Observations on Ants, Bees, and Wasps.—Part IX. By Sir JOHN LUBBOCK, Bart., M.P., D.C.L., LL.D., F.R.S., President Linn. Soc.

[Read November 17, 1881.]

Colors of Flowers as an Attraction to Bees: Experiments and Considerations thereon.

THE consideration of the causes which have led to the structure and coloring of flowers is one of the most fascinating parts of natural history. Most botanists are now agreed that insects, and especially bees, have played a very important part in the development of flowers: while in many plants, almost invariably with inconspicuous blossoms, the pollen is carried from flower to flower by the wind, in the case of almost all large and brightly colored flowers this is effected by the agency of insects. In such flowers the colors, scent, and honey serve to attract insects; while the size and form are arranged in such manner that the insects fertilize them with pollen brought from another plant.

Nevertheless these views have not escaped criticism. M. Bonnier, for instance, in an article on Nectaries, has attempted to show that they are in many respects untenable.

I do not propose on the present occasion to follow his general argument, but merely that portion of it relating to color. M. Bonnier, while not questioning the power of insects to distinguish colors, denies that they would be in any way attracted or guided by the colors of flowers. This he has attempted to demonstrate by experiment. With this view he proceeded as follows:—He took four cubes, 22 centim. by 12 (*i. e.* about 9 inches by $3\frac{1}{2}$), and colored red, green, yellow, and white, placing them 6 feet apart in a line parallel to and about 60 feet distant from the hives. He then placed on each an equal quantity of honey, and from minute to minute counted the number of bees on each cube. He found that the number of bees on each was approximately equal, and that the honey was removed from each in about twenty minutes. In the experiment he records the bees began to arrive directly the honey was arranged, and in ten minutes there were nearly a hundred bees on each cube. I presume, therefore, that the bees were previously accustomed to come to the spot in question, expecting to find honey.

I do not think, however, that any satisfactory result could be expected from this experiment. In the first place, after the first five minutes there were about thirty bees on each cube, and in less than ten minutes nearly a hundred; the color therefore must have been almost covered up. The presence of so many bees would also attract their companions. Moreover, as the honey was all removed in less than twenty minutes, the bees were evidently working against time. They were like the passengers in an express train, turned hurriedly into a refreshment room; and we cannot expect that they would be much influenced by the coloring of the tablecloth. In fact, the experiment was too hurried and the test not delicate enough.

Then, again, he omitted blue, which I hope to show is the bees' favourite color; and his cubes were all colored. It is true that one was green; but any one may satisfy himself that a piece of green paper on grass is almost as conspicuous as any other color. To make his experiment complete, M. Bonnier should have placed beside the honey on the colored cubes, a similar supply without any accompaniment of color to render it conspicuous.

I could not, therefore, regard these experiments as at all conclusive. The following experiments seem to me a more fair test:—

I took slips of glass of the size generally used for slides for the microscope, viz. 3 inches by 1, and pasted on them slips of paper coloured respectively blue, green, orange, red, white, yellow. I then put them on a lawn, in a row, about a foot apart, and on each put a second slip of glass with a drop of honey. I also put with them a slip of plain glass with a similar drop of honey. I had previously trained a marked bee to come to the spot for honey. My plan then was, when the bee returned and had sipped about for a quarter of a minute, to remove the honey, when she flew to another slip. This then I took away, when she went to a third; and so on. In this way I induced her to visit all the drops successively. When she had returned to the nest, I transposed all the upper glasses with the honey, and also moved the colored glasses. Thus, as the drop of honey was changed each time, and also the position of the colored glasses, neither of these could influence the selection by the bee.

In recording the results I marked down successively the order in which the bee went to the different colored glasses. For instance, in the first journey from the nest, as recorded below, the bee lit first on the blue, which accordingly I marked 1; when disturbed from the blue, she flew about a little and then lit on the white; when the white was removed, she settled on the green; and so on successively on the orange, yellow, plain, and red. I repeated the experiment a hundred times, using two different hives, and spreading the observations over some time, so as to experiment with different bees and under varied circumstances. Adding the numbers together, it of course follows that the preference shown for each colour is inversely as the number standing against it.

I now subjoin the numbers, giving the first day *in extenso*:—

Journeys.	Blue.	Green.	Plain glass.	Orange.	Red.	White.	Yellow.
1.	1	3	6	4	7	2	5
2.	5	4	7	6	1	2	3
3.	1	4	7	6	5	3	2
4.	2	4	6	7	5	1	3
5.	1	4	7	2	6	5	3
6.	1	2	3	6	5	4	7
7.	2	1	4	7	3	5	6
8.	3	4	6	2	7	5	1
9.	5	1	7	4	6	3	2
10.	1	6	7	5	3	2	4
11.	4	6	5	2	7	3	1
	26	39	65	51	55	35	37

In the next series of experiments the bees had been trained for three weeks to come to a particular spot on a large lawn, by placing from time to time honey on a piece of plain glass. This naturally gave the plain glass a great advantage; nevertheless, as will be seen, the blue still retained its preeminence. It seems hardly necessary to give the others *in extenso*. The following table shows the general result:—

Series.	No. of exp.	Blue.	Green.	Orange.	Plain.	Red.	White.	Yellow.
1st	11	26	39	51	65	55	35	37
2nd, May 30...	15	38	57	59	72	66	58	70
3rd, July 2...	16	44	76	82	73	53	53	67
4th, „ 4...	15	43	61	64	80	66	50	56
5th, „ 5...	10	36	47	39	40	40	36	42
6th, „ 6...	2	2	8	9	10	14	6	7
7th, „ 20...	11	33	39	50	47	49	41	49
8th, „ 23...	10	31	46	48	52	37	35	31
9th, „ 25...	10	22	54	38	52	33	35	46
	100	275	427	440	491	413	349	405

The precautions taken seem to me to have placed the colors on an equal footing; while the number of experiments appears sufficient to give a fair average. It will be observed also that the different series agree well among themselves. The difference between the numbers is certainly striking. Adding together 1, 2, 3, 4, 5, 6, and 7 we get 28 as the total number given by each journey; 100 journeys therefore give, as the table shows, a total of 2800, which divided by 7 would of course, if no preference were shown, give 400 for each color. The numbers given, however, are—for the blue only 275, for the white 349, yellow 405, red 413, green 427, orange 440, and plain glass as many as 491.

Another mode of testing the result is to take the percentage in which the bees went respectively to each color first, second, third, and so on. It will be observed, for instance, that out of a hundred rounds the bees took blue as one of the first three in 74 cases, and one of the last four only in 26 cases; while, on the contrary, they selected the plain as one of the first three only in 25 cases, and one of the last four in 75 cases.

	Blue.	Green.	Orange.	Plain.	Red.	White.	Yellow.
First......	31	10	11	5	14	19	9
Second ...	18	11	13	7	10	21	20
Third ...	25	12	8	13	16	13	13
Fourth ...	8	23	15	11	11	12	20
Fifth......	11	13	15	19	17	16	10
Sixth......	3	15	22	21	18	12	9
Seventh ..	4	16	16	24	14	7	19
	100	100	100	100	100	100	100

I may add that I was by no means prepared for this result. Müller, in his remarkable volume on Alpine Flowers, states that bees are much more attracted by yellow than by white *. In the same work he gives the following table:—

	In every 100 visits of insects there were			
Flowers.	Butterflies.	Bees.	Flies and Gnats.	Other insects.
3 yellowish-white species...	12·8	51·3	15·4	20·5
23 yellow " ...	47	27·5	28·1	7·2
16 red " ...	51·4	35·1	9·2	8·2
7 blue " ...	64·9	26·6	10·7	1·9

* 'Alpenblumen,' p. 487.

This table does not indeed show any absolute preference for one color rather than another. In the first place the number of species compared is very different in the case of the different colors; and in the second place, the results may of course be due to the taste, quantity, or accessibility of the honey (all of which we know exercise a great influence), rather than by the color of the flower. Still the table rather seems to indicate that bees preferred red, white, and yellow, to blue.

I may very likely be asked why it is that if blue is the favorite color of bees, and if bees have had so much to do with the origin of flowers, how is it that there are so few blue ones? I believe the explanation to be that all blue flowers have descended from ancestors in which the flowers were green, and that they have passed through stages of white or yellow, and generally red, before becoming blue. That all flowers were originally green and inconspicuous, as those of so many plants are still, has, I think, been shown by recent researches, especially those of Darwin, Müller, and Hildebrand.

But what are the considerations which seem to justify us in concluding that blue flowers were formerly yellow or white? Let us consider some of the orders in which blue flowers occur with others of different colors.

For instance, in the Ranunculaceæ *, those with simple open flowers, such as the buttercups and Thalictrums, are generally yellow or white. The blue Delphiniums and Aconites are highly specialized, abnormal forms, and doubtless, therefore, of more recent origin. Among the Caryophyllaceæ the red and purplish species are amongst those with highly specialized flowers, such as *Dianthus* and *Saponaria*, while the simple open flowers, which more nearly represent the ancestral type, such as *Stellaria*, *Cerastium*, &c. are yellow and white. I cannot, therefore, concur with Hildebrand in considering that red was the original color of the family.

Take, again, the Primulaceæ. The open-flowered, honeyless species, such as *Lysimachia* and *Trientalis*, are generally white or yellow; while red, purple, and blue occur principally in the highly specialized species with tubular flowers. The genus *Anagallis* here, however, certainly forms an exception.

Among the violets we find some yellow, some blue species; and

* I take most of the following facts from Müller's admirable work on Alpine Flowers.

Müller considers that the yellow is the original color. *Viola biflora*, a small, comparatively little specialized fly-flower, is yellow; while the large, long-spurred *V. calcarata*, specially adapted to Humble-bees, is blue. In *V. tricolor*, again, the smaller varieties are whitish-yellow ; the larger, and more highly developed, blue. *Myosotis versicolor*, we know, is first yellow and then blue; and, according to Müller, one variety of *V. tricolor alpestris* is yellow when it first opens, and gradually becomes more and more blue. In this case the individual flower repeats the phases which in past times the ancestors have passed through.

The only other family I will mention is that of the Gentians. Here, also, while the well-known deep-blue species have long tubular flowers, specially adapted to bees and butterflies, the yellow *G. lutea* has a simple open flower with exposed honey.

Müller and Hildebrand * have also pointed out that the blue flowers, which, according to this view, are descended from white or yellow ancestors, passing through a red stage, frequently vary, as if the colors had not had time to fix themselves, and by atavism assume their original color. Thus *Aquilegia vulgaris*, *Ajuga genevensis*, *Polygala vulgaris*, *P. comosa*, *Salvia pratensis*, *Myosotis alpestris*, and other blue flowers are often reddish or white; *Viola calcarata* is normally blue, but occasionally yellow. On the other hand, flowers which are normally white or yellow rarely, I might almost say never, vary to blue. Moreover, though it is true that there are comparatively few blue flowers, still if we consider only those in which the honey is concealed, and which are, as we know, specially suited to, and frequented by bees and butterflies, we find a larger proportion. Thus of 150 flowers with concealed honey observed by Müller in the Swiss Alps †, 68 were white or yellow, 52 more or less red, and 30 blue or violet.

However this may be, it seems to me that the preceding experiments show conclusively that bees do prefer one color to another, and that blue is distinctly their favorite.

On Anergates.

The life-history of the genus *Anergates* is, in the words of Forel, an unsolved enigma. The species was discovered by Schenk, who found a small community consisting of males, females, and workers, which he naturally supposed to belong to one species. Mayr,

* 'Die Farben der Blüthen,' p. 26.

† 'Alpenblumen,' p. 492.

however, pointed out that the workers were in fact workers of *Tetramorium cæspitum*; and it would appear that while in *Strongylognathus* the workers are comparatively few, *Anergates* differs from all other ants in having no workers at all *. The males and females live with *Tetramorium cæspitum*, and are in several respects very peculiar: for instance, the male is wingless. One might consider it rather a case of parasitism than of slavery; but the difficulty is that in these mixed nests there are no males and females of *Tetramorium*. It seems quite clear that *Anergates* cannot procure its slaves, if such they are, by marauding expeditions like those of *Polyergus*—in the first place because they are too few, and secondly because they are too weak. The whole question is rendered still more difficult by the fact that neither Von Hagen† nor Forel found either larvæ or pupæ of *Tetramorium* in the mixed nests. The community consisted of males and females of *Anergates*, accompanied and tended by workers of *Tetramorium cæspitum*. The Anergates are absolutely dependent upon their slaves, and cannot even feed themselves. The whole problem is most puzzling and interesting. On the whole I would venture to suggest that the female *Anergates* makes her way into a nest of *Tetramorium*, and in some manner contrives to assassinate their queen. It must be admitted that even this hypothesis does not fully account for the facts. Still, I have shown that a nest of ants may continue even in captivity for five years without a queen. If, therefore, the female of *Anergates* could by violence or poison destroy the queen of the *Tetramoriums*, we should in the following year have a community composed in the manner described by Von Hagen and Forel. This would naturally not have suggested itself to them, because if the life of an ant had, as was formerly supposed, been confined to a single season, it would, of course, have been out of the question; but as we now know that the life of ants is so much more prolonged than had been supposed, it is at least not an impossibility.

At any rate the four genera of so-called slave-making ants offer us every gradation from lawless violence to contemptible parasitism. *Formica sanguinea*, which may be assumed to have compa-

* In *Tomognathus sublævis*, on the contrary, a Finland species, which lives in the nests of *Leptothorax muscorum* and *L. acervorum*, the workers only are known.

† Verh. des natur. Vereins der preuss. Rheinlande und Westphalens, 1867, p. 53.

ratively recently taken to slave-making, has not as yet been materially affected.

Polyergus, on the contrary, already illustrates the lowering tendency of slavery. They have lost their knowledge of art, their natural affection for their young, and even their instinct of feeding! They are, however, bold and powerful marauders.

In *Strongylognathus*, however, the enervating influence of slavery has gone further, and told even on the bodily strength. They are no longer able to capture their slaves in fair and open warfare. Still they retain a semblance of authority, and, when roused, will fight bravely, though in vain.

In *Anergates*, finally, we come to the last scene of this sad history. We may safely conclude that in distant times their ancestors lived, as so many ants do now, partly by hunting, partly on honey; that by degrees they became bold marauders, and gradually took to keeping slaves; that for a time they maintained their strength and agility, though losing by degrees their real independence, their arts, and even many of their instincts; that gradually even their bodily force dwindled away under the enervating influences to which they had subjected themselves, until they sank to their present degraded condition—weak in body and mind, few in numbers, and apparently nearly extinct,—the miserable representatives of far superior ancestors, maintaining a precarious existence as contemptible parasites of their former slaves.

It is conceivable that the *Tetramoriums* may have gradually become harder and stronger; the marauding expeditions would then become less and less frequent. If, then, we suppose that the females found it possible to establish themselves in nests of *Tetramorium*, the present state of things would almost inevitably be by degrees established.

Thus we may explain the remarkable condition of *Strongylognathus*, armed with weapons which it is too weak to use, and endowed with instincts which it cannot exercise.

Identification of Companions.

With reference to the interesting problem as to how ants recognize their companions, I have tried the following little experiment. It is of course well known, and has been abuudantly proved by my experiments, that although, if a strange ant is introduced into a community even of the same species, she is at once attacked, yet, on the other hand, if a few ants belonging to different communities are placed together in a confined space, though at first a little shy, they gradually make friends. I thought therefore I would take a few specimens of *Formica fusca* from two different nests, which we will call nests A and B, place them together, and then, when they had lived together for some time, introduce the ants from nest A into nest B and *vice versâ*. Accordingly, having first ascertained by direct experiment, though I had myself no doubt on the point, that the ants in nest A would attack and expel an ant from nest B, and *vice versâ*, I took two ants from nest A on the 2nd December 1880, and put them in a small glass with two others from nest B.

Then, on the 23rd January, I put the two ants from nest A into nest B. One of them was at once attacked; about the other we could not be sure. Unluckily the two ants from nest B were killed by an accident.

On Feb. 24, 1881, I again took three ants from nest A and the same number from nest B, and put them together in a small glass. Then, on May 1, I put two ants from nest B into nest A. They were soon attacked very vigorously, and dragged out of the nest.

Thus, then, though these ants had lived amicably for some weeks with companions from another nest, they were not accepted as friends by the nest from which those companions were taken.

In consequence of a suggestion made by Mr. McCook, I took three specimens of *Lasius niger* and three of *Formica fusca*, and put them in water for an hour. After marking them, I put them back in the nest. The specimens of *L. niger* were put back at 11 A.M. They were quite amicably received, and the other ants began at once to lick off the paint with which they were marked. At 11.30 one was among the rest, evidently quite at home; the other I could not distinguish; but no ant was being attacked. At 12 the one was not quite cleaned; the other I could not distinguish. I looked from time to time during the afternoon, and certainly there was no fighting in the nest. The next morning I looked carefully; but there was no dead body, and I am satisfied they were amicably received.

The following morning at 7 A.M. I put in the three specimens of *F. fusca*. They were also evidently received as friends; and their companions began, as in the other case, to clean off the paint. At 7.30 they were quite at home among the others. 8, ditto. 9, ditto. 10, ditto. There could be no doubt about their recognition.

In my previous paper * I have recorded some experiments made

* Linn. Soc. Journ. vol. xiv. p. 610.

with pupæ in order to determine in what manner ants recognize their comrades.

For instance, I separated a nest of *Formica fusca* into two divisions in the spring before the season for laying eggs. Then in the autumn I took ants from one half (which I may call A) and put them into the other half (which I may call B). Thus, of course, there could be no question of individual recognition. Nevertheless, in nine cases such ants were received as friends. This season again, on the 10th April 1881, I divided a two-queened nest of *Formica*, leaving a queen in each half. At that time no eggs had yet been laid, and of course there were no larvæ or pupæ. In due course both queens laid eggs; and young ants were brought up in each half of the nest. I will call the two halves, as before, A and B. On the 15th August at 9 A.M. I put three of the young ants from A into B, and three from B into A. At 9.30 none are attacked. At 10, the same. At 10.30, the same; one is being cleaned. At 12, the same. At 2 P.M., the same. In fact they seemed quite at home with the other ants. The next morning I was unable to recognize them, the paint having been entirely removed. The ants were all peaceably together in the nest; and there were no dead ones either in the nest or in the outer box. It is evident, therefore, that they had been treated as friends.

August 17.—I put in three more from B into A at noon. At 12.30 they were with the other ants. At 1, the same. At 2, the same. At 3, the same. At 5 the same. The following morning I was still able to recognize them, though most of the paint had been removed. They also were evidently treated as part of the community.

Sept. 19.—Put in three more from A into B at 8.30 A.M. I looked at them at intervals of half an hour; but none of them were attacked. Next morning there was no ant outside the nest, nor had any been killed.

Oct. 10.—Put in three more at 7 A.M., and looked at intervals of an hour. They were not attacked, and evidently felt themselves among friends. The next morning I was still able to recognize two. There was no dead ant either in the nest or the outer box.

Lastly, on the 15th Oct. I put in four more at 7 A.M., and watched then all day at short intervals. They exhibited no sign of fear, and were never attacked. In fact, they made themselves quite at home, and were evidently, like the preceding, recognized as friends. For the sake of comparison, at noon I put in a stranger. Her behaviour was in marked contrast. The preceding ants seemed quite at home, walked about peaceably among the other ants, and made no attempt to leave the nest. The stranger, on the contrary, ran uneasily about, started away from any ant she met, and made every effort to get out of the nest. After she had three times escaped, I let her go.

Thus, then, when a nest of *Formica fusca* is divided early in spring and when there are no young, the ants produced in each half were in twenty-eight cases all received as friends. In no case was there the slightest trace of enmity.

Peculiarities of Manner in Different Species of Ants.

In one of my previous memoirs* I have observed that the behaviour of *Lasius flavus* offered in some respects a surprising contrast to that of *Formica fusca*. In experimenting on the power of recognizing friends possessed by these species, I found that while specimens of *Lasius flavus* readily, and even of their own accord, entered other nests of the same species, *Formica fusca*, on the contrary, showed a marked reluctance to do so; and I had some difficulty in inducing them to do so. At that time, however, I did not ascertain what became of the specimens thus introduced into a strange community. I thought it would be worth while to determine this; so I took six ants from one of my nests of *Lasius flavus*, marked them, and introduced them into another nest of the same species. As in the preceding cases, they entered quite readily; but though they were not at first attacked, they were evidently recognized as strangers. The others examined them carefully; and at length they were all driven out of the nest. Their greater readiness to enter a strange nest may perhaps be accounted for by the fact that, as a subterranean species, their instinct always is to conceal themselves underground, whereas *F. fusca*, a hunting species, does not do so, except to enter its own nest.

Longevity of Ants.

In my previous paper I have called attention to the considerable age attained by my ants; and I may perhaps be permitted to repeat here, *mutatis mutandis*, a paragraph from my last communication with reference to my most aged specimens, most of

* Journ. Linn. Soc. vol. xiv. p. 611.

those mentioned last year being still alive. One of my nests of *Formica fusca* was brought from the woods in December 1874; it then contained two queens, both of which are now still alive. I am disposed to think that some of the workers now in the nest were among those originally captured, the mortality after the first few weeks having been but small. This, of course, I cannot prove. The queens, however, are certainly more than seven, and probably more than eight, years old. In the following nests, viz. another nest of *F. fusca*, which I brought in on the 6th June 1875, and one of *Lasius niger* on the 30th November 1875, there were no queens; and, as already mentioned, no workers have been produced. Those now living are therefore the original ones; and they must be between six and seven years old.

I had also some workers of *Lasius niger* which I began to observe on the 6th July 1875; the last of these died on June 15th, 1881. Lastly, some of *Formica cinerea* which I began to observe on the 29th November 1875, lived till the ants in this nest died off somewhat rapidly, the last on July 23, 1881. There were no queens in either of these nests; these workers therefore must have been more than 6 years old.

On the Sense of Color among some of the Lower Animals. By Sir John Lubbock, Bart., M.P., D.C.L., LL.D., F.R.S., President Linn. Soc.

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As I have already mentioned in a previous communication* M. Paul Bert† has made some very interesting experiments on a small freshwater crustacean belonging to the genus *Daphnia*, from which he concludes that they perceive all the colors known to us, being, however, especially sensitive to the yellow and green, and that their limits of vision are the same as ours.

Nay, as I have stated (*loc. cit.*), he even goes further than this, and feels justified in concluding, from the experience of two species—Man and *Daphnia*—that the limits of vision would be the same in all cases.

* Journ. Linn. Soc. vol. xv. p. 376 (No. 87).
† Archiv. de Physiol. 1869, p. 547.