UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1324

Washington, D. C. April, 1925

THE OVIPOSITION RESPONSE OF INSECTS

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INTRODUCTION

Insects are generally attracted to materials for three purposes: (1) To obtain food for themselves or their progeny, (2) to lay their eggs, or (3) to gather material for their nests. In some instances the food of the adult and young is the same, and the eggs are laid directly on the substance which the adult eats. But there are many insects which show no such relation, in which the adult leads some part, often a considerable part, of its life in an environment very different from that of its immature forms. Furthermore, certain adult insects do not feed at all, yet are able, in some manner, to deposit their eggs in locations which favor the ready access of the young larvæ to their acccustomed food. Indeed, there is so much precision on the part of many insects in the selection of a place to deposit eggs that students were early impressed with the idea that something directs the gravid female to, and induces her to oviposit upon, food suitable for her progeny.

It is the purpose of this bulletin to discuss the various stimuli which affect the oviposition reaction of insects. Any treatment of the subject at this time must, however, be considered preliminary. Few attempts have been made to analyze this response, although numerous observations are on record which contribute toward its

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understanding. Many of these records are found in the extensive life-history literature of entomology under titles which conceal their presence. For this reason, some important contributions have probably been overlooked and, although a sincere effort has been made to cover the ground, completeness is not claimed.

The stimuli which determine when and where an insect will oviposit begin to operate far back in her life and may continue to affect her till the eggs are extruded. These influences are of two kinds, the *internal* and the *external*, and for convenience they will be taken up below in this order.

INTERNAL PHYSIOLOGICAL CONDITIONS AFFECTING OVIPOSITION

NUTRITION

There is evidence to show that the amount and character of the food of an insect affect the production of eggs. An adequate treatment of this subject would necessarily involve a discussion of nutrition and would lead beyond the limits of the present problem. It is sufficient to say here that numerous authors, including Kellogg and Bell (*44*),[1] Baumberger (*6*), Glaser (*26*), and Kopeć (*47*) have indicated that subnormal nutrition, whether due to the quantity or quality of the food, may have a decided effect on oviposition.

AGE

Among the groups of insects which possess mature eggs upon reaching the adult stage, some species, under favorable conditions, lay their eggs soon after emerging, whereas others retain them for a more or less extended period of time. The state of nutrition and weather conditions modify greatly the extent of this period (*26*, *40*). No particular attempt has been made to assemble the literature on this subject and only two references are given here. Breit (*10*) states that bombycid and noctuid moths lay eggs soon after mating, while most diurnal Lepidoptera fly around a few days before ovipositing. Age has no influence upon the oviposition of *Drosophila melanogaster* Meig., provided sexual maturity has been reached (Adolph, *1*).

FERTILITY

Fertility appears to be a stimulus for oviposition in some species, influencing not only the time of egg laying but also the number of eggs deposited. Normal oviposition of the cotton boll weevil (*Anthonomus grandis* Boh.) apparently will not take place till fertilization has been accomplished, but it usually begins soon after that (*41*). Mating accelerates the oviposition of *Heliothis obsoleta* Fab. (*62*). The fertile potato tuber moth (*Phthorimaea operculella* Zell.), according to Graf (*29*), oviposits within 24 to 48 hours after emergence and most of the eggs are laid within 4 days. The number varies from 38 to 290 eggs, the average, from 114 to 209 eggs, depending upon the nutrition of the female. Contrary to this, virgin females oviposit in from 1 to 7 days after emergence, the average time being 4.4 days. The number of eggs ranges from 1 to 51, with only 22.6 as an average. Unpublished observations of the writer on

[1] Reference is made by number (italic) in parentheses to "Literature cited," p. 13.

Ephestia kuehniella Zell. indicate that oviposition is considerably delayed and the number of eggs reduced if copulation has not taken place. Guyénot (*31*) and Adolph (*1*) obtained evidence from *Drosophila melanogaster* that mating is a stimulus for egg-laying; the former thought it was a mechanical stimulus because the first eggs deposited were frequently unfertilized. Picard (*61*) has also observed this effect in Phthorimaea and *Hesperophanes griseus* F. A recent work by Glaser (*26*) indicates clearly that association with the male sex stimulates egg production in *Musca domestica* L. and *Stomoxys calcitrans* L. Virgin females of the imported pine sawfly (*Diprion simile* Hartig) apparently wait 2 days before oviposition and although they can reproduce parthenogenetically, if not mated they lay only half as many eggs as fertile females (*53*). Mating is not a factor in the oviposition of many parasitic Hymenoptera (*34, 61*), nor in certain social Hymenoptera.[2]

INTERNAL PERIODICITIES

Adolph cites the work of Back and Pemberton (*3*) on the melon fly (*Bactrocera cucurbitae* Coq.) to show that internal periodicities may be responsible for the intermittent deposition of eggs by certain species. Such periodic egg-laying occurs in other insects (*9*) though few references to it have been found. Bishop, Dove, and Parman (*8*) mention that the house fly (*Musca domestica*) lays eggs at 8-day intervals.

EXTERNAL INFLUENCES AFFECTING OVIPOSITION

TEMPERATURE

Temperature influences the rate of many life processes, among which may be counted the activities connected with oviposition. Within the range of each species there is probably an optimum temperature for egg-laying. In the alfalfa weevil (*Phytonomus posticus* Fab.) mean daily oviposition follows in general the curve of mean daily temperature (*57*); a similar relation holds for the cotton boll weevil (*Anthonomus grandis*) (*76*). A reduction of 3° or 4° C. has been observed to lengthen the oviposition period of *Tomicus* (*Ips*) *typographicus* L. from 1 to 8 days (*35*). A cool night retards the oviposition of *Hypera punctata* Fab. and it ceases between 7° and 10° C., according to Hudson and Wood (*39*). A recent study by Detouches (*19*) on the wax moth (*Galleria mellonella* L.) shows how markedly temperature may affect the quantity of eggs laid. At 37°

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[2] Some additional instances of fertility as a stimulus for oviposition have come to light since the above was written. According to Baker and Davidson (Jour. Agr. Research, vol. 6, pp. 351–360, 1916), the female of *Eriosoma pyricola* Baker and Davidson fails to deposit the winter egg unless fertilized directly after the last integument has been cast. *Hippodamia 13-punctata L.* will oviposit without being fertilized but scarcely one-fourth of the usual number of eggs are laid (Cutright, Ann. Ent. Soc. Amer., vol. 17, pp. 188–192, 1924). Sen (Rept. Proc. 5th Ent. Meeting Pusa, February, 1923, pp. 215–225, Calcutta, 1924) was not able to obtain eggs from unfertilized females of *Aedes* (*Stegomyia*) *albopicta* Skuse even after the insects were allowed to bite and suck blood. Studies on *Chlorops taeniopus* Meig. by Frew (Ann. Appl. Biol., vol. 11, pp. 175–219, 1924) show that unfertilized females commence ovipositing 10 to 12 days after emergence, while fertilized females begin laying in 4 to 5 days. Unfertilized flies also lay fewer eggs than fertilized flies. Apparently the mite *Tyroglyphus mycophagus* (Mégnin) will not lay eggs unless it has been fertilized (Schulze, Zeitschr. wissen. Biol., Abt. A. Morph, and Ökologie, 2, Heft 1 and 2, pp. 1–57, 1924). It is not yet clear whether this stimulus is a mechanical one, as Guyénot has suggested, or an internal one resulting from substances transferred to the female during coition.

C., the optimum for larval development, the female lays from 9 to 15 eggs. When intermittent temperatures of 1° and 37° are imposed for 24-hour periods throughout the life of the moth, it lives longer and lays 25 to 35 eggs. At temperatures intermediate between 20° and 37° not over 12 eggs are laid. The vital repose obtained by the lower temperature prolongs the life of the moth and an increase in egg production results. Temperature affects both the rapidity of egg-laying and the number of eggs deposited by *Phthorimaea operculella* (*29*). Glenn (*28*) states that low temperature delays egg-laying of the codling moth (*Carpocapsa pomonella*). Isely and Ackerman (*42*), who have recently studied the oviposition of this insect, could detect no serious check in egg-laying under optimum light conditions till a temperature of 18.3°C. was reached. Below this few eggs were laid and oviposition ceased entirely at 16.7°C. The period of highest night temperature occurs immediately after sunset, which probably accounts for the heavy oviposition at this time (Siegler and Plank, *74*). Sharma and Sen (*72*) found that certain Indian mosquitoes preferred temperatures near 35° C. for oviposition, and high or moderately high temperatures under proper moisture conditions stimulate egg-laying in the house fly (*Musca domestica*) (Bishopp, Dove and Parman, *8*). It has been shown by Roubaud (*67*) that *Glossina palpalis* Desv., which deposits living larvæ, is active in this respect between approximately 23° and 28° C., whereas at 30° C. reproduction is completely arrested. *Lysiphlebus tritici* Ashm. (=*Aphidius testaceipes* Cress.), a hymenopterous parasite of the green bug (*Toxoptera graminum* Rond.) attempted to oviposit, but without success, at 1.7° C., the lowest temperature at which the oviposition activity of this species was observed (*27*). Temperature plays an important rôle in the oviposition of *Habrobracon brevicornis* (Wesmael) (*34*).[3]

HUMIDITY

Humidity is an important factor in the egg-laying activities of many if not most insects. Shelford (*73*) observed that tiger-beetles require moist soil for oviposition. By increasing the atmospheric moisture from 55 per cent to 96 per cent, egg-laying of *Tomicus typographicus* was delayed from 1 to 7 days (Hennings, *35*). Heavy precipitation delays oviposition in *Carpocapsa pomonella*, but whether from the effect of the moisture or from mechanical effects was not stated (Glenn, *28*). High atmospheric moisture favors oviposition in the blow-flies (*Calliphora* spp., *Lucilia* spp., *81*), and invariably increases the amount of egg laying in *Drosophila melanogaster* (*1*). It is also necessary for normal oviposition of the house fly (*8, 63, 64, 68*). According to Roubaud (*67*), the deposition of larvae by *Glossina palpalis* ceases when the atmospheric humidity reaches the saturation point unless the fly has previously been subjected for several days to an accelerating temperature (28° C). The humidity of the usual habitat of this species is normally 90 per cent. Certain species of mosquitoes and other insects which lay their eggs upon the surface of the water probably develop a strong hydro-

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[3] The correct name for the species used by Hase (cf. Die Naturwissenschaft, Jahrg. 11, Heft. 39, p. 801, 1923) is *juglandis*.

tropism during the breeding season. However, the recent experiments of Sharma and Sen (*72*) appear to indicate that dissolved substances influence the oviposition response.[4] According to Hase (*34*), the degree of moisture has no effect on the egg-laying of *Habrobracon juglandis*.

LIGHT

The character of the response of an insect to light has an important bearing on the kind of environment in which the eggs will be laid. If the response is positive, oviposition will take place in a well-lighted environment, unless, as sometimes happens, there is a reversion of the normal heliotropism during the egg-laying period. The opposite will be true of negatively heliotropic insects.[5] Grevillius (*30*) states that light plays an important part in the selection of a place for oviposition by the brown-tail moth (*Euproctis chrysorrhoea* L.). An appreciable degree of darkness is essential for heavy oviposition of the codling moth (*Carpocapsa pomonella*) (*42*). Dewitz (*21*) cites a number of references which indicate that the European vine moths *Cochylis* (*Clysia*) *ambiguella* Hübn. and *Polychrosis botrana* Schiff. select the shaded grape clusters for oviposition rather than those situated in strong sunlight. According to Wardle (*81*), blow-flies seldom oviposit in food exposed to the sun's rays, but they lay their eggs readily in the shade. The response to light varies with the species of blow-fly concerned, *Lucilia caesar* L. being more strongly heliotropic than *Calliphora vomitoria* L. Light stimulates reproduction in the house fly (*8*), but is without effect on the egg-laying responses of *Drosophila melanogaster* (*1*).

Few observations upon the effect of color on oviposition appear to have been made. The most important of these which the writer has seen are embodied in the recent work of Knoll (*46*) on the relation of insects and flowers. The experiments were made on *Macroglossum stellatarum* L., a European diurnal sphingid moth which lays its eggs chiefly upon cruciferous plants of the genus Galium. The oviposition flight of this moth is distinct from its flight when in search of food. Knoll found that the gravid female made typical oviposition flights to reflected light from chlorophyll solutions (alcoholic solutions of crude chlorophyll and α- and β-chlorophyll from Galium plants); the moth reacted to the colored light and not to the odor of the solutions. A number of artificial green and yellow objects induced the oviposition flight, but in only one instance was an egg deposited. To obtain the complete response, artificial flowers made of green or yellow paper dipped in beeswax and each containing a drop of the press juice from plants of *Galium mollugo* L. were used. Gravid moths flew to these objects, exhibiting the characteristic oviposition flight and laid an egg on the under side. This result was often repeated. From these experiments, Knoll con-

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[4] In a recent paper Crumb (Ent. News, vol. 35, pp. 242–243, 1924) states that certain odors arising from water are strongly attractive to gravid female mosquitoes (*Culex pipiens L.*). Experimentally, he finds dilute aqueous solutions of methane, hydrogen sulphide, old yeast infusion, and stale urine to be considerably more attractive than water alone.

[5] Thus Dietz and Zetek (U. S. Dept. Agr. Bul. 885, 55 pp., 1920) find that the eggs of the aleurodid *Aleurocanthus woglumi* Ashby are normally laid on the undersides of the leaves. The females are negatively heliotropic at the time of oviposition, for when a leaf upon which a female is ovipositing is turned over so that the light falls directly upon it, egg laying invariably ceases.

cluded that two factors were necessary to induce Macroglossum to oviposit, an optical factor, effective at a distance through yellow and green light and a chemical factor operating near at hand through the specific odor of the larval food plant, Galium. Titschack (*77*) found that the color of wool stuffs is not a factor in determining egg laying in the webbing clothes moth (*Tineola bisellliella* Hum.).

AIR AND WATER CURRENTS

Aquatic and aerial insects are oriented in their environment by the movement of the medium surrounding them. It seems probable that ovipositing insects are also affected by stream or air movement. Wardle (*81*) states that wind is antagonistic to the oviposition of blow-flies. The cyrtid fly *Pterodontia flavipes* Gray deposits its eggs on the leeward side of trees (*45*), in which location it may be oriented by air movement.

SURFACES

In many insects, contact with an appropriate surface seems to be a necessary prerequisite for oviposition. According to Loeb (*49*), a highly developed stereotropism exists in the segments of the reproductive organs of animals, and further there are indications that contact with a solid affects the behavior of living matter through an influence on the rate of certain chemical reactions. Crozier and Moore (*16*) show that the response of diplopods to surfaces in contact with the body is essentially like the response of a positively heliotropic animal to light; that is, the animal turns its head toward the side which is in contact with a solid surface. When both sides are stimulated by contact with surfaces of equal extent, the movement of the animal is along a straight path.

In the cockroach *Periplaneta americana* L., contact with suitable material is necessary to bring about the release of the egg case (*32*). According to Folsom (*25 p. 349*), some species of grasshoppers prefer hard-baked soil for oviposition. The migratory grasshopper (*Locusta migratoria* L.) in Russia evidences a choice between different kinds of soil. Isolated females insert the ovipositor into the soil a number of times before they deposit their eggs, and often a swarm which has alighted on soil too hard for oviposition will resume flight again (*80*). Baillon (*4*) also mentions that grasshoppers choose between different types of soil for oviposition. The Mormon cricket (*Anabrus simplex* Hald.) is said to prefer a somewhat firm but not very hard soil for this purpose (*13*). According to McColloch (*50*) the corn earworm moth (*Heliothis obsoleta*) deposits more eggs on corn plants which have rough hairy stalk and leaf surfaces than on plants with smooth surfaces. The moths were also induced to lay some eggs on cotton twine. Investigations of Benedict (*7*) and Titschack (*77*) on the webbing clothes moth (*Tineola bisellliella*) suggest that the tactile stimulus may be the determining factor in the selection of a place for egg laying by this species. Any rough surface was observed by Titschack to call forth oviposition, regardless of the food value of the material for the larvæ. The moths with which Benedict experimented laid their eggs on cotton and silk as well as wool, the loose threads being especially preferred. The character of the surface is apparently of importance to the potato tuber moth (*Pthorimaea operculella*). In France, Picard (*58*) states that it generally lays its eggs in the cavities which surround the buds on the surface of the tuber, in incisions of the skin, or on the clumps of dried earth which adhere to the surface. It will also oviposit on the foliage of Verbascum and Cynoglossum which is felted and plaited, in preference to that of Linaria, for although the latter is more closely allied to the Solanaceae than Cynoglossum, its leaves have smooth surfaces. In laboratory experiments, the moths often laid a part of their eggs on the muslin sides of the cage, even when potatoes were available, but eggs were placed only exceptionally on the glass walls. Graf (*29*), who has studied the potato tuber moth in America, likewise reached the conclusion that oviposition was stimulated by roughened surfaces. The Angoumois grain moth (*Sitotroga cerealella* Oliv.) does not require the presence of grain as a stimulant for egg laying, but, in captivity, will readily oviposit between strips of cardboard. Usually all the eggs are deposited in the crevice between the strips (*75*). Dewitz (*20*, *22*), while pointing out the possible rôle of odor in the attraction of the gravid female of *Cochylis ambiguella*, also states that oviposition on the grapevine bud may be attributed to a contact stimulation. In another paper (*21 p. 233*) he quotes Marchal to the effect that the female of *Polychrosis botrana* is guided during oviposition upon the smooth surface of the grape by the tactile power of the abdomen. Oviposition would not take place on grapes covered experimentally with powder or a sticky mass. The experiments of Adolph (*1*) on *Drosophila melanogaster* show that the texture of the substance with which the gravid female comes in contact exercises a marked effect upon the quantity of eggs laid. Boiled agar was more potent in this respect than any of the solutions which were used to test the effect of taste, odor, or a combination of taste and odor. The character of the nidus also has a very evident influence upon the oviposition of the house fly (*Musca domestica*). Under appropriate conditions, pine sawdust is considerably less attractive than timothy chaff or horse manure, and moist absorbent cotton (containing ammonium carbonate only) was oviposited upon only once in 11 experiments (*63*, *64*). Some observations by Picard (*60*) on the oviposition of *Pimpla instigator* F., a hymenopterous parasite of the chrysalis of *Pieris brassicae* L., and of certain other Lepidoptera, are interesting in this connection. If an old chrysalis shell or a cylinder of white paper is coated with fresh blood from a chrysalis of Pieris, the parasite will pierce it with its ovipositor. The stimulus is olfactory, but according to Picard the actual deposition of the egg depends upon a tactile stimulus produced by the resistance of the living tissue within the chrysalis. Indeed, a chrysalis shell or a hollow cylinder of paper may be many times perforated by the ovipositor, but never will an egg be laid. The importance of tactile stimuli in the oviposition response of *Habrobracon juglandis* has recently been shown by Hase (Die Naturwissenschaft. Jahrg. 11, Heft 39, pp. 801–806, 1923). Touch is probably the directing sense in the oviposition behavior of Habrocytus (*61*).

In a recent publication, Howard (*36*, *p. 36–37*) declares that the stimulus for oviposition in certain chalcidoid parasites of gall-making insects is not the morphological character of the host insect but of the gall which it inhabits. In some other parasites mentioned by this author, the stimulus seems to be furnished by the silken cocoons or webs of the host insects.

ODOROUS SUBSTANCES

A number of observations are on record which stress to a greater or less degree the importance of odor as a factor in oviposition. Scudder (*71*), in discussing the so-called botanical instinct of butterflies, excludes taste and sight but believes the oviposition behavior is in keeping with the idea that the larval food plant is detected by means of the olfactory sense. Trägardh (*79*) places great emphasis on chemotropism, and Picard (*59*) also emphasizes its importance but recognizes that light, temperature, humidity, and other physical factors play a part. Brues (*11*) states that there is much in the behavior of certain species to suggest that food plants are selected by the female insect on the basis of odor. In addition, Brues recognizes "some attribute of the plant, perhaps an odor, but far less pronounced to our senses than odor or taste" as a factor in the attraction of insects to plants. Grevillius (*30*) thought it probable that the choice of a food plant on the part of the brown-tail moth (*Euproctis chrysorrhoea*) was determined by the olfactory sense. The cotton worm moth (*Alabama argillacea* Hbn.), which lays its eggs on the leaves of the cotton plant (*Gossypium* sp.), may be attracted by the nectar glands on the leaves (*12*). In fact, moths were seen alternately feeding from these glands and ovipositing. It was found, however, that no preference was shown for the portion near the glands on the involucre. This fact induced Comstock to question whether oviposition was here determined by the presence of the nectar glands. Studies by McColloch (*50*) on *Heliothis obsoleta* show that it deposits 60 per cent of its eggs on the silks when the corn plant is in silk. Artificial silks made of cotton twine soaked in the fresh juice pressed from corn silk received 79 per cent of the eggs laid, while the controls (untreated cotton twine) received 21 per cent. Thus odor appears to be important in this case, but surfaces, according to McColloch, must also be considered. Knoll (*46*) emphasizes the effect of odor upon *Macroglossum stellatarum* when the moth is close to the plant upon which the eggs are to be laid. But green or yellow light is necessary to attract the moth to the plant from a distance. The potato tuber moth is attracted by the odor of certain plants (*61*), but, as previously mentioned, the character of the surface is also highly important. *Dewitz* (*20*) thought the vine moth (*Cochylis ambiguella*) might be attracted and induced to lay its eggs upon or near the buds of the grapevine by the odor poured from the nectaries. But, in addition, he recognized the possible effect of contact stimulation. Loeb (*49, p. 160*) states that the blowfly [6] is attracted to and will oviposit on decaying meat but not on fat. It will also deposit eggs on objects smeared over with asafetida. A positive chemotropism is responsible, according to this author, for oviposition. Fabre's observations on the blow-fly, *Calli-*

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[6] It is here called "the common house fly," but the reference is undoubtedly to one of the Calliphoras (cf. Loeb, *48*).

phora vomitoria, indicate that odor is a much more important factor in oviposition than the physical character of the material on which the eggs are laid (*23*). A variety of substances, colored paper, oilskin, tin foil, when placed over a receptacle which contained meat, were oviposited upon provided an opening was made in the cover. Dead birds wrapped in paper envelopes were visited by blow-flies, but they did not lay their eggs on the paper or attempt to oviposit in slits in the paper folds. Fabre attributes this behavior to a maternal foresight of the fly for an opening through which the progeny may find their way to food. His results, however, do not preclude the possibility that this behavior resulted from differences in odor concentration. The same explanation might also be offered to interpret his experiments on the larvipositing fly *Sarcophaga carnaria* L., (*op. cit., pp. 331–340*). Wardle (*81*) recognizes two factors concerned in the oviposition of blow-flies, (1) the nature of the foodstuffs and (2) meteorological conditions. The stimulus for oviposition, whether olfactory or gustatory he was not sure, probably resides in the exuding juices of the food substances. Howlett (*37*) induced an Indian species of Sarcophaga to deposit larvæ in a flask which contained a solution of skatole. Subsequent experiments with skatole by Lodge (Proc. Zool. Soc. London, September-December, pp. 481–518, 1916), Roubaud and Veillon (*68*), and the writer (*64*) have failed to substantiate the attractiveness which Howlett claimed for this compound. He also obtained eggs of *Stomoxys calcitrans* upon cotton wool soaked in valeric acid, but an attempt to duplicate the latter result in America failed (*65*).

In the case of the house fly (*Musca domestica*), although the odor of ammonia from ammonium carbonate will, under suitable conditions, induce the female to oviposit (*63*, *64*, *66*), the immediate environment from which the ammonia arises also shares in determining whether egg laying will occur. If we place several pieces of solid ammonium carbonate with a little water in a glass dish, female house flies are attracted by the odor, but will not oviposit in or near the dish. A very slight response is obtained with moist cotton and ammonium carbonate which is increased when butyric or valeric acid is added. Pine sawdust is better than cotton but inferior to timothy chaff or acidulated horse manure. Wheat bran is a favorable nidus in the presence of ammonium carbonate, but eggs have not been found in fresh, moist bran which does not volatilize ammonia. It has been shown conclusively that carbon dioxide, a decomposition product of ammonium carbonate, is not in itself attractive to the gravid female house fly but, together with other factors, may exert an influence upon oviposition which has not been detected (*17*, *18*, *66*, *68*). Adolph (*1*) found that odor is a slight stimulus to egg laying in *Drosophila melanogaster*, being most marked when flies could gain contact with the odorous solution. Texture, however, was more effective than odor, and suitable combinations of texture and odor (the flies were prevented from reaching the odorous substance) gave responses nearly equal to those which prevail under natural conditions. Townsend (*78*), in a study of the tachinid flies, observed that *Eupeleteria magnicornis* Zett., which deposits living larvæ on the foliage of plants, seeks for this purpose only those portions over which the host caterpillars have crawled. The parasitic larvæ are usually placed on stems where a silken thread has been left by a caterpillar, and Townsend suggests that the sense of smell induces the flies to larviposit in such locations. Picard (*60*) states that the functioning of the ovipositor of *Pimpla instigator* is a reflex determined by an olfactory sensation, but that the tactile sense governs the actual deposition of the egg in the host. The investigations of Hase show that odor is all important in the discovery of the host by *Habrobracon juglandis* but that tactile stimuli are necessary to bring about the deposition of the egg (*34;* cf. also Die Naturwissenschaft, Jahrg. 11, Heft 39, p. 801, 1923).

CONTACT WITH CHEMICAL SUBSTANCES

In addition to the effects produced by the purely physical character of surfaces there yet remains the possibility that the oviposition behavior may be influenced by direct contact of the insect's body with chemical substances. Responses due to the sense of taste and to the general chemical sense probably belong here. McIndoo (*51, 52*) believes that the senses of smell and taste in insects are inseparable. Minnich (*54, 55, 56*), however, has recently described a chemical sense analogous to taste located on the tarsi of two species of Lepidoptera, *Pyrameis atalanta* L. and *Vanessa antiopa* L. Experiments on *Drosophila melanogaster* (*1*) indicate that the taste of an aqueous glucose solution is much more effective in evoking oviposition than the odor of a solution which contains a mixture of acetic acid and alcohol, although the latter mixture has a marked food attraction for this fly (*5*). Sharma and Sen (*72*), in a study of the oviposition of mosquitoes, find that weak solutions of sodium chloride, sodium citrate, sodium tartrate, and certain other salts are conducive to egg laying, while the corresponding acids are repellent. Observations of Hancock (*33*) on the oviposition of the grasshopper *Orchelimum glaberrimum* Burm. reveal the interesting fact that this insect, when searching for a place to lay its eggs, either ignores the plants distasteful to it or subjects them to a brief mouth test (cf. *4, p. 134*). Although not proving the point, these observations suggest that taste plays a part in the selection of the plant. Brues (*11*) places taste among the senses which direct gravid female insects to plants.

DISCUSSION

Insects which spend most of their lives upon substances that offer food for themselves or their offspring probably exhibit the simplest oviposition responses. When the internal physiological conditions are right, simple contact with the stimulating medium appears to be all that is necessary to release the eggs. The behavior of the ovipositing queen bee suggests that the response is largely determined by the tactile sense and this may also be true of other colonial insects. The webbing clothes moth (*Tineola bisselliella*), which oviposits as readily upon the surfaces of indigestible materials as upon the natural food of its larva, likewise seems to lay its eggs largely in response to tactile stimuli.

Contrasted with these simpler cases, the oviposition response of many active free-living species is much more complex. The intensity and wave length of light, temperature, and humidity, rate of movement of the medium in which she lives, odor, and the physical and chemical character of surfaces aid in bringing the gravid female insect into contact with the specific larval food and induce her to release the eggs. A given set of stimuli is not effective for all species. Thus, for *Drosophila melanogaster* the stimuli may be roughly classified in the following ascending order of effectiveness: Odor, moisture, taste, odor and taste, texture, texture and odor, and a combination of texture, taste, and odor. In comparison with Drosophila, the house fly is more dependent on the odor of the medium; most substances which do not liberate ammonia probably seldom, in nature, evoke egg deposition. The response of Macroglossum to green and yellow light presents a reaction at present apparently unique among insects, but which further study may show to be widespread in those species which lay their eggs on green plants.

The experimental evidence at hand suggests, then, that a chain of stimuli is, in many species, necessary to induce egg deposition. Adolph (*1, p. 338*) sets forth this view in the following words:

> Egg laying in its nature is a complete response ("all or none"); that is, partial stimulation can not be measured. A single potent factor in the chain may never lead to the extrusion of eggs.

A similar view is gained by Knoll (*46, p. 349*) from his study of Macroglossum, by Picard (*60*) from observations on *Pimpla instigator* F., by Hase from studies on *Habrobracon juglandis*, and the results of the writer's experiments on the house fly are concordant with it.

Loeb (*49*) seems to favor the idea than an odor stimulus is sufficient to produce oviposition in certain free-living insects. He says (p. 160):

> The fact that eggs are laid by many insects on material which serves as a nutritive medium for the offspring is a typical instinct. An experimental analysis shows again that the underlying mechanism of the instinct is a positive chemotropism of the mother insect for the type of substance serving her as food; and when the intensity of these volatile substances is very high, that is, when the insect is on the material, the egg-laying mechanism of the fly is automatically set in motion. Thus the common house fly [see footnote, p. 8] will deposit its eggs on decaying meat, but not on fat; but it will also deposit it [them] on objects smeared over with asafetida on which the larvæ can not live. * * * It seems that the female insect lays her eggs on material for which she is positively chemotropic, and this is generally material which she also eats.

Fabre's observations on the blow-fly *Calliphora vomitoria* emphasize the predominance of odor in this response, and Howlett's results with Sarcophaga would appear to leave little doubt that odor alone can induce insects to oviposit. It must be said, however, that Howlett's experiments are given in little detail and might be accidental or unusual rather than the customary response of the fly in question. And the observations of Loeb and Fabre do not exclude effects due to the surface with which the flies came in contact. At all events, it is desirable that thoroughgoing evidence be obtained before accepting as fact the proposition that free-living Diptera can be induced to lay eggs solely by means of an odor stimulus. It seems necessary to stress the dependence of chemotropism upon other factors at this point because certain entomologists have rather accepted it as the stimulus responsible for the oviposition of insects. From present knowledge, however, it seems doubtful whether a free-living insect can ever be induced to oviposit by means of an odor stimulus alone.

The reaction of Drosophila to odor concentration is interesting. It has been shown by Adolph (*1, p. 334, 335*) that odor concentrations are never so low that they fail to call forth positive responses, and even very faint odors have full stimulating value. If this proves true of many insects it will perhaps explain how the faint odors emanating from the green portions of some plants may possess great stimulating value, particularly when the insect is near by.

In captivity, some species will oviposit on almost any convenient surface, but others hold strictly to specific substances and refuse to oviposit in their absence. Among Lepidoptera, for example, there are species (*Satyrus dryas*, *Carpocapsa pomenella*) which lay their eggs at random on the walls or floor of the cage, and others which refuse any but a particular food plant for this purpose (*Papilio machaon* L., *Pieris brassicae*., *Arginnis selene* Schiff., and others, *24, 43, 69*). These results show the difference in oviposition behavior that may occur in the same family of insects.

It has been observed, however, that there are occasional errors of judgment on the part of female insects which have specialized food plants; that eggs are, in fact, sometimes placed upon plants which can not nourish the larvæ. Knoll (*46*) observed the habits of *Macroglossum stellatarum* in captivity, the larva of which is closely restricted to plants of the genius Galium. After retaining the eggs a long time, the female will deposit them on any available green portion of a plant, regardless of its botanical relationships. And more recently Schwarz (*70*) concludes from observations on Catocala extending over a number of years that such mistakes in oviposition are a phenomenon of old age and a sign of physical exhaustion.

The question now arises, how has the female insect obtained the ability to respond to these stimuli which lead it almost unerringly to the specific larval food? Is it impelled by a series of tropisms, or by an instinct which is the result of natural selection, or by an acquired instinct now hereditarily fixed? The tropistic view has been advanced by Loeb (*48, 49*), Trägardh (*79*), Howlett (*37, 38*), and others. Brues (*11*) and Loeb (*49, p. 160*) have mentioned the possible relation of natural selection to food selection by the female insect. Bachmetjew (*2*) believes that the female insect must have an acquaintance with the taste of the larval food plant which it has inherited from the larva. To use his own words (*p. 713*).

> Allein der Geruchsempfindung bei der Wahl der betreffenden Pflanzeging die Geschmacksempfindung geschichtlich voran, denn um zu wissen, wo er seine Eier ablegen soll, musste der Falter zuerst mit dem Geschmack der betreffenden Pflanze bekannt gewesen sein, resp. dies von der Raupe geerbt haben.

Wheeler (*82, p. 71–72*) states that oviposition and feeding upon the host blood in the parasitic Hymenoptera are congenitally or hereditarily conditioned reflexes. Little of an exact nature seems to have been done to elucidate this important question. However, the very suggestive experimental investigation of Craighead (*14, 15*) throws considerable light upon it.[7] Craighead finds that nearly all adult cerambycids display a marked preference for the host wood in which they have fed as larvæ, and that certain species which can be induced to feed in a new host show a preference for that host when they become adults. Concerning oviposition, he says (*14, p. 220*):

Although the adults show a decided predilection for a favored host in ovipositing and even, in certain species, a preference for the plants in which the larvæ have fed for one or two generations, the instinct to oviposit seems to overbalance that of host selection, consequently new hosts are frequently selected—possibly more frequently in nature than is generally realized.

If it can be shown that the food of the larva determines the host preference of the adult, a decided step in advance will have been made. Another step then will be to explain whether the "memory" of the food plant which the larva has passed on to the adult is the result of or is influenced by the chemical or physical effects of the food in the growing larva.

CONCLUSIONS

The following internal factors may condition the oviposition responses of insects: The nutritive state as affected by the amount and chemical constitution of the food, age, fertility, and internal stimuli which determine periodic egg-laying.

The external influences which may affect the oviposition response are temperature, humidity, light (including color), air currents (and probably in some species water currents), the physical character of surfaces, the chemical constitution of substances which stimulate on contact, and the volatile constituents of substances.

The simplest oviposition responses are probably shown by insects which spend most of their lives upon substances that serve as food for themselves and their offspring.

Most free-living insects, however, require a chain of stimuli to provoke egg laying; a single stimulus is insufficient to call forth a normal response. Many species demand a specific chain of stimuli.

The odor of a substance may attract gravid female insects, but is probably never in itself sufficient to induce normal oviposition.

LITERATURE CITED

(1) ADOLPH, EDWARD F.
1920. Egg-laying reactions in the pomace fly, Drosophila. *In* Jour. Expt. Zool., vol. 31, pp. 327–341.

(2) BACHMETJEW, P.
1907. Experimentelle entomologische Studien. vol. 2, xvi+944+cviii pp., 31 figs., Sophia.

(3) BACK, E. A., and PEMBERTON, C. E.
1914. Life history of the melon fly. *In* Jour. Agr. Research, vol. 3, pp. 269–274.

(4) BAILLON, P. CAPPE DE.
1920. Contribution anatomique et physiologique à l'etude de la reproduction chez les locustiens et les grilloniens. I. La ponte et l'éclosion chez les locustiens. *In* La Cellule, vol. 31, pp. 1–245.

(5) BARROWS, WILLIAM MORTON.
1907. The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. *In* Jour. Expt. Zool., vol. 4, pp. 515–537.

[7] An important discussion by Brues of this and similar cases has recently appeared (cf. Amer. Nat., vol. 58, pp. 127–144, 1924).

(6) BAUMBERGER, J. PERCY.
1919. A nutritional study of insects, with special reference to microorganisms and their substrata. *In* Jour. Expt. Zool., vol. 28, pp. 1–81.
(7) BENEDICT, RALPH C.
1917. An outline of the life history of the clothes moth, *Tineola biscliella.* *In* Science, n. s., vol. 46, pp. 464–466.
(8) BISHOPP, F. C., DOVE, W. E., and PARMAN, D. C.
1915. Notes on certain points of economic importance in the biology of the house fly. *In* Jour. Econ. Ent., vol. 8, pp. 54–71.
(9) BOUVIER, E. L.
1922. The psychic life of insects. Trans. by L. O. Howard, New York, xvi+377 pp., illus.
(10) BREIT, JULIUS.
1899. Die Eiablage der Tagfalter in der Gefangenschaft. *In* Societas Entomologica, vol. 14, no. 12, pp. 91–92.
(11) BRUES, CHARLES T.
1920. The selection of food-plants by insects with special reference to lepidopterous larvæ. *In* Amer. Nat., vol. 54, pp. 313–332.
(12) COMSTOCK, J. HENRY.
1879. Report upon cotton insects. Washington, Government Printing Office. v+511 pp., 2 col. pls., illus.
(13) CORKINS, C. L.
1922. Notes on the habits and control of the western or Mormon cricket, *Anabrus simplex* Hald. *In* 13th Ann. Rpt. State Ent. Colorado for 1921. Cir. 36, pp. 41–55.
(14) CRAIGHEAD, F. C.
1921. Hopkins host-selection principle as related to certain cerambycid beetles. *In* Jour. Agr. Research, vol. 22, pp. 189–220.
(15) ———
1923. The host selection principle as advanced by Walsh. *In* Canad. Ent., vol. 55, pp. 76–79.
(16) CROZIER, W. J., and MOORE, A. R.
1923. Homostrophic reflex and stereotropism in diplopods. *In* Jour. General Physiology, vol. 5, pp. 597–604, illus.
(17) CRUMB, S. E., and LYON, S. C.
1917. The effect of certain chemicals upon oviposition in the house fly (*Musca domestica* L.) *In* Jour. Econ. Ent., vol. 10, pp. 532–536.
(18) ———
1921. Further observations on the effect of certain chemicals upon oviposition in the house fly (*Musca domestica*). *In* Jour. Econ. Ent., vol. 14, pp. 461–465.
(19) DETOUCHES, LOUIS.
1921. Prolongation de la vie chez les Galleria mellonella. *In* Compt. Rend. Acad. Sci., vol. 172, pp. 998–999.
(20) DEWITZ, J.
1905. Beobachtungen, die Biologie der Traubenmotte *Cochylis ambiguella* Hüb. betreffend. *In* Ztschr. Wiss. Insektenbiol., vol. 1, pp. 193–199, 237–247, 281–285, 338–347, illus.
(21) ———
1912. Bearbeitung der Literatur der Traubenwickler Nr. 2. *In* Bericht der Königl. Lehranstalt für Wein, Obst, und Gartenbau zu Geisenheim a Rh. für das Etatsjahr, 1911, pp. 218–277.
(22) ———
1912. The bearing of physiology on economic entomology. *In* Bul. Ent. Research, vol. 3, pp. 343–354.
(23) FABRE, J. HENRI.
1913. The life of the fly. Trans. by A. T. de Mattos, New York, 477 pp.
(24) FISCHER, E.
1916. Ueber die Eiablage und Paarung der Tagfalter in der Gefangenschaft. *In* Societes entomologica, vol. 31, no. 12, p. 55.
(25) FOLSOM, JUSTUS WATSON.
1922. Entomology with special reference to its ecological aspects, 3rd. ed. vii + 502 pp., 5 pls., illus.
(26) GLASER, R. W.
1923. The effect of food on longevity and reproduction in flies. *In* Jour. Expt. Zool., vol. 38, pp. 383–412.

(27) GLENN, PRESSLEY A.
1909. Influence of climate on the green bug and its parasite. *In* Bul. Univ. Kansas, vol. 9, no. 2, pp. 165–200, illus.

(28) ———
1922. Codling moth investigations of the State Entomologist's Office, 1915, 1916, 1917. Bul. State Ill. Dept. Registration and Education, Div. Nat. Hist. Survey, vol. 14, art. 7, pp. 219–281.

(29) GRAF, J. E.
1917. The potato tuber moth. U. S. Dept. Agr. Bul. 427. 56 pp., map, illus.

(30) GREVILLIUS, A. Y.
1905. Zur Kenntnis der Biologie des Goldafters (*Euproctis chrysorrhoea* (L) Hb.) und der durch denselben verursachten Beschädigungen. *In* Beiheft Botan. Centralb. 18, Abt. 2, Heft 2, pp. 222–322, 8 figs.

(31) GUYÉNOT, ÉMILE.
1913. Études biologiques sur une mouche, *Drosophila ampclophila* Löw. VII. Le déterminisme de la ponte. *In* Compt. Rend. Soc. Biol. Paris, vol. 74, pp. 443–445.

(32) HABER, V. R.
1920. Oviposition by a cockroach, *Periplaneta americana* Linn. (Orth.) *In* Ent. News, vol. 31, pp. 190–193.

(33) HANCOCK, JOSEPH L.
1904. The oviposition and carnivorous habits of the green meadow grasshopper (*Orchelimum glaberrimum* Burmeister). *In* Psyche, vol. 11, pp. 69–71.

(34) HASE, ALBRECHT.
1922. Biologie der Schlupfwespe *Habrobracon brevicornis* (Wesmael) Braconidae. Zugleich ein Beitrag zur Frage der biologischen Bekämpfung von Schadinsekten. *In* Arbeiten aus der Biologischen Reichsanstalt für Land-und Forstwirtschaft, vol. 11, Heft 2, pp. 95–168.

(35) HENNINGS, CURT.
1907. Beiträge zur Kenntnis der die Insektenentwickelung beeinflussenden Faktoren. *In* Biol. Centralb. vol. 27, pp. 324–337.

(36) HOWARD, L. O.
1924. On entomological societies. Insect parasites of insects. Address of the retiring president. *In* Proc. Ent. Soc. Wash., vol. 26, pp. 25–46.

(37) HOWLETT, F. M.
1912. The effect of oil of citronella on two species of Dacus. *In* Trans. Ent. Soc. London, pp. 412–418, pls. 39–40.

(38) ———
1921. The practical application of insect psychology. *In* Rpt. Proc. 4th Ent. Meeting held at Pusa on the 7th to 12th February, 1921, pp. 368–377, Calcutta.

(39) HUDSON, H. F., and WOOD, A. A.
1923. Oviposition of Hypera punctata. *In* 53rd Ann. Rpt. Ent. Soc. Ontario, 1922, pp. 70–72.

(40) HUTCHISON, R. H.
1916. Notes on the preoviposition period of the house fly, *Musca domestica* L. U. S. Dept. Agr. Bul. 345, 13 pp.

(41) HUNTER, W. D. and HINDS, W. E.
1904. The Mexican cotton boll weevil. U. S. Dept. Agr. Div. Ent. Bul. 45, 116 pp.

(42) ISELY, DWIGHT, and ACKERMAN, A. J.
1923. Life history of the codling moth in Arkansas, with special reference to factors limiting abundance. Univ. Ark. Agr. Expt. Sta. Bul. 189, 57 pp.

(43) JENNE, E. L.
1909. The codling moth in the Ozarks, U. S. Dept. Agr. Bur. Ent. Bul. 80, pt. 1, pp. 1–32, illus.

(44) KELLOGG, V. L., and BELL, R. G.
1903. Variations induced in larval, pupal, and imaginal stages of *Bombyx mori* by controlled varying food supply. *In* Science, n. s., vol. 18, pp. 741–748.

(45) KING, J. L.
1916. Observations on the life history of Pterodontia flavipes Gray (Diptera). *In* Ann. Ent. Soc. Amer., vol. 9, pp. 309–321, pls. 15, 16.
(46) KNOLL, FRITZ.
1922. Insekten und Blumen. Experimentelle Arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Pflanzen und Tieren. III. Lichtsinn und Blumenbesuch des Falters von *Macroglossum stellatarum*. *In* Abhandl. Zool.-Bot. Gesell. Wein, vol. 12, Heft. 2, pp. 123–377, pls. 7–9, illus.
(47) KOPEĆ, STEFAN.
1924. On the heterogeneous influence of starvation of male and of female insects on their offspring. *In* Biol. Bul., vol. 46, pp. 22–34.
(48) LOEB, JACQUES.
1890. Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen. Würzburg, 118 pp.
(49) ———
1918. Forced movements, tropisms, and animal conduct. Philadelphia and London, 209 pp., illus.
(50) MCCOLLOCH, JAMES W.
1922. The attraction of *Chloridea obsoleta* Fabr. to the corn plant. *In* Jour. Econ. Ent., vol. 15, pp. 333–339.
(51) MCINDOO, N. E.
1916. The sense organs on the mouth-parts of the honey bee. *In* Smithsn. Misc. Collect., vol. 65, no. 14, pp. 1–55.
(52) ———
1922. The senses of insects. *In* Ann. Rpt. Smithsn. Inst. for 1920, Pub. 2622, pp. 461–483.
(53) MIDDLETON, WILLIAM.
1923. The imported pine sawfly. U. S. Dept. Agr. Bul. 1182, 21 pp., illus.
(54) MINNICH, DWIGHT E.
1921. An experimental study of the tarsal chemoreceptors of two nymphalid butterflies. *In* Jour. Expt. Zool., vol. 33, pp. 173–203.
(55) ———
1922. The chemical sensitivity of the tarsi of the red admiral butterfly, *Pyrameis atalanta* Linn. *In* Jour. Expt. Zool., vol, 35, pp. 57–81.
(56) ———
1922. A quantitative study of tarsal sensitivity to solutions of saccharose, in the red admiral butterfly, *Pyrameis atalanta* Linn. *In* Jour. Expt. Zool., vol. 36, pp. 445–457.
(57) PARKS, T. H.
1914. Effect of temperature upon the oviposition of the alfalfa weevil (*Phytonomus posticus* Gyllenhal). *In* Jour. Econ. Ent., vol. 7, pp. 417–421.
(58) PICARD, F.
1913. La teigne des pommes de terre (*Phthorimaea operculella*). *In* Ann. Service des Épiphyties, vol. 1, pp. 106–176, illus.
(59) ———
1919. Contribution à l'étude du peuplement d'un végétal. La faune entomologique du figuier. *In* Ann. Service des Épiphyties, vol. 6, pp. 34–174.
(60) ———
1921. Le déterminisme de la ponte chez un Hyménoptère térébrant, le Pimpla instigator L. *In* Compt. Rend. Acad. Sci., vol. 172, pp. 1617–1619.
(61) ———
1922. Contribution à l'étude des parasites de Pieris brassicae L. *In* Bul. Biol. France et Belg., vol. 56, pp. 54–130.
(62) QUAINTANCE, A. L., and BRUES, C. T.
1905. The cotton bollworm, U. S. Dept. Agr., Bur. Ent. Bul. 50, 155 pp.
(63) RICHARDSON, CHARLES H.
1916. A chemotropic response of the house fly (*Musca domestica* L.). *In* Science, n. s., vol. 43, pp. 613–616.
(64) ———
1916. The response of the house fly (*Musca domestica* L.) to ammonia and other substances. N. J. Agr. Expt. Sta. Bul. 292, 19 pp.

(65) RICHARDSON, CHARLES H.
1916. The attraction of Diptera to ammonia. *In* Ann. Ent. Soc. Amer., vol. 9, pp. 409–413.
(66) ——— and RICHARDSON, EVA H.
1922. Is the house fly in its natural environment attracted to carbon dioxide? *In* Jour. Econ. Ent., vol. 15, pp. 425–430.
(67) ROUBAUD, E.
1909. Recherches biologiques sur les conditions de viviparité et de vie larvaire de Glossina palpalis R. Desv. *In* Compt. Rend. Acad. Sci. vol. 148, pp. 195–197.
(68) ROUBAUD, E., and VEÍLLON, R.
1922. Recherches sur l'attraction des mouches communes par les substances de fermentation et de putréfaction. *In* Ann. Inst. Pasteur, Paris, vol. 36, pp. 752–764.
(69) SCHWANZ, WILHELM.
1912. Ueber die Eiablage der Tagfaltersweibchen. *In* Internat. Ent. Ztschr., Jahrg. 6, no. 11, pp. 73–75.
(70) SCHWARZ, ERNST.
1923. The reason why Catocala eggs are occasionally deposited on plants upon which the larva can not survive; and a new variation (Lepid., Noctuidae). *In* Ent. News, vol. 34, pp. 272–273.
(71) SCUDDER, SAMUEL HUBBARD.
1889. The butterflies of the eastern United States and Canada with special reference to New England. Cambridge, Mass., vol. 2, pp. x+767–1774.
(72) SHARMA, H. N., and SEN, S. K.
1921. Oviposition in Culicidae. *In* Rpt. Proc. 4th. Ent. meeting held at Pusa on the 7th to 12th February, 1921, Calcutta, pp. 192–198, pls. 31–35.
(73) SHELFORD, VICTOR ERNEST.
1907–10 Life histories and larval habits of the tiger beetles. *In* Jour. Linn. Soc. London (Zool.), vol. 30, no. 197, pp. 157–184.
(74) SIEGLER, E. H., and PLANK, H. K.
1921. Life history of the codling moth in the Grand Valley of Colorado. U. S. Dept. Agr. Bul. 932, 119 pp., 7 pls., illus.
(75) SIMMONS, PEREZ, AND ELLINGTON, GEORGE W.
1924. Biology of the Angoumois grain moth. Progress report. *In* Jour. Econ. Ent., vol. 17, pp. 41–45.
(76) SMITH, GEORGE D.
1921. Studies in the biology of the Mexican cotton boll weevil on short-staple upland, long-staple upland, and sea-island cottons. U. S. Dept. Agr. Bul. 926, 44 pp., 1 pl., illus.
(77) TITSCHACK, E.
1922. Beiträge zu einer Monographie der Kleidermotte, *Tineola bisselliella* Hum. *In* Ztschr. Techn. Biol., vol. 10, pp. 1–168.
(78) TOWNSEND, CHARLES H. T.
1908. A record of results from rearings and dissections of Tachinidae. U. S. Dept. Agr., Bur. Ent. Tech. Ser. 12, pt. 6, pp. 95–118, illus.
(79) TRÄGARDH, IVAR.
1913. On the chemotropism of insects and its significance for economic entomology. *In* Bul. Ent. Research, vol. 4, pp. 113–117.
(80) UVAROV, B–P.
1923. Quelques problèmes de la biologie des sautereiles. *In* Ann. Service des Êpiphyties, vol. 9, no. 2, pp. 84–108.
(81) WARDLE, R. A.
1921. The protection of meat commodities against blowflies. *In* Ann. App. Biol., vol. 8, pp. 1–9.
(82) WHEELER, WILLIAM MORTON.
1922. Social life among the insects, Lecture II. Wasps solitary and social. *In* Sci. Monthly, vol. 15, pp. 68–88.

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