JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 MAY-JUNE, 1914 No. 3

CONSPICUOUS FLOWERS RARELY VISITED BY INSECTS[1]

JOHN H. LOVELL,
Waldoboro, Maine

There are many cultivated flowers adapted to winged pollinators, which are rarely visited by insects although they are of large size and display the most brilliant hues. Among the species enumerated by Plateau as illustrations are the red geranium (*Pelargonium zonale* Willd., hybrid Lepidopterid flowers from Southern Africa), the scarlet sage (*Salvia splendens* Sellow, ornithophilous, from Brazil), the cardinal flower (*Lobelia cardinalis* L., ornithophilous, from North America), and the splendid gaudy flowers of *Passiflora incarnata* L. (probably ornithophilous,[2] from North America).[3] Other neglected flowers employed by Plateau for experimental purposes were *Lilium candidum* L. (hawk-moth flowers), *Passiflora adenophylla* Masters (?), (probably a hybrid), *Œnothera speciosa* Nutt. (hawk-moth flowers), *Pisum sativum* L. (almost invariably self-fertilized, probably introduced from Western Asia into Europe in prehistoric times),[4] *Pelargonium zonale* Willd., *Clematis Jackmanni* Jack. (hybrid pollen flowers), and *Petunia hybrida* Hortul. (hybrid, the South American species are ornithophilous?). That anthophilous birds and insects have played an important part as pollinators in the phylogenetic history of the flowers enumerated, in the

[1] The pollination of green or inconspicuous flowers has been considered by the writer in an earlier paper. *Am. Nat.*, **46**:83–107, 1912.

[2] In Alabama Trelease saw the flowers visited by humming-birds. Knuth, Paul, "*Blütenbiologie*," **3**: 510.

[3] Plateau, F., "Les insectes et la couleur des fleurs," *L'Année Psychologique*, **13**:72.

[4] De Candolle, A., "Origin of Cultivated Plants," p. 329.

lands where they are or were endemic, will not be questioned by any orthodox floroecologist. But manifestly when they are cultivated in widely separated stations, under the most diverse conditions, there is a strong probability that in many localities their normal pollinators will be entirely absent or extremely rare; while the flowers themselves modified both in form and function by artificial selection and hybridization may cease to remain equally attractive, e.g., double flowers may be devoid of both nectar and pollen. On the other hand why should we expect common Hymenoptera and Diptera frequently to visit flowers from which they can not legitimately obtain nectar, and to which they are not beneficial; or why should we look for diurnal insects as common visitors to crepuscular flowers? One of the advantages of reciprocal adaptation between flowers and their pollinators is the exclusion of injurious and useless forms.

But Plateau assumes that all bright-hued flowers, according to the theories of Muller and Knuth, no matter what their manner of pollination, should frequently be visited by diurnal insects. The rarity of insect visitors to many beautiful flowers with very showy colors, he remarks, places the biologists of the school of Hermann Muller in a singularly embarrassing position.[5]

He summarizes his views as follows:

"My observations establish the truth of the fact, well-known though not sufficiently insisted upon, of the existence of many plants with flowers formed on the entomophilous type and presenting large dimensions as well as brilliant colors, which attract almost no diurnal insects.

It follows that the attractive rôle, or, as it is often called, vexillary rôle of the forms and colors of floral envelopes is either nul or of very little importance.

Causes of attraction other than colored surfaces are necessary to bring pollinators to flowers and to lead them to return again after a first visit; they are an odor, which is agreeable to the insects, and a sweet liquid, which permits them to appease their hunger and provide food for their young.[6]

Unfortunately for the general acceptance of Plateau's conclusions, they are not of universal application, but are controverted

[5] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., **2**:5, 1910.

[6] *Loc. cit.*, pp. 51–2.

by the characters of various natural flowers. (The cornflower, (*Centaurea Cyanus* L.), *Gentiana acaulis* L., and several other gentians have conspicuous nectariferous flowers, which are visited by numerous insects although they are devoid of scent. Bees frequently gather pollen from poppy flowers, which are not only nectarless but possess a faint unpleasant odor. From the wind-pollinated, purple flowers of the elm, which are both nectarless and odorless, honey-bees in immense numbers sometimes procure pollen for early brood-rearing; while many other anemophilous species are also valuable to the bee-keeper as sources of pollen.) Nor is it stated that (there are many conspicuous flowers, which are neglected by insects notwithstanding they are strongly odoriferous, as the sweet pea,) *Lilium candidum*, and varieties of *Pelargonium*, which have the entire plant pleasantly scented. Finally, (if a flower is rich in nectar, it may be both inconspicuous and odorless and yet receive numerous visits.) According to Fritz Muller, there is in South Brazil a species of *Trianosperma* which is visited very abundantly all day long by *Apis mellifera* and species of *Melipona*, although the flowers are scentless, greenish and to a great extent hidden by the foliage.[7] It is thus apparent that the visits of insects in large numbers are not dependent on the presence of an agreeable odor.

But, assuming the validity of his conclusion that bright coloration is without significance because certain conspicuous flowers are commonly neglected by insects, (Plateau performed a long series of experiments, in some instances introducing honey and in others odoriferous sweet syrups into neglected flowers with the result that in most cases insects were attracted, often in large numbers.) In his earlier experiments of 1897, he employed only honey diluted with water. When a small quantity of this mixture was placed on the handsome flowers of *Pelargonium zonale*, *Phlox paniculata* and *Anemone japonica*, it was speedily discovered by numerous Diptera and Hymenoptera. Similar results were obtained with greenish or dull-colored flowers. The vexillary organs are, therefore, asserted to be of little or no importance.[8]

Knuth considered these experiments of no value since " they

[7] Müller, H., " Fertilization of Flowers," p. 270.

[8] Plateau, F., "Comment les fleurs attirent les insectes," 3me part., *Bull. de l'Acad. roy. de Belgique*, **33**:27–37, 1897; 4me part., loc. cit., **34**:604–10, 1897.

only prove that the odor of honey exercises a great power of attraction which has long been known. It is only necessary to place honey anywhere to secure the immediate appearance of numerous insects which are fond of it."[9] To this criticism, Plateau replied:

" Quelle pauvre argumentation! Knuth ne s'aperçoit pas qu'il me donne pleinement raison. En effet, s'il a suffi de l'introduction d'un peu de miel dans des fleurs habituellement négligées pour y amener les Insectes, c'est que l'éclat des corolles ne compte guère et que le perfum de la substance que ces animaux recherchent avidement a constitué seul l'excitant déterminant leurs actes. J'avais donc démontré ce que je voulais démontrer."[10]

Plateau's conclusion that certain conspicuous flowers, which are devoid of nectar and pollen, ~~or nearly so~~, are neglected because insects fail to notice their colors, ~~it is believed~~, can readily be shown to be fallacious. The flowers are neglected not because they escape attention, but because ~~anthophilous~~ insects have learned from experience their inability to procure food materials from them. They do not neglect them entirely, but visit them occasionally,[11] although they do not often repeat their futile visits since " memory appears to replace both odor and color as the directive stimulus of first importance."[12] In his experiments with odoriferous essences, that is, odors without a sweet syrup, Plateau recognized the fact that if they are employed alone a Hymenopteron or Dipteron entering the corolla and finding nothing will not return again.[13] This statement is

[9] Knuth, Paul, " Handbook of Flower Pollination," translated by J. Ainsworth Davis, **1**:206.

[10] Plateau, F., " Recherches expérimentales sur les fleurs entomophiles," etc., p. 8.

[11] This statement will be supported later by a large number of observations.

[12] Coulter, Barnes and Cowles, " Textbook of Botany," 2 (Ecology by H. C. Cowles) :850. On the memory of honey-bees cf. Forel, A., "Ants and Some Other Insects," translated by W. M. Wheeler, p. 28; and on the memory of place in bees cf. Buttel-Reepen, H. V., "Are Bees Reflex Machines," translated by M. H. Geisler, pp. 19–39. In the autumn of 1912 I placed a dish containing fragments of comb honey in a secluded spot nearly surrounded by a steep bank and willow bushes. A few bees were brought to the honey and it was soon visited by a large number. After they had been fed several times the dish was removed and everything left as at first. Two weeks later I examined the place but failed to discover a single bee. The weather was, moreover, growing colder and they were no longer flying freely. I now placed on the same spot as previously another dish of comb honey; and two hours afterwards I found it swarming with bees. During two weeks they had evidently kept this locality under constant surveillance, inspecting it from time to time, although there was nothing to attract their attention.

[13] Plateau, F., " Recherches expérimentales," etc., p. 10.

equally applicable to color. Neither color nor odor separately or together will attract insects continuously, if they can obtain no spoil.

Plateau was equally mistaken in supposing that the addition of an agreeable odor is indispensable; for it is only necessary to introduce a solution of sugar and water, which is odorless, to bring insects to the flowers in great numbers, as will be shown experimentally. In the absence of accessible food materials pleasantly scented flowers will not be visited more frequently than would be the case if they possessed only bright coloration. Insects will not repeatedly visit an inflorescence because they experience an aesthetic pleasure. This is well shown by *Lathyrus odoratus* L., or the sweet pea, which, notwithstanding its strong fragrance and brilliant hues, is very rarely sought by insects, because the nectar is inaccessible to nearly all of them. An ample, available food supply will alone secure continued and frequent visits of insects to flowers. Since it can be shown, therefore, that an inflorescence can be rendered very attractive to insects without the addition of an odor, it logically follows from Plateau's own method of reasoning that conspicuousness is beneficial.

When Plateau introduced honey into certain selected flowers, they received two allurements, an agreeable odor and a sweet liquid food, which sharply distinguished them from the flowers left in their natural state. In effect, the flowers containing honey became distinct physiological varieties. Color and odor were not brought, therefore, into competition on equal terms; the flowers in their natural state possessed only color and form, while those into which honey was introduced possessed color, form, an agreeable odor and a liquid food. Manifestly, the latter flowers were given the greater advantage, and it is unfair to conclude that because they received the greater number of visits, odor was essential and color was of no significance. Throughout Plateau's experiments, the presence of the vexillary organs was a source of error. As he had assumed that they were of no value, it is difficult to understand why he did not remove the floral envelopes, when the flowers would of necessity have been compelled to depend wholly on the odoriferous liquid food. Finally, to have made the competition impartial, an odor-

less syrup should have been introduced into the empty flowers. The experiments were, therefore, not well adapted for the purpose intended and the results obtained, as interpreted by Plateau, are misleading.

In another series of experiments, Plateau unsuccessfully attempted to draw insects to flowers by means of the odoriferous essences of lavender, thyme, sage, and mint. "The Labiatae are habitually much visited by bees and I hoped in giving the preference to essences extracted from these plants to see bees and allied insects drawn to the flowers." Essences of orange and bergamot were also employed. But the attraction proved very small or non-existent. Certain essences as thyme and sage were feebly attractive, while mint was even repellent.[14]

Knuth makes the following comment: "From these experiments it follows that solutions of odoriferous plant extracts, which ought to attract insects, do not do so."[15] Plateau subsequently attributed the failure of the flowers to attract insects to the too violent and medicinal odors of the extracts employed; they never possessed the delicate perfume of the plants from which they were extracted. In a new series of experiments undertaken in the spring and summer months of the years 1907-9, instead of odoriferous essences, odoriferous liquid foods, which it had been previously ascertained were attractive to insects, were introduced into neglected flowers. The sweet liquids employed were anisette[16] (essence of anise, syrup of sugar and diluted alcohol), the cooked juice of cherries, syrup of cassonade[17] (syrup of brown sugar to which a few drops of rum had been added), and syrup of Angelica[18] (syrup of cane sugar flavored with a strong aromatic essence obtained from the petioles of *Angelica officinalis*). Fifty-five experiments were performed with these syrups, but descriptions of only a part of them were published, those being selected

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[14] Plateau, F., "Comment les fleurs attirent les insectes," 5me part., *Bull. de l'Acad. roy. de Belgique*, **34**:872–5, 1897.

[15] Knuth, P., "Handbook of Flower Pollination," **1**:207.

[16] A bee-keeper in California reported that he found essence of anise very useful in attracting swarms of bees to empty hives, while another bee-keeper in Ohio did not find it of much value. Gleanings in Bee Culture, **40**:482.

[17] This is somewhat similar to the mixture used in "sugaring" for moths. *Psyche*, **19**:195.

[18] The tender stalks are preserved in sugar and sold as a confectionery.

which most strongly sustained his views, while a few particulars were given in regard to his other experiences.[1]

There will be described in the present paper a few of the more interesting experiments performed by Plateau on relatively large and brilliantly colored flowers seldom visited by insects, following which will be given the observations of the writer on similar flowers. Among the familiar species selected by Plateau was a purple-flowered variety of *Clematis Jackmanni* Jack., a hardy perennial vine widely cultivated both in Europe and America. The flowers are nectarless, but bees obtain from them a small amount of pollen. A vine of *C. Jackmanni superba* is described by Plateau as covering a wall three meters in height and displaying many hundred magnificent blue-violet flowers, which are said to have been wholly ignored by insects. On a very warm clear day anisette was introduced into eleven flowers, near each other, and constituting a group by themselves. In the hour following, they were visited by fourteen bumblebees and six flies belonging to the family Syrphidae. In four instances bumblebees examined adjacent flowers which remained in their natural condition.

The facts related by Plateau are not called in question; but it should be noted again that the ungarnished flowers possessed only conspicuousness and pollen, while the eleven flowers containing anisette possessed conspicuousness, pollen, an agreeable odor and a sweet liquid; evidently color was not here brought directly into competition with odor. Let us now endeavor to determine whether the purple flowers are as completely neglected by insects as Plateau supposed; and whether insects can not be induced to visit them in large numbers without the addition of an agreeable odor! The purple-flowered *Clematis* on which my observations were made was a small vine bearing only eleven flowers wholly or partially expanded. The flowers were of large size, pale purple, nectarless, and odorless. As regards brilliancy of coloring and number, they were at a great disadvantage compared with the inflorescence described by Plateau. They were very frequently examined during the entire period of blooming.

[1] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., 2:1–55, 1910.

On June 11, 1912, a warm clear day, a honey-bee was observed at 12:35 p. m., gathering pollen, also a wild bee which flew away so quickly that it could not be determined. The honey-bee visited four or five flowers before returning to the hive. A few minutes later a second and third honey-bee came for pollen; and during the succeeding hour one or two workers were constantly visiting the flowers for this purpose. One of them remained for a long time, and the loads of purple pollen in the pollen-baskets were plainly visible. Two females of *Halictus craterus* came for pollen. A bumblebee inspected the flowers, but did not alight. A small undetermined bee flew from flower to flower apparently looking for pollen. At 1:35 p. m., there were no insects on the flowers; but a little later a small species of *Halictus*, and also a female of the larger *Halictus craterus* arrived and removed all the pollen remaining available. On three other occasions a female *Halictus craterus* was seen collecting pollen, which in one instance colored purple the under side of the abdomen and the brushes on the posterior legs. No attempt was made to capture any of the bees since this would have lessened the normal number of visits.

The nectarless flowers of *Clematis* were not, therefore, entirely neglected by insects; but were visited by a number of bees sufficiently large to remove all the pollen they produced, and to have effectively pollinated the stigmas had they been in a normally receptive condition, and as this is all that is required, additional visits would have been of no advantage. The sterility of the flowers is not thus due to the absence of pollen-carriers as Plateau supposed. The flowers should be examined immediately after anthesis before the pollen has been removed; since Plateau makes no mention of the pollen he probably did not observe whether it was removed or not.[20] I inspected the flowers many times without finding any insects, and it is easy to understand how a casual observer might gain the impression that they were entirely neglected. Plateau's failure to discover insects on the flowers in their natural condition may have been partly due to an insufficient number of observations, partly to location, and partly to the absence of suitable species of bees. Bumblebees are not well adapted for gathering the scanty supply of pollen, and prob-

[20] Cowles has suggested that Plateau failed to see the earlier visits of his insects, Cowles, H. C., "Insects and Flower Colors," *Bot. Gaz.*, **39**:70, 1905.

ably seldom make the attempt. After the pollen has been entirely removed there is, of course, no reason why bees should continue their visits. In an earlier paper I have shown that flowers frequently visited by bees were almost entirely deserted when the corollas were removed; there is, therefore, good reason to believe that the purple sepals of *Clematis* attract the attention of insects.

I next proceeded to place on a few flowers an odorless sweet liquid for the purpose of ascertaining whether they would not be visited by bees in large numbers. White granulated sugar dissolved in equal parts of water yields an odorless and colorless syrup, as is admitted by Plateau.[11] June 16 and 17 were cloudy, rainy days, but the 18th was fair. At 8 o'clock a. m., a small quantity of syrup of sugar was placed on three flowers. No visitors were observed until 9:15, when two females of *Halictus craterus* began feeding on the syrup; five minutes later there was a honey-bee at the syrup and a female of *Halictus craterus* gathering pollen. Sugar syrup was now placed on a fourth flower. At 10:00 o'clock there were three honey-bees and one female *H. craterus* feeding on the syrup, a second female *H. craterus* on a flower without syrup, and a third hovering in the air. Ten minutes later a honey-bee left a flower on which there was syrup and flew to two empty flowers; but, after carefully examining their centers and finding nothing, it returned to the flower on which it had previously been at work. The bees were compelled to learn by experience which flowers contained syrup and which did not. I replenished the supply of syrup from time to time as it was consumed, and at 12:15 p. m., there were seven honey-bees sucking on the flowers. On the morning of June 19 I again put syrup of sugar on the flowers, and presently three or four bees were at work. It seemed needless to continue the experiment further, for the bees came from my apiary and it was only a question of time and of supplying the syrup in sufficient quantity to have attracted them in great numbers. During the latter part of this experiment there were eighteen flowers in bloom. Plateau's assumption that the flowers would not be visited unless they were given an agreeable odor was shown to be wholly erroneous; the addition of an odorless sweet liquid secured the visits of insects in far greater numbers than were observed by him.

[11] Plateau, F., "Recherches expérimentales," etc., p. 19.

Another common flower selected by Plateau for experiment was the edible garden pea, *Pisum sativum* L. The flowers are rarely pollinated by insects, and self-fertilization is almost invariable. It was for this reason selected by Mendel for his celebrated experiments in hybridization. He says: "Among more than 10,000 plants which were carefully examined there were very few cases where an indubitable false impregnation had occurred." [22] During four summers, however, Müller frequently saw the flowers visited by both sexes of *Megachile pyrina*, and the females both sucked nectar and collected pollen.[23] Plateau's observations were confined to walking on two occasions through many cultivated fields of peas, in one of which he saw a single *Bombus agrorum*.

Plateau introduced anisette into a dozen, or, on one day, two dozen flowers of *Pisum sativum* growing in his garden, which were carefully observed for from one to three hours on five days. The anisette was renewed each day. Twenty visits were made by species of *Bombus* and *Megachile*; and ten visits by flies and small bees which could not possibly effect pollination. Plateau attributed the small number of insects attracted by the odoriferous liquid food to frequent interruptions by rain.

The flowers of the common garden pea are rarely visited by insects, not because they are nearly odorless and the coloration is of no value, but because of the difficulty of depressing the carina. This species no longer exists in the wild state; and, according to De Candolle, was probably introduced into Europe from Western Asia.[24] Muller says: "In its original home the pea no doubt adapted itself to some strong and at the same time diligent and skillful species of bee, which could easily depress the carina, and was plentiful enough in ordinary weather to act as the regular fertilizing agent. Under such conditions, the advantages of firm closure would outweigh the disadvantages. In our climate the pea fails to find bees adapted to its flowers, and it would be much better for it under these altered conditions to have its flowers less firmly shut." [25]

During the summer of 1912, I saw the flowers of the garden

[22] Bateson, W., "Mendel's Principles of Heredity," p. 342. Bateson is of the opinion that Thrips may be a source of error.
[23] Müller, H., "Fertilization of Flowers," p. 214.
[24] De Candolle, A., "Origin of Cultivated Plants," p. 329.
[25] "Fertilization of Flowers," p. 214.

pea visited a few times by females of *Bombus fervidus* only; but in other seasons I have occasionally observed honey-bees endeavoring to find nectar in the flowers. The visits of the bumblebees were made in the legitimate way, but I was unable to approach near enough to determine whether the carina was actually depressed or not. In each instance, the bee visited only three or four flowers, probably because it experienced difficulty in obtaining the nectar which was not abundant.

In this connection, it is a matter of surprise that Plateau passes over the flowers of the sweet pea, *Lathyrus odoratus* L., without mention. This species belongs to the same family as the garden pea, to which it is closely allied in form and structure, though differing in details. Although the blossoms have a strong and pleasant odor suggestive of honey in addition to the most brilliant hues, it is yet more sparingly visited by insects than the garden pea. According to Plateau, the nearly scentless flowers of the garden pea require an agreeable odor to attract insects; but the fragrance of the sweet pea, which is so pleasing that any effort to improve it would be as futile as the proverbial attempt to paint the lily, does not give the inflorescence any permanent advantage over that of the garden pea. If the absence of insects from the garden pea shows that the influence of its coloration is of no significance, then it may be inquired does not the absence of insects from the sweet pea prove that both color and odor are of no importance? Bees neglect to visit the sweet pea frequently not because these two allurements are of no benefit, but because they have learned from experience that they can not obtain nectar. To attract numerous visits, both the garden pea and the sweet pea require an available food supply.

Place a honey-bee on one of the wings of the sweet pea, and it is at once apparent that it is neither large enough nor strong enough to depress the carina. Repeated examinations of the flowers continued through several weeks of the summer of 1912 failed to reveal a single visit by any species of bee. But by September 22, the autumnal honey-flow from the golden-rods was over, and the honey-bees were at liberty to give more attention to the few other flowers still remaining in bloom. On this date I repeatedly saw honey-bees alight and examine the flowers of the sweet pea, but they made no attempt to depress the keel. One probed diligently between a wing petal and the

keel, while another sought for nectar under the calyx lobes, at one time standing on the back of the standard. None of their efforts proved effectual.

Neither can any of our Maine bumblebees depress the carina. On September 26 I saw a female *Bombus fervidus* visit illegitimately twenty flowers in succession. Standing sideways on the flower, clinging to one of the wings and the calyx, she inserted her tongue in a crevice between the standard and a wing petal. Subsequently she robbed many other flowers of their nectar in the same way. The nectar was also obtained in a similar manner by a worker of *Bombus consimilis.**

Until the summer of 1912 I did not suppose that any of our indigenous bees could properly pollinate the flowers; but on August 17 and September 15 and 22, a female leaf-cutting bee, *Megachile latimanus*, was observed to visit the flowers legitimately. She manifested so little fear that I was able to watch her movements at close range. The stigma protruded for a long distance, touching the abdominal scopa on one side and on the other the brush of hairs on the tibia of the posterior leg. Both brushes were thickly covered with pollen. In England, also, according to Punnett, a species of *Megachile* is able to depress the carina.[28] Muller saw only *Anthidium manicatum* sucking on the flowers.

Neither color alone in the garden pea nor color and odor combined in the sweet pea will induce frequent visits, if nothing is to be gained thereby; but, if an odorless sweet syrup is placed on the flowers, bees will resort to them in large numbers. On the morning of August 16 I placed syrup of sugar on a number of sweet pea blossoms. Three times during the afternoon I found a worker of *Bombus consimilis* feeding on the syrup—probably the same bee in each instance. On the 17th I renewed the supply of syrup, and at about 12:30 p. m., a honey-bee discovered it; an hour later there was three honey-bees. Before the close of the afternoon, four honey-bees and two bumblebees were sucking the syrup, or flying about the flowers to which it

*_Bombus consimilis_ Cr. is doubtless correctly regarded as a synonym of _B. vagans_ Sm., but as the local specimens agree exactly with a set of the three forms of _B. consimilis_ obtained from the Ac. Nat. Sci Phil. the name has been permitted to stand in this paper.

[28] Punnett, R. C., "Mendelism," p. 188.

adhered in small drops. It is evident that they must have occasionally inspected the blossoms, or they would not have discovered the colorless and odorless liquid. By frequently replenishing the syrup, an indefinite number of bees might have been attracted. There was sugar syrup on about ten flower clusters. An available and abundant food supply is required, therefore, to secure numerous and continued visits.

Let us now inquire whether similar results can not be obtained in the case of the garden pea, *Pisum sativum*. On a clear and moderately warm morning (July 31, 1913), at 8:00 o'clock, about forty flowers of this species were dipped in sugar syrup, a few, small drops of the thin, colorless and odorless solution adhering to each corolla. The garden was in a secluded location, which had not been planted previously for many years, and was nearly surrounded on two sides by a tall cedar hedge. During the half hour following, a honey-bee inspected the flowers on another row of peas, but failed to find the flowers garnished with sugar syrup. At 8:40 a. m., a white-banded wasp, *Vespa consobrina* Sauss, was also seen examining the flowers on another row of peas, and presently, more fortunate than the bee, it came to the flowers on which there was sugar syrup. For the larger part of the day this wasp, and a little later a second wasp of the same species, worked diligently gathering the sweet liquid. I recorded many of their visits, but it would be tedious to relate them in detail.

At 9:10 a. m., a honey-bee was observed inspecting ungarnished flowers of the garden pea; it alighted on the carina and then sought unsuccessfully to reach the nectar through the side of the flower. Ten minutes later a honey-bee discovered the flowers with syrup, and subsequently it continued to return to them at intervals until 10:20 a. m., when I closed the experiment. It met with many disappointments as it often examined ungarnished flowers. The pea blossoms were also visited by a yellow-banded wasp, *Vespa germanica* Fab. At 4:00 p. m., I found both species of *Vespa* still resorting to the flowers.

On August 2, a hot, clear day, at 12:30 p. m., forty flowers of the garden pea were supplied with sugar syrup, which was almost immediately found by a honey-bee and a *Vespa consobrina*. At 12:45, a second honey-bee and a *Vespa germanica* came to

the flowers. In another part of the garden a female *Megachile melanophaea* (one of the larger leaf-cutting bees), was observed to visit ungarnished flowers in the normal way. At 1:15 o'clock there were two honey-bees, two *Vespa consobrina* and the small pale blue butterfly, *Lycaena pseudargiolus*, sucking syrup from the flowers; and fifteen minutes later one honey-bee, two *V. consobrina* and two *V. germanica*. The visits continued until 2:45 p. m., when I closed the experiment.

The number of visits by bees and wasps received by the flowers of the garden pea garnished with sugar syrup, during the time they were under observation, was much greater than I had expected. Under the conditions I should not have been surprised had there been no visits by Hymenoptera. On the night preceding August 2 there had been much rain, and the following morning was very foggy, so that the leaves of the pea vines at noon were covered with small drops of water, which could not be distinguished from drops of sugar syrup. The bees made many fruitless visits to flowers without syrup and also to flowers on the wrong row. But both bees and wasps soon learned to confine their attention chiefly to the end of the row with garnished flowers.

There were many small Syrphid flies, as well as larger flies, flitting about among the foliage of the pea vines. Although they not infrequently came to the flowers on which there was sugar syrup, but little importance was attached to their visits, as evidently they might be largely the result of chance. One or two smaller bees belonging to the genera *Sphecodes* and *Prosopis* were also among the visitors. But the larger aculeate Hymenoptera, whose visits are manifestly purposive, were regarded as much better adapted for observation than small, little specialized insects. It was conclusively shown that an available food supply, without the addition of an agreeable odor, would induce numerous visits of honey-bees and social wasps to the odorless flowers of *Pisum sativum*.

The many horticultural varieties, known under the name of *Petunia hybrida* and cultivated in all gardens, have resulted, as is well understood, from crossings between *P. nyctaginiflora* Juss. and *P. violacea* Lindl. They offer this very interesting peculiarity, from the point of view of the present work, of receiving no visits from the domestic bee, notwithstanding the brilliancy and dimensions of their beautiful, infundibuliform, white,

rose, violet, or purple flowers."[2] Plateau, however, observed visits by many bumblebees, and species of Diptera belonging to the genera *Eristalis* and *Syrphus*.

Plateau employed in his first experience a large group of Petunias, surrounded by other plants, as *Tagetes patula* and *Scabiosa atropurpurea*, attractive to bumblebees, flies and butterflies; while among the Petunias there was a single stalk of *Borago officinalis* which alone was visited by honey-bees. On a clear but cool August morning, at 9:30 o'clock, he introduced the odoriferous juice of cooked cherries into six flowers near the stalk of borage. At 3:30 p. m., of the same day, the honey-bees discovered the cherry juice and entirely abandoned the borage flowers for the Petunias. During an hour there were fourteen arrivals, each individual visiting many of the garnished flowers, and rarely a few of the empty flowers. Essentially similar results were obtained in Plateau's other observations on Petunias.

The two common species of *Petunia* endemic to South America have long narrow tubes, are strongly scented in the evening, and are either adapted to crepuscular Lepidoptera or are ornithophilous; in either case we should not expect to find honey-bees among their legitimate pollinators. The hybrid forms of cultivation, moreover, are destitute of nectar; and even if it were present the throat of the corolla is so obstructed by the filaments and style that it would be inaccessible to them. Plateau asserted that an odoriferous syrup was required to attract visits by honey-bees, but it can readily be shown that the presence of an odorless, sweet liquid will render their visits very numerous. A medium sized group of single-flowered Petunias of various colors was selected for my observations.

On July 31, 1913, there were only two flowers in bloom, into both of which I introduced sugar syrup. A bumblebee inspected both flowers but overlooked the syrup. On the 2nd there were two fully expanded flowers, and one which had wilted and closed. A honey-bee examined all three, and remained a long time in one of the open flowers. As the sugar syrup had evaporated, the supply was renewed. The honey-bee returned and thirty minutes later was still visiting the flowers. On the following day a female *Bombus consimilis* was a visitor.

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[2] Plateau, F., "Recherches expérimentales, etc." *Mem. de l'Acad. roy. de Belgique*, 2me sér., 2:46, 1910.

On August 10, I introduced sugar syrup into nearly all the expanded flowers. *Vespa consobrina* was a constant visitor throughout the day, and subsequently *Vespa germanica* was also observed on the inflorescence.[23] At 2:30 p. m., a honey-bee appeared and continued its visits for half an hour. The day following was very cold and windy for mid-summer; but the 12th was clear and warm. At 9:05 a. m., I introduced sugar syrup into the expanded flowers. A honey-bee was soon at work, and by 11:00 o'clock the number had increased to three; at 12:45, there were four honey-bees and a *V. consobrina*; at 2:35 there were five honey-bees and a *V. consobrina*; and at 6:00 p. m., the wasp and six honey-bees. The number of flowers in bloom was about thirty-five. The weather continued fair on the 13th, and in the morning I found four honey-bees on the flowers. A new supply of sugar syrup was provided, and by 9:10 a. m., there were twelve honey-bees at work. Manifestly, it was needless to continue the experiment further. Thus, without the addition of an agreeable odor, but merely by introducing a supply of an odorless, colorless syrup the visits of honey-bees were induced in great numbers.

Although sugar syrup was not again introduced into the flowers, on August 14, 15 and 16 I saw honey-bees examining the inflorescence, doubtless remembering their former experience. On September 2, a honey-bee alighted on two flowers and examined others; by this time most, if not all, of the flowers into which syrup had been introduced had wilted. Bumblebees were also seen to visit the flowers occasionally, but not finding nectar, they did not remain long. There were many small Diptera flying about the foliage of the Petunias, but little or no significance was attached to their visits. A small bee of the genus *Halictus* also alighted on the corollas.

Pelargonium zonale Willd., says Plateau, is one of the more noteworthy forms of plants with very brilliant flowers which are almost wholly ignored by insects; the beds of scarlet Pelargoniums, commonly called red geraniums, of which there are a profusion in public gardens, permit us to establish this fact each year. A large bed of *Pelargonium zonale* displayed more than fifty umbels of scarlet flowers; into three umbels on the left side

[23] For the determination of the specific names of these wasps I am indebted to Mr. S. A. Rohwer.

of the bed Plateau introduced the cooked juice of cherries, and in two umbels on the right side anisette was used. Immediately many flies belonging to the families Muscidae and Sarcophagidae, and later two Syrphidae and three wasps were attracted to the odoriferous liquids. The clusters which remained in their natural state are said not to have received a single visit.

A large plant of *Pelargonium zonale*, of the variety called " General Grant," produced in my garden during the larger part of the summer of 1912 numerous bright scarlet umbels. The nectaries had disappeared and the stamens were largely petaloid so that the flowers yielded neither nectar nor pollen; notwithstanding frequent inspections no insect visits were observed during the larger part of the season. On September 23, at 1:00 p. m., odorless sugar syrup was introduced into two umbels near the center of the plant. From the 23rd to the 26th, no insects found the syrup, which was renewed from time to time as it evaporated. The 26th was warm and clear, and in the afternoon I saw a honey-bee inspect a cluster of flowers near the ground, but it did not alight. The weather continued fair on the 27th, and at 7:00 a. m., there were no insects on the flowers; but at 9:00 o'clock there were, at least, a dozen honey-bees feeding on the syrup, which was speedily consumed. There were six other fully expanded umbels on which there was no syrup, and it was interesting to note how the bees searched them again and again in their efforts to find more of the edible liquid. Two other umbels with a few buds partially open were also carefully examined. Their attention at first was entirely confined to the gaudy flowers, but later they discovered some of the liquid, which had dripped on a few leaves, and removed it. Their number continued to increase so long as I supplied the syrup. Later they flew to a bed of *Portulaca grandiflora* Lindl., to the inflorescence of which they had never before been seen to pay any attention, and inspected flower after flower but seldom alighted.[29]

Evidently the bees had learned from past experience to associate the presence of nectar with conspicuousness, and though they had never found any food in these particular flowers, they had no doubt continued to occasionally inspect them, as in the

[29] During a part of the time this experiment was in progress one of the colonies in my apiary was allowed to remove the honey from a few partially filled combs; and it subsequently occurred to me that this probably stimulated the bees to search the flowers more diligently for nectar.

single instance observed on the 26th, when a bee inspected an empty umbel but failed to visit those containing syrup. After they had found syrup on two of the umbels, they examined all the others very thoroughly, and also other flowers in the garden previously neglected. They discovered the syrup on the flowers long before they did that which had dripped on a few leaves, and the discovery of the latter was incidental to their visits to the flowers. The bright coloration was clearly an advantage in this instance in enabling honey-bees in large numbers to find the odorless sweet syrup. Obviously highly specialized bees are much better adapted for the purpose of such an experiment than the common flesh-flies observed by Plateau.

Plateau made many additional experiments in the course of which he introduced odoriferous syrups into the flowers of *Lilium candidum* L., *Passiflora adenophylla* Masters, *Œnothera speciosa* Nuttal, *Linum perenne* L., and *Convolvulus sepium* L., with the result that insects in variety were attracted. But it is unnecessary to consider his experiences further since insects in large numbers may also be attracted to conspicuous, neglected flowers by means of an odorless sweet liquid. Since Plateau knew that sugar syrup was odorless it is natural to inquire why he failed to employ it in control experiments. On four occasions he did introduce syrup of sugar into the flowers of *Lilium candidum*, in three instances into two flowers and in one instance into six flowers. He says that, as he foresaw, syrup of sugar without odor did not show any power of attraction.[10] But a small number of Diptera, as *Syritta pipiens*, *Melanophora roralis*, *Anthomyia radicum* and *Calliphora erythrocephala*, did find the syrup and profit by their discovery. No information is given as to the length of time the flowers were under observation. The number of visits received, however, was about the same as in the case of *Polygonum Convolvulus*, when anisette was added to eight groups of flowers on a very warm clear day. Certainly the list of Diptera recorded gave promise that many visits would have been received had the supply of syrup been continued for a longer period. *Lilium candidum* is a campanulate flower two or three inches long adapted to pollination by hawk-moths, and it is easy to understand that some time might elapse before the deeply concealed syrup was found by Hymenoptera. No

[10] " Recherches expérimentales sur les fleurs entomophiles," etc., p. 19.

mention is made of the use of sugar syrup in any other control experiments, an omission which can hardly be regarded as excusable.

It seems desirable, therefore, in this connection to give a few additional instances observed by myself, where the introduction of sugar syrup resulted in frequent visits of bees. A group of *Zinnia elegans* Jacq., in my garden, was almost wholly neglected by insects. On the morning of August 16, I introduced syrup of sugar into several capitula, renewing the supply the following day. During the forenoon of the 17th, a honey-bee examined the ray flowers of two ungarnished capitula, and then, coming to a head, containing syrup, sucked for a short time. Later a worker of *Bombus consimilis* found the syrup. At 12:30 p. m., there were on the flowers two honey-bees and two worker bumblebees, *Bombus consimilis* and *B. terricola*. At 3:30 p. m., there were seven honey-bees and one bumblebee on the flowers—there was syrup in a dozen capitula. The honey-bees also examined the capitula which remained in their natural condition. The experiment was now discontinued. Three days later, on August 20, a honey-bee, undoubtedly one of the former visitors, examined many capitula; evidently it remembered its previous experience.

The brilliantly colored flowers of the scarlet runner, *Phaseolus multiflorus* Willd. var. *coccineus* Lam., contain nectar; but owing to the difficulty of depressing the carina, are much neglected by insects. Occasionally in this locality females of *Bombus fervidus* visit the flowers legitimately. I have also seen a honey-bee for several hours fly from flower to flower inserting its tongue in the opening beneath the standard, and apparently able to reach a very small quantity of the nectar. On the morning of August 16, I put sugar syrup on a few corollas, and during the afternoon there were always from four to six bees on the flowers. They also inspected flowers on which there was no syrup. On the 17th, I renewed the supply of syrup and the bees continued their visits during the entire day.

Honey-bees have not sufficient strength to depress the carina and obtain the nectar normally; but if the nectaries are punctured they will then visit the flowers in great numbers. Every year the scarlet runner is under cultivation in my garden, but I have never known bumblebees to bite holes in the flowers except

in 1908. On August 14 of that year, the vines were in full bloom, and there were present many workers of *Bombus terricola*, which perforated the flowers as fast as they matured—so far as I could discover not a single blossom escaped. The holes were all on the under side of the calyx on the left hand side, which may be explained by the fact (also observed by Müller[31]) that the more powerful bees almost invariably alight on the left ala. The honey-bees promptly discovered the holes and used them most diligently for extracting the nectar. There was no pretence on the part of either honey-bees or bumblebees of making normal visits. The absence of bees from the flowers of the scarlet runner does not, therefore, prove that their brilliant hue is of no advantage, or that an agreeable odor is required, for it is only necessary to render the nectar easily accessible by punctures to induce the visits of bumblebees and honey-bees in great numbers.

The correlation existing between the accessibility of nectar and the number of honey-bees present is also most instructively shown by the inflorescence of red clover, *Trifolium pratense* L. The flowers are pollinated chiefly by bumblebees, which are frequent visitors, and in their absence are largely sterile. An historical illustration is the well-known experience of the agriculturists of New Zealand, in which country at the time of its discovery there were neither honey-bees nor bumblebees. In consequence the yield of seed did not become commercially profitable until in 1855, when about one hundred bumblebees were imported from Europe.[32]

The nectar of red clover is secreted at the base of a tube a little over 9 mm. in length, where it is beyond the reach of the tongue of the honey-bee. This has occasioned much regret among bee-keepers, for the flowers not only secrete nectar very freely but the quantity is not greatly affected by weather conditions. Repeated attempts have been made to develop a strain of red clover bees, but the gain in tongue length has invariably

[31] Müller, H., "Fertilization of Flowers," p. 216. Both honey-bees and bumblebees almost invariably alight on the left ala. The reason for this is that the spirally coiled carina closes the entrance beneath the standard on the right hand side. Usually the alae stand apart, but when one occasionally overlaps the other, honey-bees alight on the center. Bumblebees visit the flowers of the common, garden bush beans in a similar manner.

[32] Knuth, P., "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, **2**:292. Jarvis, P. D., "Bumblebees that Fertilize Red Clover," *Rep. Ent. Soc. Ont.*, **36**:128. Graenicher, S., "New Zealand's Experience with the Red Clover and Bumblebees," *Bull. Wis. Nat. Hist. Soc.*, **8**:166.

proved only temporary. Under normal conditions, then, honey-bees do not frequently resort to the red clover fields; but occasionally in very dry weather the floral tubes become so short that large yields of honey are obtained. Two or three times during the last thirty years at Borodino, N. Y., red clover has been a very valuable source of honey; and one season fully sixty pounds, on an average, to a colony was secured.[33] An apiarist in Michigan reports that in one year his bees stored 500 pounds of pure red clover honey as surplus.[34] The black bees stored none, the hybrids only a little, while the bulk of the 500 pounds was gathered by Italian bees. The length of the tongue of the common black bee is 6 mm., of the pure Italians, not over 7 mm., while that of the hybrids is intermediate. Thus there was presented the singular spectacle of fields of red clover visited by thousands of Italian bees, while the black bees were absent. Had the drought shortened the corolla tubes another millimeter the nectar would have been accessible to black bees, and they, too, would have been present.

But undoubtedly the most remarkable illustration ever recorded of the relation of rainfall to the length of the corolla-tubes, and consequently of the accessibility of the nectar to honey-bees, was observed by an apiarist at Medina, Ohio. Of two apiaries belonging to him one is located near Medina, and the other two miles north of that city. A few years ago (1906) there was a drouth at the north bee-yard, and the floral tubes of the red clover were so much shorter than usual that honey-bees were able to reach the nectar. When one of the farmers began to cut his field of red clover that season, the cutter knives of the mower stirred up so many bees that they attacked the horses and their driver. So numerous and pugnacious were they that it looked as though they would prevent anyone from cutting off their supply of honey.

Singularly enough at Medina and the south bee-yard, there was an abundance of rain. Here, when he went over a big field covered with a luxuriant growth of red clover scarcely a bee could be found. The corolla-tubes were so long that the bees could not obtain the nectar, and consequently, there were none on the clover heads. Thus two bee-keepers, living only a few

[33] Doolittle, G. M., " Honey from Red Clover," *Gleanings in Bee Culture*, **34**:993.
[34] Hutchinson, W. Z., " Red Clover," *The Bee-Keepers' Review*, **21**:342.

miles apart, might have arrived at diametrically opposite conclusions as to the value of red clover as a honey plant.[35]

It is clear that the presence or absence of honey-bees in large numbers on the flowers of red clover is not determined by the color or odor, but by the accessibility or inaccessibility of the nectar. Drouth may not render the nectar accessible more than once in ten years, but when it does happen, the bees promptly avail themselves of the opportunity. Evidently they must inspect the flowers each season, but, finding no booty, they do not often repeat their visits. The utter inconsistency with the facts of the claim that the absence of insects from certain conspicuous flowers proves that bright coloration is of no advantage and that an agreeable odor is a necessity, could not be better shown than in the instance where the Italian bees were able to obtain the nectar and the black bees were not.

The flowers of alfalfa, *Medicago sativa* L., a leguminous plant very extensively cultivated in the west for forage, offers very similar phenomena. In the irrigated regions of California and Colorado, nectar is yielded so abundantly that alfalfa surpasses all the other local honey plants in importance, even the famous purple, black and white sages of the former state. But in Kansas, for example, the results are strikingly different. In the Western part of the state along the river bottoms the flowers can usually be depended on for nectar during most of the season, while around Topeka, bees only occasionally visit the bloom. A bee-keeper who has lived in Eastern Kansas for thirty-five years states he has never seen a bee on the flowers, or known of a pound of alfalfa honey being produced in that section.[36] Where alfalfa, then, secretes nectar freely the vast acreage is constantly the resort of millions of bees; but in localities where it is nectarless,

[35] Root, E. R., "Red Clover as a Honey Plant," *Gleanings in Bee Culture*, **34**: 990. The three apiarists cited in this article are careful observers and recognized authorities on bee-culture. Buttel-Reepen has remarked: "It seems to me that the biological knowledge concerning *Apis mellifica* which has been gained by practical bee-keeping has scarcely entered scientific literature . . . In proof of this there are the vague, defective assertions which are found in the newest editions of scientific works." "Are Bees Reflex Machines," p. 1.

[36] Root, E. R., "Bee-keeping in the Semi-arid Regions of Oklahoma, Kansas and Nebraska," **41**:345. In the eastern states of North America, white clover, *Trifolium repens* L., is the foremost honey plant, and the domestic bee stores from its bloom annually hundreds of tons of an excellent, white honey; but in France and Switzerland it yields no appreciable quantity of nectar and one may travel several kilometers and not see a bee on it. "White Clover in Europe," *Am. Bee Journal*, **53**:331.

their visits are so rare that the flowers appear to be entirely deserted through a long series of years. Honey-bees do not usually visit the flowers legitimately, but procure the nectar through a crevice in the side.

An excellent illustration on a scale of great magnitude showing that honey-bees are guided by the memory of past experience in gathering nectar is furnished by the honey-flow of buckwheat, *Fagopyrum esculentum* Moench., which Buttel-Reepen describes as follows:

" If colonies stand in buckwheat, the flight is lively in the mornings until ten o'clock; then it lessens, and is entirely quiet for the greater part of the day, beginning vigorously again the next morning. The buckwheat nectar flows only in early morning; so, as the nectaries dry up, the bees fly out a couple of times and then discontinue their vain flight. In spite of the shimmering sea of flowers, *in spite of the strong fragrance*, only a few bees may usually be found after ten o'clock in the buckwheat field." [37]

The period of time during which the flowers of buckwheat secrete nectar varies in different localities. In this region the bees continue to work on them, according to observations made by a young friend of the writer, until about 12:30 p. m. Their visits then quickly decrease in number until about 1:00 o'clock, when they cease entirely. But for an hour or more afterwards, the bees may be seen occasionally flying from blossom to blossom, pausing, however, for only an instant, as they apparently discover at once that the flowers are now nectarless. At Delanson, N. Y., buckwheat yields nectar most abundantly between 9:00 o'clock in the morning and 2:00 p. m. A bee is seldom at work on it much earlier or much later, notwithstanding there are hundreds of colonies of bees in the vicinity. In parts of the west, buckwheat is a more uncertain honey plant than in the east and in some years the flowers fail to become nectariferous, when they are almost wholly deserted by bees.[38] Again a sudden shower followed by a fall in temperature may bring the buckwheat harvest to an abrupt and premature close in August, when ordinarily it would continue into September. Such an interruption of the

[37] Buttel-Reepen, H. V., "Are Bees Reflex Machines? " translated by Mary H. Geisler, p. 29.

[38] Root, A. I. and E. R., " The A B C and X Y Z of Bee Culture," p. 71.

honey season occurred at Delanson in 1906. For several days a hive on scales had shown a gain of eight pounds a day; but during the night of August 24 there was a light shower and a decline in temperature of 11 degrees F., after which the hive on scales did not show a gain of half a pound any day that fall. The bees immediately ceased visiting the flowers, and in countless thousands attempted to rob each other and the honey house.[39] Owing to the intermittent nature of the flow of nectar, bees are more irritable during the buckwheat harvest than during that of any other plant. The time of the flight of the bees thus always coincides with the period of active secretion of nectar, or if the flowers are nectarless they neglect them almost entirely.

The preceding experiments and studies of honey plants show that honey-bees learn from observation and are guided by the memory of past experience. Flowers rich in accessible food supplies receive numerous visits, but if for any reason the flow of nectar suddenly ceases the bees immediately discontinue their visits. If the inflorescence of a plant species yields abundant nectar in one locality but is devoid of nectar in another, even though only a few miles intervene, the flowers in the former place will be frequently visited and in the latter deserted. But honey-bees do occasionally visit and examine conspicuous flowers from which they can not obtain food materials, and it is upon this premise that the argument of the present paper is based. *A priori* reasoning alone would lead the floroecologist, who believes that conspicuousness is an advantage to flowers to this conclusion, thus Campbell remarks that "it is safe to say that no showy flower is entirely destitute of insect visitors."[40] Much evidence has already been adduced in support of this statement, but it is desirable to give additional observations, made especially for this purpose. The casual observer will often fail to discover a single visitor, and may easily conclude that they never attract the attention of insects; but long continued investigation proves this to be a mistake.

The variegated flowers of the Sweet William, or bunch pink, (*Dianthus barbatus* L.), display the most vivid shades of crimson and scarlet; and, as the name indicates, exhale a pleasant fra-

[39] Alexander, E. W., "Buckwheat as a Honey Producer," *Gleanings in Bee Culture*, 35:394.

[40] Campbell, D. H., "Plant Life and Evolution," p. 227.

grance. They are adapted to pollination by butterflies and day-flying moths. The nectar, while not abundant, is sufficient in quantity to yield a sweet taste to the tip of the tongue; and it lies at the bottom of a calycine tube 15 mm. long, far beyond the reach of honey-bees. Previous to July 11, 1912, I failed to record a single bee visitor. On this date I saw a honey-bee inspect several clusters of flowers, but it never actually alighted, although flying close to the inflorescence. On the 23rd, a honey-bee visited a few flowers. At about 11:00 a. m., August 6, a warm clear day, two and at one time three honey-bees were observed on the flowers. They were carefully watched for ten minutes, and one of them vainly endeavored, standing in various positions, to reach the nectar by thrusting its tongue down the center of the flower. Others probed between the petals, even looking under the corolla. An hour later, a bee was still found on the clusters; at intervals, wasps and flies also examined the flowers. Observations extending through the entire season show that the flowers are very far from being wholly neglected by Hymenoptera and Diptera, although a few inspections might readily lead to this belief.

The flowers of the bee larkspur (*Delphinium clatum* L.), which are normally pollinated by bumblebees, have so long a spur that the nectar is wholly inaccessible to honey-bees. In my garden they are very rarely visited by insects of any kind. On the morning of July 11, a honey-bee after visiting one or two flowers, desisted from its useless efforts. On July 24, in the afternoon, a honey-bee visited several flowers in an unsuccessful attempt to find nectar. It pushed its tongue as far as possible into the mouth of the spur, and also looked for nectar under the upper perianth segment. On August 4, a bee inspected two blue floral leaves, which had fallen from a flower to the green foliage, thus showing that a single detached petal could gain its attention.

On July 16, a large moth poised before several flowers and obtained the nectar without difficulty; in the evening the white center contrasts so strongly with the blue ground color that the attention of crepuscular Lepidoptera might easily be gained.

During the summer of 1910, no insects were seen to visit the flowers of the pansy (*Viola tricolor* L.). By October 1, nearly all the wild and cultivated flowers had perished, but a few

pansies still remained in bloom. October 7 was cold and rainy, but the day following was clear, warm and calm, and at 10 a. m., a honey-bee spent more than ten minutes on the pansy flowers searching for nectar. Two Syrphid flies (*Eristalis tenax*) were also flying from flower to flower looking for pollen, but making no attempt to find nectar. On the afternoon of the 10th, a worker of *Bombus consimilis* and a male of *B. fervidus* were examining the flowers for nectar; and on the 11th a worker of *B. consimilis* and a white butterfly. Thus the pansies are not so much neglected as at first appeared probable, but in the absence of more desirable flowers are frequently visited by insects.

On the morning of October 28, 1912, two honey-bees were examining the larger, neutral flowers of *Hydrangea paniculata* Sieb., but they soon learned that they were nectarless and passed over to the smaller, perfect flowers. On July 16, a species of *Megachile* visited two flowers of the climbing honeysuckle (*Lonicera Periclymenum* L.), a hawk-moth flower; but its stay was very brief, as it could not reach the nectar. It then flew to another moth flower (*Œnothera biennis* L.), which was closed. Finding no opportunity to get flower food it returned to the honeysuckle; but meeting with no better success than on its previous visit, it abandoned that part of the garden altogether. In the evening, while the hawk-moths were industriously at work on the honeysuckle flowers, they repeatedly inspected large, red roses blooming on a bush a few feet away. The roses are pollen flowers and devoid of nectar, but the hawk-moths were compelled to learn this fact by direct examination. Another pollen flower is the poppy, but before the anthers dehisc honey-bees may often be seen searching for nectar at the base of the petals. Honey-bees have likewise been observed looking for nectar under the calyx segments of flowers belonging to the Labiatae.

Further examples that honey-bees occasionally examine carefully flowers, which are commonly neglected, might be multiplied indefinitely; but sufficient instances have been given for the purpose of the present paper. It has been shown that such visits are actually made, and that they are infrequent because the bees remember their inability to obtain flower food. Nevertheless, in the aggregate they do waste much time in fruitless visits to a great variety of flowers, which for one reason or another

yield no booty; but this loss is reduced to a minimum by their ability to learn from experience. They are able to store up in their brains, as described by Forel, various sense impressions of color, form and spatial position, by which their movements are subsequently guided and which prevent them from indefinitely making useless visits. " It results, therefore, from the unanimous observations of all the connoisseurs that sensation and perception, and association, inference, memory and habit follow in the social insects the same fundamental laws as in the vertebrates and ourselves."[1] But he adds that " the above mentioned faculties are manifested in an extremely feeble form beyond the confines of the instinct-automatism stereotyped in the species."[2]

In closing this paper it is desirable to remind the reader that the visits of bees to flowers are, of course, often influenced by other factors besides the characters of the flowers, as temperature, rainy or foggy weather, the number of insects in the locality, and especially by the blooming period of common plants very rich in nectar. During the honey-flow from the more important honey plants, bees restrict their visits very closely to a single species, and there is no occasion nor would it be for their advantage to pay attention to flowers containing little or no nectar. Plateau himself noticed that when the apricots expanded their flowers, the Hymenoptera abandoned the violets, and he was forced to discontinue his experiments with artificial flowers.[3] During a honey-flow the entire force of field bees of each colony is largely governed by a common impulse, and their attention may be fairly termed obsessional. The hives may then be opened and the honey exposed with scarcely any danger of robbing. Buttel-Reepen tells of a bee-keeper who placed a dish of honey over his strongest colony during the buckwheat honey-flow, and after eight days of good forage the bees had not touched the honey, although it was pure.[4] Manifestly, under these conditions

[1] Honey-bees will not visit bright-hued pieces of paper or cloth, whether large or small, attached to a line and suspended over a bed of flowers, or crude floral groups painted on large screens or walls, because they are not deceived by these objects, or images, any more than ourselves. Cf. Plateau, F., " Le Macroglosse," *Mem. Soc. ent. de Belgique*, **12**:141–80, 1906.

[2] Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 21.

[3] Plateau, F., " Les fleurs artificielles et les insectes," *Mem. de l'Acad. roy. de Belgique*, **1**:24, 1906.

[4] Buttel-Reepen, H. V., "Are Bees Reflex Machines," p. 27.

small groups of conspicuous, nectarless flowers, and even those containing nectar, will be likely to be passed over unheeded.

CONCLUSIONS

Entomophilous flowers are usually characterized by the possession of either bright coloration, or odor, or both, although apparently to some extent the two qualities are mutually exclusive. Both allurements are useful in attracting the attention of insects; but the absence of either conspicuousness, or odor, or both, will not necessarily cause a flower to be neglected if it contains an ample supply of pollen or nectar. But under similar conditions, small, green, odorless flowers, even if rich in nectar, will not be discovered as quickly as nectariferous flowers, which are conspicuous or agreeably scented.[1] On the other hand, the possession of both color and odor will not ensure frequent visits in the absence of available food materials. The experiments afford no evidence that bees visit flowers for the purpose of experiencing an aesthetic pleasure.

Insects, especially bees, occasionally examine the neglected, conspicuous flowers of cultivation; but, obtaining no food materials, or very little, they do not often repeat their visits. Many neglected flowers are pleasantly scented, and the addition of another agreeable odor is neither necessary nor beneficial.

When odoriferous fruit syrups are introduced into conspicuous flowers, commonly neglected, a group of miscellaneous insects, especially Diptera, will be attracted; but the inference that, therefore, color is no advantage and that an agreeable odor is required is fallacious. For the introduction of an odorless syrup into similar flowers will induce insect visits in large numbers; also when flowers, with the nectar inaccessible to honeybees and, consequently, seldom visited by them, have the nectaries artificially punctured, or the floral tubes shortened by drouth, they are then visited by bees in countless thousands without the addition of either an agreeable odor or a sweet liquid. Flowers which in one locality freely secrete nectar and are visited by numerous insects are sometimes in other localities nectarless and almost entirely neglected. Insects, therefore, perceive the colors and forms of neglected flowers, and the rarity of their

[1] Lovell, John H., "The Pollination of Green Flowers," *Amer. Nat.*, **46**:83–107, 1912.

visits is the result of their memory of the absence of food materials, not because the flowers lack an agreeable odor, which is often not the fact.

The flowers into which Plateau introduced odoriferous sweet liquids were thus artificially converted into distinct physiological varieties. Since flowers possessing conspicuousness, an agreeable odor, and a liquid food were opposed to flowers possessing only conspicuousness, it is clear that color was never directly brought into competition with odor—the latter was invariably given the advantage.

Colors and odors attract the attention of insects, but bees in their visits to flowers, previously examined by them, are guided largely by the memory of past experience; they are able to associate different sense impressions and unconsciously make analogous inferences.