advance guard of the beetle had begun to penetrate into the mountains in all three States.

The spread of the beetle was facilitated by the river valleys. The movement into the mountains was largely in the valleys of the Potomac, Susquehanna, Delaware, and Hudson Rivers. Its spread northward in Connecticut and Massachusetts was in the Connecticut River Valley and along the coast. Its westward spread in New York was in the Mohawk River Valley.

Soils

There was little difference in the density of grub populations developing in the sands, sandy loams, and loams. In field surveys Smith and Hadley (1926) found 30 percent of the grubs in sands, 35 percent in sandy loams, and 35 percent in loams. The pupation

and the emergence of the adults, however, were 10 to 14 days later in the sands than in the sandy loams and loams.

The density of the grub population decreased progressively with the increment in the pH of the soil. The number of eggs deposited and the number of grubs developing in soils with a pH about 4.0 were two to 10 times greater than in soils with a pH about 7.0. The range in the pH tolerated by the grubs was not established. The populations built up faster and dense populations persisted longer in soils with a low pH than in the other soils. (Wessel and Polivka 1952; Polivka 1960a, 1960b)

Wind

The direction of the wind during the summer affects the spread of the beetle. The flight of the beetle is essentially aimless and usually of short duration. In the absence of chemotropic stimulus, the beetles tend to drift with the wind. The prevailing winds are westerly during the summer in southern New Jersey. Fox (1927) found that in the 10 years following the discovery of the beetle, it had spread eastward about 42 miles through the New Jersey Pine Barrens, even though this area was not favorable for it, but it had spread only 28 miles westward in more favorable country. The massive flights of the beetle over the Atlantic Ocean occurred with westerly winds, whereas the massive flights westward across the Delaware River and Delaware Bay usually coincided with the periods the wind had shifted to the east.

Temperature and Rainfall

Although the temperature and moisture of the soil do not affect the flight of the beetle, these factors are important in the survival of the insect. The beetle is adapted to a country where (1) the mean soil temperature during the summer is between 17.5° and 27.5° C., (2) the soil temperature during the winter is above -9.4°, and (3) the precipitation is adequate and rather uniformly distributed throughout the year, averaging not less than 250 mm. (10 inches) during the summer.

Soil temperatures in the summer favorable for the hatching of the eggs and the development of the newly hatched grubs occur over much of the eastern part of the United States.

There is usually an insignificant mortality of the hibernating grubs during the winter in southern New Jersey and southeastern Pennsylvania. The average winter mortality during 1927-34 was only 3 percent (Fox 1937). The soil temperature at a depth of 7.5 mm. (3 inches) during 1925-38 did not fall below 0° C., except dur-

ing the winters of 1926, 1927, 1934, and 1936. With a snow cover during the winters of 1926, 1927, and 1934, the soil temperature did not go much below 0°, even when the air temperature was far below freezing, and the winter mortality these years was about the same as during milder winters (Fox 1935; Hawley and Dobbins 1941). In 1934 a mortality of 33 to 100 percent occurred in those areas where there was a freezing rain instead of snow even though the soil temperature did not fall below -3.1°. (Hawley and Dobbins 1941)

The winter mortality in Connecticut ranged from 17 to 42 percent in the absence of a snow cover, but it was only about 1 percent when snow was on the ground (Schread 1944, 1945). The winter mortality was high during some years in Indiana (Gould 1963).

The normal summer rainfall is about 300 mm. in southern New England, southeastern New York, the eastern half of Pennsylvania, New Jersey, Delaware, and Maryland and about 250 mm. in the Central States (Hawley 1949). Summer droughts at irregular though rather frequent intervals are characteristic of these areas. In southern New Jersey there were 11 years during 1916-46 when the summer rainfall was less than 250 mm. Years with less than 250 mm. of summer rainfall occur more frequently in the Central States. As noted previously, a marked deficiency of rainfall during the summer reduced the beetle population the following summer.

Progressive Spread in Square Miles

Almost each year during the period 1916-52 the limits of the natural spread of the beetle was determined, maps were prepared, and the square miles occupied by the beetle were estimated. While the insect was spreading naturally, it was also becoming established at points beyond the periphery of the generally infested area where it had been carried inadvertently by man. In determining the area over which the beetle had spread, the colonies beyond the periphery were not included until the vanguard of beetles advancing from the generally infested area met and merged with them. The absorption of these colonies sometimes resulted in a large increase in the generally infested area, such as the addition in 1952 of 2,562 square miles in North Carolina and 1,170 square miles in Ohio.

The progressive increase in the generally infested area during this period is summarized in table 7. The data are based on the published reports of Hadley (1922, 1923, 1924), Smith (1924, 1925), Smith and Hadley (1926), Fox (1927, 1932, 1934), Hawley and Dobbins (1945), and Hawley (1950) and the unpublished reports of T. N. Dobbins, H. Fox, I. M. Hawley, R. T. White, and H. J. Willard.

The area occupied by the beetle increased from not more than 0.5 square mile in 1916 to 76,504 square miles in 1952, when the beetle had spread over all or parts of 14 States and the District of Columbia. The beetle had spread over all of New Jersey by 1943, all of Delaware by 1942, all of the District of Columbia by 1941, and all of Rhode Island by 1931. Fleming (1963a) estimated that by 1962 the beetle had spread over 100,000 square miles in the eastern part of the United States. It probably occupied 150,000 square miles in 1970, when it had invaded all or parts of 19 States and the District of Columbia and part of one Province in Canada.

Progressive Invasion of States

New Jersey

The beetle extended its range eastward in New Jersey to the Atlantic Ocean in 1926. It reached Delaware Bay to the south in 1930 and except for Cape May County, where the heavily forested country impeded its progress, all of the State south of latitude $40^{\circ}30' N.$ was occupied by the beetle. All of Cape May County was infested in 1932. By 1935 all of New Jersey except the mountainous northwest part was occupied by the beetle. This part of the State was infested in 1943. (Fox 1927, 1932, 1934; Hawley and Dobbins 1945)

Pennsylvania

The beetle flew across the Delaware River from New Jersey and established itself in Pennsylvania during the summer of 1920. The main lines of advance westward were in the Schuylkill River Valley and through the troughlike Chester Valley, which extends diagonally across Chester County into Lancaster County. By 1932 the beetle had spread over all of Bucks, Montgomery, Philadelphia, and Delaware Counties and had penetrated into Chester, Northampton, Lehigh, and Berks Counties. In 1935 its range included most of the open rolling farming country lying east of the lower reaches of the Susquehanna River and southeast of the Appalachian Mountains.

The beetle moved up the Susquehanna River Valley and reached Harrisburg in 1937, where it joined the isolated colony in this area. By 1941 there had been considerable dispersion through the open country west of the Susquehanna River and a slight movement westward in most of the Appalachian Mountain region. In 1943 the beetle continued moving westward in the open farming country of southern Pennsylvania and began to penetrate into the mountains. Its movement up the Susquehanna River reached Sunbury. By 1946

1941-----	7,431	6,114	1,550	1,733	3,016	620	62	85	--	--	--	--	--	--	--	20,611
1942-----	7,767	6,529	1,965	2,056	5,114	1,720	62	895	152	--	--	--	--	--	--	26,200
1943-----	8,224	7,169	1,965	2,418	5,887	2,200	62	1,085	190	--	--	--	--	--	--	29,200
1944-----	8,224	8,327	1,965	3,352	6,762	2,401	62	1,432	210	165	--	--	--	--	--	32,900
1945-----	8,224	8,327	1,965	3,652	6,762	2,401	62	1,432	210	165	--	--	--	--	--	33,200
1946-----	8,224	9,097	1,965	4,458	7,557	3,025	62	2,092	400	365	255	--	--	--	--	37,500
1947-----	8,224	9,467	1,965	5,038	7,857	3,795	62	2,292	955	515	580	--	--	--	--	40,750
1948-----	8,224	10,597	1,965	5,163	8,027	3,970	62	3,217	1,485	530	710	--	--	--	--	43,950
1949-----	8,224	12,902	1,965	5,313	8,402	4,390	62	3,757	1,575	550	770	--	--	--	--	47,910
1950-----	8,224	13,827	1,965	5,403	9,842	4,515	62	5,202	2,225	595	1,190	--	--	--	--	53,050
1951-----	8,224	17,361	1,965	5,628	10,142	4,755	62	6,652	3,465	935	1,248	129	55	--	--	60,612
1952-----	8,224	20,616	1,965	5,703	10,142	4,790	62	11,652	3,850	4,085	1,248	250	185	2,562	1,170	76,504

it had moved through several gaps in the Appalachian Mountains and was established to the west of the mountains.

By 1952 the isolated colonies in Washington, Beaver, Lawrence, Mercer, Butler, Allegheny, Westmoreland, Armstrong, Indiana, Cambria, and Somerset Counties in western Pennsylvania had consolidated and had united with the vanguard of beetles moving up the Ohio River Valley from West Virginia. The movement westward along the Pennsylvania-Maryland border had almost reached Somerset County. In the northern part of the State the movement up the north branch of the Susquehanna River had passed the Pennsylvania-New York border, and the movement along the west branch of the river had penetrated into Clinton County. The beetle had not reached the northern tier of counties west of Bradford County or the central and the extreme southwestern parts of the State. (Hadley 1922, 1924; Fox 1934; Hawley and Dobbins 1945; Hawley 1950; White and Willard unpublished)

Delaware

The beetle moved southward from Delaware County, Pa., in 1926 and occupied a small part of New Castle County north of Wilmington. By 1931 it had reached the western suburbs of Wilmington and had penetrated along the Delaware River to below New Castle. During 1933 large swarms of beetles flew from the densely populated area in New Jersey across the Delaware River and upper Delaware Bay into Delaware, increasing the population already in New Castle County and extending their range southward to Dover in Kent County. By 1937 the beetle had spread over much of the northern two-thirds of the State. The entire State except the extreme southern part of Sussex County was infested in 1941. The invasion of Delaware was completed in 1942. (Fox 1927, 1932, 1934; Hawley and Dobbins 1945)

New York

The beetle had no difficulty in flying across the narrow Arthur Kill, separating Staten Island, N.Y., from New Jersey, and establishing itself in the southwestern part of the island in 1932. It spread over all the island in 1933.

In 1933 large swarms of beetles flew over the Atlantic Ocean from Monmouth County, N.J., and were washed up dead and alive on the southern shore of Long Island and on the beaches of New Jersey. By 1935 the beetle had established itself in the western one-fourth of Long Island and in the metropolitan area of New York City and had

penetrated up the Hudson River Valley into Westchester County. It infested the western half of Long Island in 1941 and the entire island except the north-central part in 1944.

By 1941 the beetle occupied all of Westchester, Rockland, and Putnam Counties and the eastern part of Orange County in the Hudson River Valley. During the next 3 years it extended its range westward in Orange County and along both sides of the Hudson River into Ulster and Dutchess Counties. By 1949 it had moved westward from Orange County into Sullivan County and northward in the Hudson River Valley into Greene, Columbia, Albany, and Rensselaer Counties. It had also moved westward in the Mohawk River Valley from Albany County into Schenectady County. By 1952 the beetle had gone farther north in the Hudson River Valley into Saratoga and Washington Counties and farther west in the Mohawk River Valley into Montgomery County.

The beetles moving up the north branch of the Susquehanna River had passed the Pennsylvania-New York border by 1952 and had become established in Chemung and Tioga Counties in south-central New York. (Fox 1934; Hawley and Dobbins 1945; Hawley 1950; White and Willard unpublished)

Maryland

Isolated colonies of beetles had been found in Maryland as early as 1926, but most of them had been eliminated or retarded in development by the use of traps and insecticides (Cory and Langford 1944, 1955).

The beetle invaded Maryland from Chester County, Pa., and New Castle County, Del., in 1933 and established itself in the northeastern part of Cecil County at the head of Chesapeake Bay. By 1935 it had occupied practically all of Cecil County and had moved westward into Harford County on the Maryland-Pennsylvania border and southward into Kent County on the eastern side of the bay. During the next 4 years it occupied all of Cecil and Harford Counties. It moved from Harford County through the southern part of Baltimore County into the northern part of Anne Arundel County, and it extended its range southward through Kent County into Queen Annes and Caroline Counties. By 1943 the beetle occupied all of Queen Annes, Caroline, Talbot, Worcester, and Somerset Counties and all but a small part of Dorchester and Wicomico Counties on the east side of Chesapeake Bay, and on the west side of the bay it occupied all of Baltimore, Howard, Anne Arundel, and Prince Georges Counties and most of Montgomery County and had penetrated into Charles County. It had moved westward from Baltimore County

and occupied all of Carroll County. It had also moved from Montgomery County up the Potomac River Valley into Frederick and Washington Counties in the Blue Ridge Mountains.

By 1949 the beetle had spread over all of Maryland, except Garrett and Allegany Counties in the extreme northwest and the southern part of St. Marys County on Chesapeake Bay. Three years later only Garrett County had not been invaded by the beetle. (Hawley and Dobbins 1945; Hawley 1950; White and Willard unpublished)

Connecticut

Several isolated colonies were found in Connecticut as early as 1926. In 1937 the beetle moved eastward from Westchester County, N.Y., into the southwestern part of Fairfield County. By 1941 the beetle occupied the western half of Fairfield County and had spread along the coast into New Haven County. Two years later the beetle occupied all of Fairfield and New Haven Counties. It had moved northward from Fairfield and New Haven Counties into Litchfield County, eastward from New Haven County into Middlesex County, and eastward from Hartford County into Tolland County. It occupied all of the Connecticut River Valley from the coast to the Connecticut-Massachusetts border.

By 1949 the beetle had spread over all of Connecticut except parts of Litchfield, Windham, and New London Counties. In 1952 only a small part of Litchfield County in northwestern Connecticut had not been invaded. (Britton and Johnson 1928; Hawley and Dobbins 1945; Hawley 1950; White and Willard unpublished)

District of Columbia

There was a vigorous isolated colony of beetles in Washington, D.C., in 1927. The advance guard of beetles moving through Prince Georges County, Md., merged with this colony in 1941. (Hawley and Dobbins 1945)

Virginia

The beetle was first found in Virginia in 1928 in the Potomac Railroad yards south of Washington, D.C. Several important isolated colonies developed in Virginia during the next few years. In 1939 the beetle began to move from the District of Columbia into Fairfax County.

During the next 3 years the beetle spread over all of Fairfax and Loudoun Counties and most of the adjacent Prince William

County. By 1949 it occupied all of Prince William County and had spread southward and occupied all of Stafford and King George County and parts of Spotsylvania, Caroline, and Westmoreland Counties. It had spread westward from Prince William County through a part of Fauquier County into Culpeper and Rappahannock Counties and from Loudoun County through Clarke County into Frederick County. By 1952 the beetle occupied most of the counties in eastern Virginia, and it had moved southwesterly from Culpeper County through Orange and Albemarle Counties into Nelson County. (Hawley and Dobbins 1945; French et al. 1949; Hawley 1950; White and Willard unpublished)

Massachusetts

The vanguard of beetles moving up the Connecticut River Valley crossed the Connecticut-Massachusetts border and merged with the colony in Hampden County in 1942. The beetle continued to move northward in the valley, passing through Hampshire County into Franklin County in 1946 and reaching the border between Massachusetts and New Hampshire and Vermont in 1949.

In eastern Massachusetts the beetle moved from Rhode Island into the northwestern part of Bristol County in 1946. During the next 3 years it occupied all of Bristol County and penetrated into Norfolk County to the north and Plymouth County to the east. By 1951 it occupied about one-half of Norfolk and Plymouth Counties and it had spread from Norfolk County into the southeastern part of Worcester County and the southern part of Suffolk County. In 1952 it occupied all of Suffolk County and spread northward into Middlesex and Essex Counties. (Hawley 1950; White and Willard unpublished)

West Virginia

Some isolated colonies had been in West Virginia since 1932. In 1944 the beetle moved from Clarke and Loudoun Counties in Virginia into Jefferson County. During the next 3 years it occupied all of Jefferson and Berkeley Counties and penetrated into Morgan County. By 1951 it had moved westward in the valley of the north branch of the Potomac River into Hampshire, Mineral, and Grant Counties. Isolated colonies had been in northern West Virginia for many years. In 1952 the vanguard of beetles moving westward from Grant County met and merged with these colonies and thus extended the natural distribution of the beetle to and up the Ohio River Valley. (Craig 1945; Hawley 1950; White and Willard unpublished)

Rhode Island

In 1946 the beetle moved from New London County, Conn., through Washington County and merged with the colony in Newport County. By 1950 all the State was occupied by the beetle except a few areas on the Rhode Island-Connecticut border. The entire State was occupied by the beetle in 1951. (Hawley 1950; White and Willard unpublished)

New Hampshire and Vermont

The beetle moving up the Connecticut River Valley reached the border between Massachusetts and New Hampshire and Vermont in 1949 and by 1951 had met and merged with the colonies in Cheshire County, N.H., and in Windham County, Vt. It extended its range in 1952 through Cheshire and Sullivan Counties into Grafton County in New Hampshire and through Windham County into Windsor County in Vermont. (White and Willard unpublished)

North Carolina

The vanguard of beetles moving southward from Norfolk County in Virginia in 1952 met and merged with the colonies in northeastern North Carolina. By the end of the summer it occupied much of Currituck, Camden, Pasquotank, Gates, Perquimans, Chowan, Bertie, Martin, Washington, Tyrrell, Beaufort, and Hyde Counties. (White and Willard unpublished)

Ohio

By the end of the summer of 1949 one or more isolated colonies of beetles had been found in 47 of the 88 counties in Ohio (Polivka 1950). In 1952 the vanguard of beetles moving up the Ohio River Valley from West Virginia met and merged with the colonies in eastern Ohio. It also spread across the valley from Pennsylvania and merged with the colonies in Trumbull and Mahoning Counties. (White and Willard unpublished)

ARTIFICIAL SPREAD

United States

The adult beetle is more likely to be carried from the infested area by fruit and vegetables and the immature stages in soil about the roots of plants than by any other commodity. Federal Quarantine 48 was promulgated in 1920 to regulate the interstate movement of

all agricultural products. The States occupied by the beetle established quarantines to supplement the Federal quarantine and regulate the intrastate movement of these products. The quarantines were very effective in preventing the artificial spread of the beetle by agricultural products, but they did not regulate the movement of other articles of commerce.

There was always the hazard of beetles hitchhiking in private cars, trucks, railroad cars, ships, and airplanes and escaping when their conveyance reached its destination. Trucks and railroad cars carrying agricultural products were fumigated or treated with an insecticide dust during the flight of the adult beetle, but treatment was not used in trucks and railroad cars carrying other products. Insecticides were applied to airplanes leaving infested airports when adult beetles were present. Although the opportunity for the artificial spread of the beetle in this manner at times seemed to be great, the establishment of isolated colonies at remote places did not seem to be in proportion to this hazard.

The U.S. Department of Agriculture in cooperation with State agencies has operated traps for many years in the vicinity of freight yards, truck depots, airfields, and other places throughout the country where beetles might be carried accidentally.

In 1930 when the beetle had spread naturally over 5,700 square miles in New Jersey, Pennsylvania, and Delaware, it was found at 61 localities beyond this area—nine in Connecticut, five in Massachusetts, three in Rhode Island, four in New York, 15 in Pennsylvania, two in Delaware, 10 in Maryland, 12 in Virginia, and one in the District of Columbia. The most remote of these discoveries was at New Castle, Pa., an airline distance of approximately 285 miles. (Hadley and Stockwell 1931)

The more remote points at which the beetle was discovered in 1931 included Boston, Mass. (270 miles), Buffalo, N.Y. (290 miles), Columbus, Ohio (430 miles), Richmond, Va. (250 miles), and Charleston, S.C. (575 miles) (Fox 1932).

In 1933 when the beetle had spread naturally over 8,800 square miles in New Jersey, Pennsylvania, Delaware, New York, and Maryland, there were 330 localities beyond this area where beetles had been discovered prior to and during that summer, including two localities in Maine, four in New Hampshire, five in Vermont, 30 in Massachusetts, four in Rhode Island, 23 in Connecticut, 56 in New York, 17 in New Jersey, 78 in Pennsylvania, six in Ohio, one in Michigan, six in West Virginia, 57 in Maryland, seven in Delaware, 16 in Virginia, 14 in North Carolina, and two in South Carolina. (Fox 1934)

In 1943 when the beetle had spread naturally over 29,200 square miles in New Jersey, Pennsylvania, Delaware, New York, Maryland, Connecticut, the District of Columbia, Virginia, and Massachusetts, there were 581 localities beyond this area where beetles had been discovered prior to and during that summer, including 17 localities in Maine, seven in New Hampshire, 10 in Vermont, 45 in Massachusetts, 19 in Connecticut, nine in Rhode Island, 72 in New York, 85 in Pennsylvania, 76 in Ohio, 10 in Michigan, 17 in Indiana, nine in Illinois, one in Iowa, one in Missouri, two in Kentucky, three in Tennessee, 28 in Maryland, 73 in Virginia, 40 in West Virginia, 36 in North Carolina, eight in South Carolina, nine in Georgia, three in Florida, and one in Louisiana. (Hawley and Dobbins 1945)

In 1949 when the beetle had spread naturally over 47,910 square miles in New Jersey, Pennsylvania, Delaware, New York, Maryland, Connecticut, District of Columbia, Virginia, Massachusetts, West Virginia, and Rhode Island, there were 570 localities beyond this area where beetles had been discovered prior to and during that summer, including 17 in Maine, seven in New Hampshire, 11 in Vermont, 29 in Massachusetts, seven in Connecticut, 73 in New York, 74 in Pennsylvania, 76 in Ohio, 15 in Michigan, 17 in Indiana, 10 in Illinois, one in Iowa, one in Kansas, one in Missouri, three in Kentucky, five in Tennessee, nine in Maryland, 85 in Virginia, 45 in West Virginia, 58 in North Carolina, eight in South Carolina, 12 in Georgia, five in Florida, and one in Louisiana. (Hawley 1950)

The beetle was found at one locality in California in 1961 (Gammmon 1961).

Even with the quarantine restrictions it was not possible to prevent all the artificial dispersion of the beetle. At many isolated localities where one or a few beetles were discovered, no beetles were found in subsequent years or the increase in the population was so slow that the insect was of little economic importance. The application of insecticides to the soil and to foliage eliminated many newly established colonies or greatly retarded the normal increase in the population. At other isolated localities vigorous colonies developed. Some of these colonies spread over large areas and beetles became numerous enough to seriously damage foliage by their feeding. (Hawley 1950)

In 1958 a survey south and west of the area then regulated by Federal and State quarantines showed that isolated colonies of beetles occurred in 13 States—Georgia, Illinois, Indiana, Iowa, Kentucky, Michigan, Missouri, North Carolina, Ohio, South Carolina, Tennessee, Virginia, and West Virginia; no beetles were found this year

in Wisconsin. The colonies in North Carolina, Virginia, and West Virginia were too extensive and complex to determine their boundaries. It was estimated that colonies of beetles occupied 1,338,000 acres in South Carolina, Georgia, Kentucky, Ohio, Illinois, and Indiana. A relatively small infested acreage was found in Iowa, Michigan, Missouri, and Tennessee. (Gentry 1959)

Canada

Beetles were found in large numbers in 1944 in a rose garden in Halifax, Nova Scotia, adjacent to the ship terminal. The colony was apparently started by beetles hitchhiking on ships from the United States. Although not reported previously, the beetles apparently had been there for several years. The application of insecticides to turf and the use of foliar sprays were effective in eliminating them. No beetles have been found since 1953.

Bermuda

In July and August 1938 many beetles invaded ships plying between New York City and Bermuda, while the ships were in dock at New York, and when they proceeded down the New Jersey coast. Many dead but no living beetles were found on the ships on arrival at Bermuda after a voyage of 2 days. (Waterston 1938) During the summer of 1939 two living beetles were found in aircraft and six near the docks; one dead beetle was found in a trap (Waterston 1940). In 1940 one beetle was caught in a garden near the docks and two living beetles were found on a ship from New York City (Waterston 1941). In 1941 two living beetles were found on a ship from New York City and another on a ship from Philadelphia, Pa., but no beetles were caught in traps set throughout Bermuda (Waterston 1942).

No further interceptions of beetles were made until 1946, when living beetles were found in aircraft from New York City and Baltimore, Md., and on a ship from New York (Waterston 1943, 1947). During 1948 and 1949 living beetles were found in ships and in aircraft arriving from the United States, but none were captured in traps set up throughout the island (Bedford 1949, 1950).

Although living beetles were intercepted on ships and in aircraft, there is little possibility of the insect becoming established in Bermuda because of its very dry summers.

Europe

Bourke (1961) reported that occasionally large numbers of living beetles were removed from civil and military aircraft arriving in Europe from the United States. The possibility of the insect being introduced into Europe has increased with the volume, speed, and range of international aviation, but so far no permanent colonies of the beetle have been discovered in Europe.

Based on moisture and temperature requirements for the development and survival of the beetle (see p. 97), Bourke (1961) concluded that there is little possibility of the insect becoming established in the Mediterranean region because of the lack of summer rainfall or in the United Kingdom, Ireland, and continental Europe north of about latitude 53° N. because the summers are too cool. In central Europe south of this latitude the normally light precipitation during the summer, except in the fertile valleys of the mountainous areas, would inhibit the establishment of the insect. The climate most suitable for the establishment of the beetle occurs in central France, southern Germany, and parts of Switzerland, Austria, Czechoslovakia, Hungary, Poland, and Romania, where summer rainfall is abundant and temperature is favorable.

PROBABLE ULTIMATE SPREAD IN NORTH AMERICA

The establishment of the beetle at many points in the eastern one-third of the United States demonstrates that the insect is generally adapted to the environmental conditions of this region. The climate here more nearly duplicates that of the insect's native Japan than in other regions. There is much interest in how much farther the beetle might spread in the North American Continent.

The most obvious environmental factors modifying the spread of the beetle, a subterranean insect for most of its life, are the temperature and rainfall. The predictions of Fox (1939) on the ultimate spread of the beetle were based on the temperature and moisture requirements of the insect (see p. 97) and on a comparison of the climate of Japan with the climatic conditions of the United States and Canada. The ultimate spread of the beetle in this continent is discussed further by Hawley (1952) and Fleming (1963a).

Eastward

The Atlantic Ocean is an insurmountable barrier to the eastward spread of the beetle.

Northward

It was predicted that the northern limits of the beetle's spread in the eastern half of the United States would probably be in the more elevated sections of northern New England and New York and in extreme northern Michigan. In these areas where precipitation is normally adequate throughout the year the northward spread is less likely to be inhibited by the severity of the winters than by the cool summers. The normal protective covering of snow in the winter tends to keep the subterranean habitat of the grub well within the limits of its cold tolerance. The low temperatures of late spring and early summer so retard the development of the beetle that emergence and egg deposition can hardly occur before August 1. Although the eggs might hatch, it is unlikely the young grubs could survive. No beetles have been found in these areas, but beetles have been found in the upper Connecticut River Valley in New Hampshire and Vermont, along the shores of Lake Champlain in Vermont and New York, and along the St. Lawrence River in New York. The beetle has some difficulty in surviving in this northern area. Although the populations were light, beetles could be found easily some years but were very scarce or absent other years.

Elsewhere in the East it was predicted that the beetle was likely to extend its range across the border into the southern parts of the Canadian Provinces of Ontario and Quebec. No beetles were found in Canada in 1934 (Sheppard 1935). During the 1940's the beetle spread from western New York and southern Michigan into the Niagara peninsula in southern Ontario (McLaine 1942; Sheppard 1943). The beetles were eliminated by the use of traps and insecticides. Since then beetles have been found occasionally in the peninsula and along the St. Lawrence River west of Montreal in Quebec.

It was predicted that the beetle could not become established in the region lying west of and in the same general latitude of the Great Lakes and extending to the Missouri River. This region includes much of Wisconsin and the northern half of Iowa, Minnesota, North Dakota, and South Dakota. In the winter the precipitation is light and there are prolonged periods of very low temperature. During a

prolonged period of subfreezing temperature coinciding with the absence of snow, the soil would progressively freeze and the temperatures would be lowered to the limit of cold tolerance of the grubs, resulting in practical, if not complete, extermination of the insect. The beetle has not become established in this region.

Westward

It was predicted that the beetle would likely extend its range westward from the Appalachian Mountains into Kansas and Nebraska to about the 100th meridian. Since the summer rainfall in this region is less than on the Atlantic seaboard and droughts tend to be more frequent and severe, the beetle may have some difficulty in becoming established and the populations are likely to increase slowly. It has become established in Kentucky, Tennessee, Ohio, southern Michigan, Indiana, Illinois, southern Iowa, and eastern Missouri, and it has been found in southern Wisconsin and eastern Kansas.

The semiarid region west of the 100th meridian to the high mountain ranges, including western Kansas, western Nebraska, eastern Colorado, and eastern Wyoming, is practically an insurmountable barrier to the westward spread of the beetle. The country is so dry during the summer that the beetle could not survive except in irrigated areas. The beetle has not been found in this region. With this barrier it can reach the more westerly parts of the country only by being carried there by man.

The rainfall in summer in the higher mountain ranges, such as the Rocky Mountains and the Cascade Range, would be sufficient for the development of eggs and young grubs, but the low summer temperatures at such altitudes would probably preclude the beetle's establishment.

The Great Basin, bounded by the Sierra Nevada Mountains on the west, the Columbia Plateau on the north, and the Rocky Mountains on the east, includes the western part of Utah, almost all of Nevada, and contiguous parts of Idaho, Oregon, and California. The drainage from the high mountains on the east and west flows into various basins to form lakes, which are saline because of the concentration of minerals. In the summer this region is warm to hot and there is no precipitation. It is a desert except the irrigated areas along the streams and at the base of the mountains. Its eastern border is one of the principal irrigated districts in the United States. Where the summer temperature is favorable, the irrigated areas of the Great Basin appear to be desirable for the establishment of the beetle.

It was predicted that the scanty rainfall on the Pacific coast in the summer would make the beetle's establishment difficult. The cool summers of northern California, western Oregon, and western Washington are also unfavorable. In central and southern California, where temperatures are more favorable, extensive irrigation makes large areas suitable for the beetle. The beetle was carried to and became established in Sacramento, an oasis in an arid land, but the use of traps and insecticides eliminated the colony.

Southward

It was predicted that there was no climatic barrier to the spread of the beetle southward along the Atlantic coast into Florida and along the gulf coast into Alabama, Mississippi, Louisiana, and eastern Texas. Since the beetle can pass through its complete life cycle at 27.5°C ., the mean summer temperature of southern Florida would be no obstacle to its establishment. With copious rainfall, especially in the warmer half of the year, and temperatures rarely falling below 10° in the winter, the beetle not only would be able to survive but probably would have two generations a year.

Although beetles were found at several localities in South Carolina, Georgia, Florida, and Louisiana, vigorous colonies have developed only in the mountainous areas of western South Carolina and western Georgia. The mean summer temperature near the southern extremity of Japan is 25°C . In the Southern States the vigorous colonies are near or north of this isotherm; south of the isotherm the beetle failed to become established or the colonies are relatively weak. The summer isotherm of 25° is about the southern limit of the beetle's spread.

SUMMARY

Little was known about the biology of the Japanese beetle (*Popillia japonica* Newman) when it was discovered in southern New Jersey in 1916, probably because it is a pest of minor importance in its native Japan. In the United States the adult seriously damaged orchard crops, small fruits, certain field crops, and ornamental trees and shrubs. The grub destroyed large areas of turf in lawns, golf courses, and pastures and injured the roots of other plants.

The adult beetle is metallic green with coppery brown elytra, which do not cover the abdomen completely and expose a row of five spots of white hairs on each side of the abdomen and a pair of white spots on the dorsal side of the last abdominal segment. These white spots

distinguish the beetle from all other beetles that resemble it. The sexes are separated by slight differences in the shape of the tibia and tarsus of the prothoracic legs. The mature grub is creamy white with a yellowish-brown head. After feeding, the accumulation of fecal matter in the hindgut gives the posterior part of the abdomen a grayish to black appearance. The grub is distinguished from other scarabaeoid grubs by a V-shaped arrangement of spines on the raster. The three larval instars are separated most readily by the size of their heads. The digestive, respiratory, circulatory, and reproductive systems of the insect are discussed.

The cycle of embryogenesis and the biochemical changes during embryonic development are described. The egg must absorb moisture as a prelude to and during embryonic development. No eggs hatched below 15°, and 34° C. was near the upper limit for development.

The range of temperature for the development of the beetle from egg to adult is between 17.5° and 27.5° C. The average weight during postembryonic development at 25° increased from 2.3 mg. with the newly hatched grub to 270.8 mg. with the mature third-instar grub, and then it decreased to 254.5 mg. with the prepupa, 235.6 mg. with the pupa, and 150.4 mg. with the adult. A close relationship exists between the weight of the grub and the volume of its cells but not with the number of cells in the body.

Only first-instar grubs that have fed sufficiently to accumulate a reserve of food are able to hibernate overwinter. Second- and third-instar grubs, the overwintering stages, are adapted to withstanding long periods of inactivity at temperatures below the development threshold, except when the alimentary tract is cleared for molting. Hibernating grubs are killed by prolonged exposure to -9.4° C.

The immature stages are adapted to living in moist soil and apparently lack the ability to conserve body moisture. The fatal limit in the loss of weight by desiccation is 50 percent by the grubs, 44 percent by early prepupae, 34 percent by late prepupae, and 31 percent by pupae.

The life cycle of the beetle is completed in 1 year in most areas where it is established. Beetle emergence is retarded progressively from the southern to the northern part of the infested area. Beetles begin to emerge from the ground the third week of May in central North Carolina but not until the first week of July in southern New Hampshire and southern Vermont.

Most of the beetles emerge from the ground in the morning of clear warm days and usually climb on low-growing plants and rest before flying. The length of life depends on the environment, but the normal lifespan is 30 to 45 days.

Mating usually takes place in the early morning or evening on plants, but it may occur on the ground. The female usually mates between each oviposition period. Coitus may be brief or prolonged for several hours. The promiscuousness of the beetle undoubtedly is of importance in maintaining the racial characteristics.

The female beetle tends to deposit her eggs in a suitable site in the proximity of the plant upon which she is feeding. The type of ground cover affects the choice of the site. She burrows into the ground in the afternoon and deposits an egg at three or more sites. She may emerge from the soil in the morning or prolong her stay in the soil for 3 or 4 days. After emerging and spending 1 or more days feeding and mating, she returns to the soil to deposit another complement of eggs. Usually a female lays 40 to 60 eggs during her life.

On clear summer days when the temperature reaches about 21° C. and the relative humidity is below 60 percent, beetles begin to fly in all directions. The flight is swaying, undulating, and aimless, except in response to chemical stimuli of food plants, and there is a tendency to drift with the wind. Most of the flights are for short distances, but the beetle is capable of flying 5 miles with the wind.

The beetle is a polyphagous insect. It is particularly attracted to certain species of *Acerraceae*, *Anacardiaceae*, *Betulaceae*, *Clethraceae*, *Ericaceae*, *Fagaceae*, *Gramineae*, *Hippocastanaceae*, *Juglandaceae*, *Lauraceae*, *Leguminosae*, *Liliaceae*, *Lythraceae*, *Malvaceae*, *Onagraceae*, *Platanaceae*, *Polygonaceae*, *Rosaceae*, *Salicaceae*, *Tiliaceae*, *Ulmaceae*, and *Vitaceae*. Odor is probably the most important factor in the beetle's selection of a plant, but being a gregarious insect, it tends also to alight on plants upon which other beetles are feeding.

Of the 433 species of plants classified according to their susceptibility to attack by the beetle, the beetle has not been observed feeding on 140 species. It occasionally injures 122 species lightly, particularly in areas of dense population. It generally injures 67 species lightly, 59 species moderately, and 47 species severely, often causing defoliation.

Japanese beetles prefer to feed on plants exposed to the direct rays of the sun, beginning to feed at the top of a plant, regardless of its height, and working downward. Feeding is most extensive on clear summer days when the temperature is between 21° and 35° C. and the relative humidity is above 60 percent. There is little feeding on cloudy or windy days and no feeding on rainy days.

Beetles feed on the upper surface of the foliage of most plants, chewing out the tissue between the veins and leaving a lacelike

skeleton. They eat the maturing silk of corn as it grows and feed on the developing kernels. They feed on ripening fruit until all that is edible is consumed.

During the first week or 10 days after beetles begin to emerge from the ground, feeding is confined to low-growing plants. Then they move from low-growing plants to fruit and shade trees. As the leaves on the trees become less attractive, the beetles leave the trees and become abundant on flowers then in bloom and in fields of corn, asparagus, and clover.

During the summer practically all the grubs in turf are within 4 inches of the soil surface. As the surface layer cools to 15° C., the grubs begin to move downward. Movement ceases when the temperature reaches 10°. Most of the grubs hibernate 2 to 8 inches below the surface. As the ground warms in the spring, the grubs begin to move toward the surface. During May and June practically all of them are within 4 inches of the surface. The grubs go deeper in cultivated land than in turf.

Grubs feed on the roots of a wide variety of plants. The feeding may not be suspected until the plants are badly damaged.

During 1920-29 the area occupied by the beetle was almost spherical in shape with a very densely populated central core surrounded by a zone where the population decreased progressively until it was very light at the periphery. The size of the area increased each year. When the population in the central core began to decrease, a dense population developed in a slightly broken band surrounding the core. These densely populated spots moved outward and continued to develop at the more favored sites. As the beetle spread, the outline of the infested area became slightly arcuate and finally very irregular with prominent arms extending up the river valleys.

The natural spread of the beetle is affected largely by the topography of the land, the direction of the wind, and the temperature and rainfall. The spread is facilitated in nearly level or gently rolling country, such as on the coastal plain and in the river valleys.

The beetle is adapted to a country where (1) the mean soil temperature during the summer is between 17.5° and 27.5° C., (2) the soil temperature during winter is above -9.4°, and (3) the precipitation is adequate and rather uniformly distributed throughout the year, averaging not less than 250 mm. during the summer.

The area occupied by the beetle increased from not more than 0.5 square mile in 1916 to 76,504 square miles in 1952, and probably 150,000 square miles in 1970. The beetle has spread largely by its own efforts over all or parts of 19 States, the District of Columbia, and part of one Canadian Province.

It was carried also to more distant points by man. Although the Federal and State quarantines were very effective in preventing the artificial spread of the beetle by agricultural products, they did not regulate the movement of other articles of commerce. In 1949 when the beetle had spread naturally over 47,910 square miles, there were 570 isolated localities beyond this area where beetles had been discovered. It did not become established at many of these localities, but at some places vigorous colonies developed.

The 1939 prediction on the probable ultimate spread of the beetle in North America has been largely confirmed. The northern limits appear to be in the elevated sections of northern New York and New England, in extreme northern Michigan, and in the region lying west of and in the same general latitude of the Great Lakes and extending to the Missouri River. The western limit appears to be about the 100th meridian. Beyond this meridian the semiarid region is practically an insurmountable barrier. The beetle can reach the Pacific coast only by being carried there by man. It has not become established in Florida and along the gulf coast as predicted, because the summer isotherm of 25° C. appears to be about the limit of its southern spread.

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