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OBSERVATIONS ON LEAF-CUTTING ANTS

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It is not often that one has so good a "set up" for certain observations as that provided by a colony of *Atta cephalotes polita*[1] near the laboratory of the Institute for Research in Tropical America in the Panama Canal Zone. Accordingly, I dropped the work which I had intended to do during a short stay there and concentrated my attention on these ants.

The colony was a small one, as such colonies go, and had at that time only one trail along which they were bringing pieces of leaves. Therefore, watching this trail gave one a fairly comprehensive idea of the external activities of the colony. Furthermore, the entire trail between the nest and the trees whose leaves were being cut, a distance of only about 15 meters, was along a net-work of lianas, so that the ants could be seen easily. And, finally, this liana trail was so arranged that one could select reasonably straight 50-centimeter stretches at almost any steepness of grade that one wished. This latter feature made it possible to study the relation between grade and speed of walking under natural conditions. Unfortunately, my stay at the laboratory was such a short one that I had time to study carefully only three grades: a steep downgrade, a steep up-grade, and a relatively level stretch.

Since temperature has so marked an effect on the activities of insects—a thing that has not been well investigated for tropical species and really what led me to go to Panama—the constancy of temperature near the ground in a tropical forest greatly simplified matters. During the hours in which these ants were carrying leaves the temperature was never below 26° nor above 28° C. Likewise, the humidity was very constant at that time, near the end of the dry season (the latter part of March). Light was the most variable of the important environmental factors if, as I believe, it is important.

Many accounts[2] of leaf-cutting ants give the reader an impression that these ants work chiefly at night. This may be true of some species

[1]Identifications kindly made by Professor Wheeler.
[2]Including the ancient Guatemalan myth quoted by Wheeler in his valuable paper on 'Fungus-growing Ants of North America' (1907, Bull. Amer. Mus. Nat. Hist., XXIII, pp. 669–807).

and in other cases there seems to be a variation depending on several factors. Belt said: "In dry and hot weather, when the leaves would get dried up before they could be conveyed to the nest, the ants, when in exposed situations, do not go out at all during the hot hours, but bring in their leafy burdens in the cool of the day and during the night." The colony reported upon here had its nest and its entire trail in the comparative shade of the forest. I am not in a position to know how it may be with this nest at other seasons, but certainly during the period covered by these observations there was no activity outside of the nest before sunrise or after sunset even during the time of full moon. In fact, the setting out from the nest to work in the morning and the quitting work in the evening were among the most interesting things noticed on the liana trail.

In the early morning a few workers could be seen congregating in the outer gallery of the nest near the exit. As they moved back and forth they oradually came nearer the outer opening. Then several would wander outside, only to go back again. A little later one or two of these would retrace their steps. Then, as though at a signal, a number would go out at once, some of them possibly continuing to the tree but others, like the storied plumber returning to the shop for a forgotten tool, would go back. What is the signal that sends this first band of workers out to their tree? Doubtless "stimulus" would be a more technical term than "signal," but I confess that it seems cold and not descriptive of what I saw.

When returning individuals of the first wave reached the nest with cut leaves a second and larger wave of ants would leave and these seemed to go along the trail as though they were decidedly interested in getting there, not vacillating so much as the first group. To describe this I would be more willing to use the word "stimulus," for the bringing in of pieces of leaves seemed to arouse the nest to real activity.

To use another simile from human affairs, one might say that the first workers to start were like children going to school on a warm spring day, playing as they go and running this way and that. Then the bell rings and they more or less quickly settle down to the affairs of the day. Putting it in a statistical way, the following records of ants passing a point about three feet from the nest (and, so, beyond the zone of apparently aimless wanderings) will make the description more definite. Ants going back to the nest without a burden (piece of leaf) will be referred to as "unladen."

March 20.—There had been a rain during the night and the morning was cloudy. At 9:10 ants were taking out dirt but the leaf-carrying squad was not at the nest-opening. At 9:25 ants were gathering in the nest-gallery about two inches from the surface. At 9:55 the first carrier left the nest but went back at once. The gallery near the exit was rather crowded. At 10:03 a carrier went to the liana (the trail to their tree) about twenty inches from the nest but returned and almost immediately another went out and along the liana until at about thirty inches from the nest it was caught and carried off by a larger ant (*Paraponera clavata*), which had been standing there poised and motionless, facing the nest, for twenty minutes or so. Then something happened and work started suddenly, for between 10:08 and 10:10 forty-five ants poured out of the nest and along the liana trail, only two going back. In the next five minutes 64 went out and one returned. Between 10:15 and 10:20 only 24 went out and 15 returned unladen, not having gone as far as their tree; and in the next five minutes only 12 went out but 21 returned unladen. The first wave of carriers was apparently over but the sun broke through the clouds and, whether that had anything to do with it or not, from 10:30 to 10:35 there were 59 outgoing ants and only three going back unladen. In the following three five-minute periods there were 25 outgoing and 10 returning unladen; 158 (including a big "soldier") outgoing and 12 returning unladen; and 43 outgoing and 12 returning unladen. Then it became cloudy again and in the following successive five-minute intervals the ratios between outgoing ants and those returning unladen were: 4 to 19; 1 to 41; 14 to 44; 32 to 32; and 24 to 22. It seemed as though the cloudiness was driving the ants back. Between 11:15 and 11:20 there were 12 outgoing but among the 57 incoming ants one had a piece of leaf; and between 11:25 and 11:30, while 25 went out and 26 returned, two of the latter had burdens. Then successive intervals gave the counts shown in Table I.

TABLE I

Time	Outgoing	Ingoing	
		Unladen	Laden
11:30–11:35	79	9	7
11:35–11:40	138	4	7
11:40–11:45	75	11	19
11:45–11:50	97	7	22
11:50–11:55	60	5	26

The day's work was now under way.

March 21.—Only a light haze. Preliminaries much as yesterday. No ants went down the trail before 9:00, but then they started as is shown in Table II, an hour earlier than yesterday.

TABLE II

Time	Outgoing	Ingoing	
		Unladen	Laden
9:00– 9:05	28	1	
9:05– 9:10	69	7	
9:10– 9:15	34	11	
9:15– 9:20	13	26	
9:20– 9:25	34	13	
9:25– 9:30	21	32	
9:30– 9:35	11	25	1
9:35– 9:40	126	22	
9:40– 9:45	64	8	1
9:45– 9:50	33	24	2
9:50– 9:55	21	13	3
9:55–10:00	22	68	4
10:00–10:05	2	16	9
10:05–10:10	9	8	14
10:10–10:15	38	6	21
10:15–10:20	56	20	20

The suddenness with which work starts as well as what seems to be the stimulus of the first leaves to be brought in is illustrated by this apparently typical day.

No detailed accounts such as these were made the next two days and on March 24, the sun having risen in a nearly cloudless sky, the ants were already on the trail at 8:10, when I arrived. However, Table III illustrates the apparent effect of bringing in the first pieces of fresh leaves, as well as the greater activity on a bright day. (Note that this table does not include the first wave of carriers starting out from the nest.)

TABLE III

Time	Outgoing	Ingoing	
		Unladen	Laden
8:15– 8:20	8	4	
8:20– 8:25	5	6	1
8:25– 8:30	13	4	
8:30– 8:35	49	9	2
8:35– 8:40	189	10	9
8:40– 8:45	177	14	17
8:45– 8:50	131	12	20
8:50– 8:55	147	15	36
8:55– 9:00	47	15	26
9:00– 9:05	35	11	18
9:05– 9:10	61	17	37
9:10– 9:15	81	40	45

Other days had indicated the probable connection between the strength of the sunlight and the hour at which these ants started to work. Unfortunately, I had no instrument that would measure the light accurately enough to determine satisfactorily the amount of such a correlation, and future students should not forget that ultra-violet is probably of great importance.[1] However, during the evening of March 24, I made a canopy of black focusing cloth over the nest, arranging it so that it was at least six inches above any surface on which the ants would walk the next day. Sunrise of March 25 was unusually bright and there were practically no clouds until late afternoon, but not an ant left the shaded nest until 8:55, when a few of the smallest workers that do not seem to be of much value as carriers ventured forth. By 9:00, however, some of the regular carriers had left the edge of the shade and reached the bright sun and then the egress began in earnest, as is shown by the following counts of outgoing ants in the successive five-minute intervals of the next hour: 18, 76, 32, 75, 22, 24, 11 (removed the canopy; carriers with fresh leaves were coming back), 92, 83, 60, 56, and 123.

March 26 was another bright day and when I arrived at 8:00 A.M. the ants were already bringing in great quantities of leaves. The next day, also very bright, I arrived at 7:10 and found that the ants were already starting out.

[1]See Lutz, 1924, Ann. N. Y. Acad. Sci., XXIX, pp. 181–283.

There seems little room for doubt that light is a controlling factor, but it may act in conjunction with a physiological rhythm and, of course, we have as yet no measure of the amount of light which is necessary to start things going.

Deferring for a bit of discussion of the other points, Table IV, giving data for the partly cloudy afternoon of March 19, is presented as fairly typical of the quitting of outside work for the day. The count was made at a place on the trail about thirty feet from the nest.

TABLE IV

Time	Outgoing	Ingoing	
		Unladen	Laden
3:47– 3:52	6	13	16
3:56– 4:01	9	13	23
4:02– 4:07	6	15	22
4:09– 4:14	3	21	13
4:15– 4:20	1	15	20
4:21– 4:26	4	13	12
4:27– 4:32	3	14	20
4:33– 4:38		8	14
4:39– 4:44		4	9
4:45– 4:50		1	2
4:51– 4:56		1	6
4:57– 5:02		1	
5:03– 5:08			

By taking the algebraic sums of the numbers of outgoing and in coming ants one can determine the number of ants that were out on the trail at any time. For example, at noon of March 20 there were about 580 ants of this colony either going out, cutting leaves, or coming in.

Knowing how many leaves or pieces of leaves are carried to the nest in a day seemed to be of interest. Instead of spending a whole day to count them, I made a total of 57 five-minute counts at different times of several days, these counts being made after work had gotten well under way in the morning and before it had begun to slacken in the afternoon. The number of burdens passing a given point in any observed five minutes between these limits ranged from 12 to 69, the average being 24.9. Saying that the average rate is five per minute, the number of burdens in an average day of about eight hours work would be about 2400 pieces. Certainly 3000 pieces would seem to be a big day's work for this nest.

We have seen that there were 580 ants outside the nest at noon of March 20. Presumably, each was a potential carrier, although many came back to the nest unladen. Also, an unknown number of carriers were inside the nest at that time. If we estimate that the total number of carriers was only 600, it would mean that these workers do not average more than five pieces of leaf each per day, and it is quite probable that the average is less than four.

Now, the ants carrying leaves take, on the average, about 36 seconds to go a meter if they travel right along. Unladen ants can go even faster. The trip from nest to tree and back again was about 30 meters. An ant should make this, on the average, in 17 minutes. If we allow it five minutes to cut its piece out of a leaf, another five minutes to put it away in the nest, and three minutes for other purposes such as cleaning its antennæ, an ant might be expected to make a round trip in half an hour or at least sixteen, instead of four of five, such trips in an eight-hour day. If we wish to know whether any come up to this expectation it will be necessary to mark and watch individual ants and, furthermore, we do not know how much time the carriers give to gardening mushrooms and feeding larvæ, incidentally getting fed themselves, but a "sluggard" who is disposed to argue might get considerable satisfaction in going to these ants.

Part of the difference between possible and actual work done is due to unladen ants interfering with laden ones. The speed of a meter in 36 seconds noted above was the average of about 300 observations of carriers whose progress was not interrupted on the timed stretch. Frequently, however, an incoming laden carrier is stopped momentarily by an outgoing sister who apparently is interested in what is being carried. To see how much this visiting during working hours cost the colony, 300 observations were made on all carriers, including those that were stopped a bit by outgoing ants, and it was found that the average time taken to go a meter was about 40 seconds. This is an average delay of about four seconds per meter or, since the outgoing ant stopped as long as she delayed the incoming one, 120 seconds for the round trip of 30 meters. If there are 3000 round trips per day this is a loss of 100 ant-hours per day. It may be necessary, but an efficiency expert might object.

That part of the trail which in my notes is called No. 6 was 41 feet from the nest and was a 93 per cent down-grade to the incoming laden ants. No. 5 was 33 feet from the nest and practically level, having a grade of only 3.9 per cent. No. 3 in my notes was ten feet from the nest and had a 76 per cent grade up which the laden ants must climb before descending a grade nearly as steep to their nest on the side of the hill. Uninterrupted ants covered a 50-centimeter stretch down the steep grade of No. 6 in average time of 17.6 seconds. They did 50 centimeters on the practically level No. 5 in an average time of only 15.7 seconds but it took them an average of 22.2 seconds on the steep up-grade of No. 3. Clearly, it is not as easy for these ants to carry burdens down the steep No. 6 as it is on the level, and it is still more difficult to carry up the steep No. 3. In fact, one ant was nearly a minute struggling fifty centimeters up the latter slope. This is the sort of thing that we might expect and the reason for mentioning it here is that the average time on this slope does not seem to have been increased by interruptions, for the average when I timed each of a hundred ants that came along was also 22.2 seconds. On the next hardest slope, the steep down-grade of No. 6, there was a 5.7 per cent delay, the average time of a hundred carriers being 18.6 seconds. But on the nearly level there was a 16.6 per cent delay, the average time being 18.3 instead of 15.7 seconds to go fifty centimeters. Just what this means is not clear. Possibly it is that when the ants are on difficult going they are not so likely to stop to visit as elsewhere. It does not do to "humanize" insects but, although trained in a mechanistic school, the more I have studied insects—possibly it is the older I get—the less inclined I have become to think of them as purely tropism-ruled, instinct-bound machines. Even so, the following observations rather surprised me.

Occasionally a carrier would get into trouble with its burden because the burden catches on something, the wind blows it off balance, or for some other reason. At such times both outgoing ants and those that are returning to the nest unladen gather round and pull the leaf this way and that. In the mixup the original carrier sometimes loses its piece of leaf entirely, one of the others carrying it off. Under these circumstances the original ant, having been on its way to the nest, would have been expected on the chain-instinct theory to continue going there, especially as it is quite common for these ants to return unladen; but things seemed to happen otherwise. The ant that had been relieved of its burden usually returned to the tree and the other ant carried the burden to the nest.

In order to get enough observations to be fairly certain of this point, I robbed twenty carriers, pulling the leaf away with fine forceps in as natural a fashion as possible. Usually the robbed ant would run about a bit as though looking for what it had lost and would spend a few seconds cleaning itself before setting out in earnest. Two of the twenty went on to the nest unladen but the other eighteen started back for the tree. One of these latter stopped an ingoing carrier and tried to take its burden but, failing, continued on its way. Of course, we can say that it is the presence of a burden that stimulates the carrier to go toward the nest and when this is lost it goes in the other direction, but then we must look for the stimulus that sends other ants from the tree to the nest unladen. To me it seems easier to believe that these creatures think.

The workers of this species are of several sizes, including small ones called subminims. After watching affairs on the liana trail for several hours I called them "bad little boys," but the sex of that is wrong, and after more watching I called them "just kids" that will never grow up. They are among the first out in the morning and among the last in at night, lingering around the entrance to the nest, but they seem to do little that is very useful. When a carrier is in trouble with its burden these subminims, if anywhere near, rush in and pull with the rest. In such a case the piece of leaf when finally balanced over a carrier's back will almost certainly have at least one of these subminims resting calmly on it and riding back toward the nest. However, these subminims do not always wait for trouble but often on their own initiative stop an incoming carrier and get on its leaf for a ride. Sometimes, when another carrier's leaf touches the one a rider is on, the rider will change conveyances and continue its journey on the other leaf. When reaching the steep up-grade of No. 3 about ten feet from the nest the riders often got off. I imagine that this action was not out of consideration for their struggling sister but either because progess was not sufficiently steady or because the subminims seemed rarely to ride all the way into the nest at any rate.

In order to determine more easily the proportion of leaves having riders, I hung a small mirror a short distance from the liana and on the side opposite me. I could then see both sides of an incoming leaf at once. Observations on more than thirteen hundred leaves at different times of the day and on different parts of the trail showed that subminims were hitch-hiking on five per cent of them. On stretch No. 5, thirty-three feet from the nest, they were riding on only about 1.3 per cent of the leaves but on No. 3, the steep up-grade ten feet from the nest, they were on 8.1 per cent of the leaves and then, as was said before, some got off so that on No. 1, three feet from the nest, they were on only 4.8 per cent of the leaves that passed. Since they weigh so little (about 1 mg.), their riding probably does the colony little harm and they seem to enjoy it greatly.

In discussing the carrying of burdens by these ants it should be remembered that they lift the pieces of leaf and actually carry, not drag, them. The relation between the weights[1] of ants and the weights[1] of the burdens they were carrying is shown in Table V and Figure 1. Small ants can not carry excessively large burdens, possibly partly because of the difficulty in balancing a large piece of leaf. The maximum (relative to the size of the ant) load observed was ten times the weight of its carrier. This is the instance noted in the table in the class A, 2.75, B, 30.25 and the ant was making an average speed of 1.56 cm. per second up the 76 per cent grade.

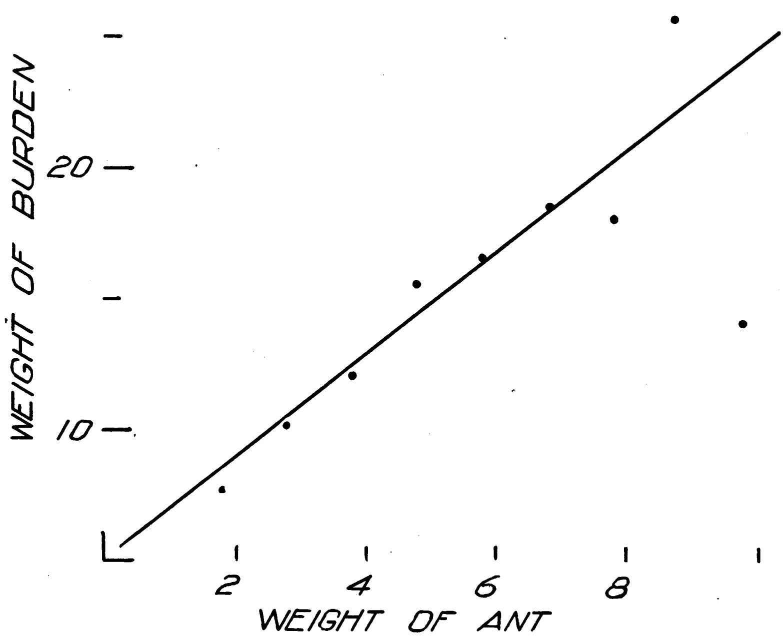

Fig. 1.—The relation between average weights of individual *Atta cephalotes* and the average weights of the burden carried.

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[1]These weights are those of specimens preserved in 75 per cent alcohol. The differences between them and "living weights" are less than the units of measuring and these, in turn, are less than the unit of grouping. Furthermore, it is a question of relative rather than of superexact absolute weights.

TABLE V

Weight of Ant

		1.75	2.75	3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	
Weight of Burden	2.25	1	8	5										14
Weight of Burden	6.25	4	22	18	8	4	2	1					1	60
Weight of Burden	10.25	2	29	28	16	13	4	2		2				96
Weight of Burden	14.25	1	14	22	17	15	1	2	1	1				74
Weight of Burden	18.25		8	8	12	4	5	1						38
Weight of Burden	22.25		1	5	7	7	6		1	1				28
Weight of Burden	26.25		1	4	4	5		3						17
Weight of Burden	30.25		1		1	4	2	1						9
Weight of Burden	34.25				3	1								4
Weight of Burden	38.25						1		1					2
		8	84	90	68	53	21	10	3	4			1	342

The fact that there is a correlation between the size of an ant and the weight of its burden does not, however, prove that there is a "choice" on the part of the ant. Still less does it prove that they deliberately cut a piece fitted to their strength. It merely means that if they try to start with an oversized piece—and I have often seen them do it—they do not get far with it and, so, do not get into the line of march. On the other hand, large ants more often than not carry burdens which seem unduly small. As a matter of fact, the average load, as observed, for the ants of this colony was roughly five milligrams more than twice the weight of the carrier. This is the formula of the straight line shown in Figure 1.

As would be expected, the data show at a glance that, in general, the greater the ratio of the weight of burden (B) to the size of the carrying ant as measured by its weight (A) the less the speed (S) expressed in centimeters per second. On the 76 per cent upgrade this correlation is -0.747 ± 0.029; on the 4 per cent upgrade it is -0.746 ± 0.027; and on the 93 per cent downgrade it is -0.634 ± 0.038. The equality of this correlation coefficient on the steep up-grade and on the nearly horizontal seems somewhat more surprising than the lessened correlation between B/A and S on the steep downgrade. One might have expected that the relative burden would have affected the speed less on the practically level stretch than on the steep upgrade. A possible explanation is that some other factor than weight is involved. Such a factor may be the difficulty of balancing a large piece of leaf.

Table VI

Speed on a +4 Per Cent Grade

Weight of Burden/Weight of Ant	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	
0.5						3	1	1	1			6
1.5					3	8	7	6	2	1	1	28
2.5				3	5	4	8	3				23
3.5			2	10	12	3	1	1				29
4.5		1	4	7	2	1	2					17
5.5		2	7	4								13
6.5	2											2
7.5			1		2							3
8.5	1											1
	3	3	14	24	24	19	19	11	3	1	1	122

Table VII

Speed on a +76 Per Cent Grade

Weight of Burden/Weight of Ant	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	
0.5					1		1			2
1.5					3	9	4		1	17
2.5			1	8	12	4	1			26
3.5			5	16	6	1				28
4.5		1	6	4	2	1				14
5.5		4	4		1					9
6.5	1		2	1						4
7.5		2								2
8.5										
9.5										
10.5			1							1
	1	7	19	29	25	15	6		1	103

Table VIII

Speed on a —93 Per Cent Grade

Weight of Burden/Weight of Ant	1.75	2.25	2.57	3.25	3.75	4.25	4.75	5.25	
0.5					1			1	2
1.5			2	3	8	1	1		15
2.5		2	10	13	9	4	1		39
3.5	3	4	12	5	3		1		28
4.5	3	5	4	6	1				19
5.5	3	3	2						8
6.5		2	1						3
7.5	1								1
	10	16	31	27	22	5	3	1	115

It is a favorite indoor sport of some people, after noting the ratio between the weight moved or the distance jumped by an insect and the size of the insect, to say that if the insect were as large as a man, a horse, or what-not, it could do most surprising things. This idea dies hard but can be passed with only a reference to Miall's discussion in his well-known 'The Structure and Life-history of the Cockroach,' where other discussions are cited.

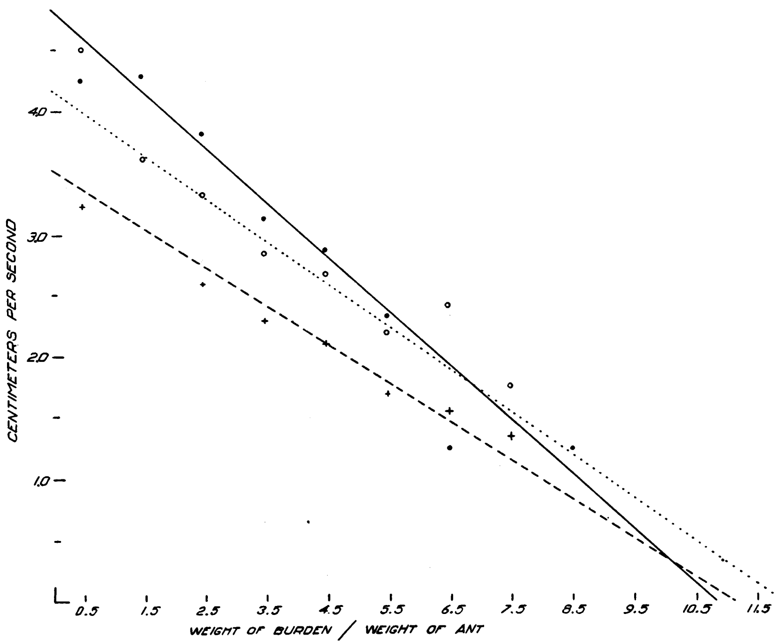

Fig. 2.—The relations between the average speed of *Atta cephalotes* and the relative weight of the burden carried on a + 4 per cent (dots), a —93 per cent (circles), and a + 76 per cent grade (crosses).

The present data do not tell very exactly how large a relative burden these ants can carry because, if the burden was so great that a carrier's speed was reduced to almost zero, other ants would gather around and by interferring would spoil the record. Fitting approximate straight lines to the graphs of average B/A plotted against average S and extending these lines to zero S we get an indication that a load of eleven or twelve times an ant's weight is about all it can carry. See Figure 2. The fact that each of these three lines (one for each of the path-grade considered) intersect the speed base-line at about the same point is another indication that some factor in addition to the weight of the burden influences the speed with which the burden is carried and that, were it not for this other factor, much larger pieces of leaf could be brought in.

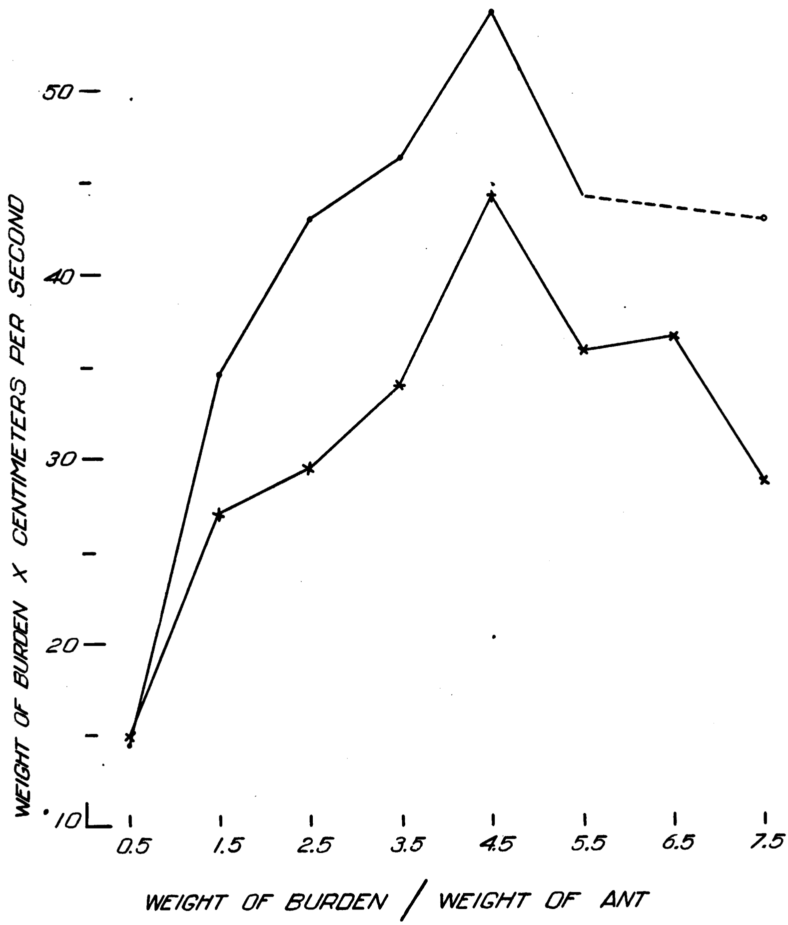

Fig. 3.—The relations between the burden-carring efficiency of *Atta cephalotes* and the relative weight of the burden carried on a + 4 per cent grade (dots) and + 76 per cent grade (crosses).

It would be interesting to know what is the maximum relative burden which it is PROFITABLE for an ant to carry. The colony may be considered as desiring that the largest number of milligrams of leaf be moved a given

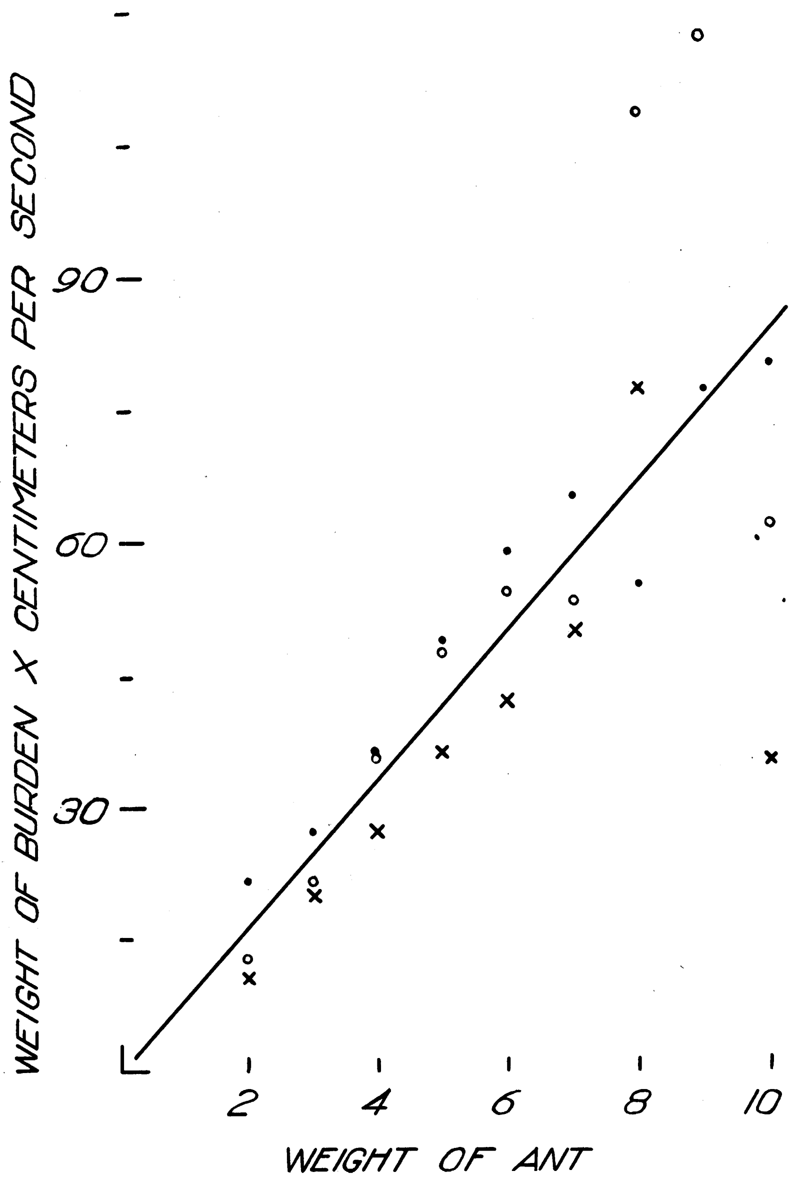

Fig. 4.—The relations between the weights of *Atta cephalotes* and their burden-carrying efficiency on a + 4 per cent (dots), a — 93 per cent (circles) and a + 76 per cent grade (crosses).

distance in a given time, in other words that burden times speed (BS) be as large as possible. Plotting BS against B/A for the practically level and the steep up-grade we get (Figure 3) curves which indicate that a load of about four and a half times the weight of the carrying ant is the most profitable load. Probably carrying this question into calculus would not give a more accurate answer because we have no basis on which to write a formula for the curves. However, since the average relative burden carried is only 3.1 times the weight of the carrier, it would seem that the ants might profitably cut rather larger pieces of leaf.

The relative burden carried decreases as the size of the ant increases. Thus, ants of the 2.25 mg. class averaged a load of 4.0 times their weight; 3.25 mg. ants, 3.6 times; 4.25 mg. ants, 3.3 times; 5.25 mg. ants, 3.1 times; 6.25 to 8.25 mg. ants, 2.6 times; and larger ones a load of only 1.9 times their own weight. We can not say definitely that this means that the smaller ants are more energetic than their larger sisters but the end-result is of that nature.

Which size of ant does the best work for the colony as judged by the milligram-centimeter transportation of leaf per second on a given trip? (Unless we mark individual ants we can not know how many trips per day the various sizes average.) The answer to this question is to be had by plotting BS against A, as is done in Figure 4. Combining the data of the three grades, practically horizontal, steep up, and steep down, we probably have a fair average of the whole trail. Apparently the relation is a straight-line one. Using the method of least squares and weighted averages we get, as a formula for the best line: Burden $\times$ Speed $= 8.67 \times$ Weight of Ant—1.20, the units being milligram, centimeter and second. For practical purposes it is sufficiently close to say that the transporting efficiency of these ants varied as eight and a half times the size of the ants as measured by their weight. Since the burdens carried varied by a lesser factor times the weight of the ant, it is clear that the greater efficiency of the larger ants is due to greater speed as well as to their carrying burdens that average absolutely larger although, as compared with the size of the ant, their burdens are relatively smaller than those carried by their smaller sisters. On this basis it seems just as well that the "minims," the exceedingly small members of the colony, stay in the nest attending the growing fungi, instead of attempting to do leaf-carrying work which their larger sisters do so much better.

Knowing the gradient of the path, the weight of the burden, the weight of the ant and the speed, one is tempted to hunt for a formula that would accord with the laws of mechanics and give us a measure of the power being used by the ants. I have spent in such an attempt an amount of time worthy of a better cause but have failed. Keeping in mind that an ant must lift and carry its own weight as well as that of its burden and that the strength of its muscles do not vary in simple proportion to their weight, putting in a factor to take care of trouble the ants have in balancing their burden, and making similar attempts to include other factors resulted in giving a theoretical speed that was too small on the up-grade or too great on the level. The missing factor seems to be that there is a speed on each grade which suits the ants and that they are not mere machines endowed with a given power which they use to the full according to the simple laws of physics. When going on the level they "take it easy" and when they come to an up-grade they use more power so that their speed, while not so great as on the level, is greater than any of my mechanistic formulæ anticipate.

In an attempt to discover something more about the different functions of ants of different sizes my plan of work for the early morning of March 27 was to station myself at the 50 cm. stretch called No. 5 on the liana trail before any ants reached there and then to collect and preserve the ants as they came along. They were picked off by hand, being careful to touch the liana as little as possible. The idea was to see whether the first lot of outgoing ants were chiefly relatively small ones, as I supposed they were. The plan failed in an interesting way.[1]

About fifteen feet after leaving the nest on the side of the hill the ants' trail descended to a roughly horizontal liana which was only about a foot from the ground near the beginning of No. 4. About eighteen feet beyond this point was No. 5. What happened this morning can best be told in chronological fashion.

7:10. The first outgoing ants have left the nest but have not yet reached No. 5.

7:15–7:20. Five ants (average weight 2.9 mg.) reached No. 5.

7:20–7:25. Fifteen ants (average weight 2.6 mg.) reached No. 5. In the little time they had to exhibit signs of disturbance before being picked off, most of them seemed puzzled and excited by something.

7:25–7-30. Nine ants (average weight 2.0 mg.) reached No. 5. Others are on the liana going back and forth just before crossing the line.

7:30–7:35. Only two small ants (0.6 and 1.5 mg.) crossed the line onto No. 5. Two *Cryptocerus umbraculatus* came along apparently undisturbed by anything.

[1]Not entirely failed, however. Of the 72 ants collected as described in what follows, 19 averaged 1.25 mg.; 30, 2.25; 14, 3.25; 6, 4.25; 2, 5.25; and one weighed 6.2 mg. In other words, these early-going ants were really small ones, averaging about 2.5 mg.

7:35–7:45. No leaf-cutting ants came on No. 5 in these ten minutes. Most of those that had nearly reached this point had gone back a considerable distance toward the nest. One *Cephalotes atratus* and two *Cryptocerus umbraculatus* came and were collected. Then the leaf-cutters seemed to get another urge to follow the day's routine.

7:45–7:50. The indication of this is that thirteen (average weight 2.3 mg.) reached No. 5 in this five-minute period. One *Neoponera striatinodis* also came.

7:50–7:55. Most of the outgoing ants are stopping before they reach No. 5 but five small ones (average weight 1.1 mg.) crossed the line, also two of *Cryptocerus umbraculatus.*

7:55–8:00. No leaf-cutters but two of *Cryptocerus umbraculatus.* At this time a dozen or more of the leaf-cutters are congregated about two feet before reaching No. 5. They seem to be waiting for something or else they were afraid to go on. At any rate, they went back.

8:05–9:05. In this entire hour only six leaf-cutters reached No. 5. There were, however, eleven of *Cryptocerus umbraculatus,* each being collected as it came along but NONE having acted as though there were anything unusual about the trail. The sun was bright all of this time and a number of leaf-cutters, perhaps forty or fifty, are congregated about the nest as though waiting for some signal. A few are wandering off the trail, going on a small branch near No. 4 to the ground.

In all of this time no "soldiers" had appeared and, so, either they do not exercise their supposed function thirty feet from the nest or what I did was not looked upon as an "attack." Notice that two hours have passed since the first ants started out to get leaves. The day's activities should have been well advanced and leaves coming in rapidly. At 8:50 I broke some pieces of leaf from a bush and dropped them near the nest opening. The ants took them in and at 9:00 a crowd started out of the nest and along the liana. The reaction was so promising that at 9:02 I dropped some more leaves on the ground near the nest and then went ahead to No. 5 to watch results.

9:05–9:10. The first ant to come near No. 5 seemed to dislike the trail there and turned back at once. Of a large number that almost crossed the line all but ten turned back. These ten were rather large, average weight being 3.8 mg.

9:10–9:15. The "wave" of outgoing ants had not quite stopped. Seven (average weight 2.1 mg.) crossed the line but the others went back and traffic in the forward direction entirely ceased.

Meanwhile, those ants which had wandered off of the trail near No. 4 and onto the ground began taking pieces of fallen leaves to the nest. At 9:40 ants were coming down No. 3 in large numbers, some going to the ground and coming back with pieces of leaves, others going on the regular trail but turning back at some point before crossing the line onto No. 5. No ants having ventured on this fatal strip during the past twenty-five minutes, I decided to stop the plan of collecting them.

At 9:43 one reached the edge of No. 5 but turned back. More are coming and at 9:46 eighteen are in the crowd milling about near the line. At 9:47 one crossed No. 5 and went about three feet beyond; then returned across No. 5 to the crowd that was stalled there. At 9:48½ five ants broke through whatever was preventing them from going ahead and then the rush began. Between 9:50 and 9:55 twenty-four went across, eight coming back before they reached the tree. The first ant carrying a leaf on the return trip passed No. 5 at 10:24. In the succeeding five minutes thirteen with leaves and sixteen without leaves passed going toward the nest; there were twenty-one outgoing ants. The arrival of these leaves at the nest caused great commotion there and a perfect upwelling of workers that started along the trail at once. There was no more hesitation at No. 5.

All of this proves very little about ants but in certain ways it seemed interesting. The finale was a beautiful demonstration of the effect which follows the first arrival of a band of workers bearing fresh leaves. The stimulus of the few pieces which I dropped on the nest or that of the fallen leaves which the workers carried in from the ground near No. 4 was as nothing compared to the explosive effect of what happened when the regular line of fresh leaves arrived.

Most clearly, what I did at No. 5 made an impression upon the remaining ants which resulted in overcoming their habit and—may one say it?—the urge to go along the liana for leaves to cut. The possibility that the captured ants communicated their distress by sound[1] may be ruled out at once, since whatever it was persisted long after the captured ants were dead.

Of the remaining possibilities, there is the probable and generally accepted factor of odor but it will have been noticed that this odor must have acted at a distance because the outgoing ants stopped before actually reaching No. 5; see, for example, the notes for 8:00 A.M., when the ants were huddled two feet away. If it was odor, it may have been the

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[1]Lutz, 1924, 'Insect Sounds,' Bull. Amer. Museum Nat. History, L, pp. 333–372.

odor of my fingers when they accidentally touched the liana in picking off the ants or it may have been some odor given off by the captured ants. I had previously determined that by rubbing the liana trail with my fingers I could so affect not only the leaf-cutters but also the other species of ants traveling this trail that they would hesitate when they came to the spot and even occasionally turn back. However, in today's work I took pains to avoid as much as possible touching the liana. Since ants of other species were not in the least disturbed by what I did today it seems clear that I really had avoided leaving an odor which would interest them. On the other hand, the leaf-cutters are much more disturbed by today's events than they ever were when I deliberately rubbed the trail.

This might indicate that the odor, if odor it be, is caused by the captured ants, but in previous days when collecting the more than four hundred ants carrying burdens I exercised no care, either as to touching the liana with my fingers or as to squeezing the ants, and no such effect as this was evident. Accordingly, one wonders whether odor was really the controlling factor.

If it was neither sound nor odor that upset the routine of these ants, what was it? I have a notion that upsetting the routine was what upset it. To an extremely methodical man this will be more understandable than it is to those of the other extreme; and ants, like insects in general, are quite methodical.

I have tried to picture in these notes how the colony, if undisturbed, does very much the same thing day after day, beginning with the first band that, when some condition, possibly light, becomes right, suddenly leaves the nest to go along the trail for the distant tree. Not all of this first band, and possibly none of them, go directly to the tree but, having gone a certain distance, an ant turns back while others go a bit farther, and so on. Finally the tree is reached and some ants come back with leaves, others without. When the leaves reach the nest, the stream of outgoing ants, which has rarely entirely stopped, is suddenly increased. This is routine; and a striking part of it is that at all times, even when the main body of moving ants is out-bound at the very start of the day a given ant does not go far before it meets at least one ant going in the opposite direction and stopping to exchange antennal touchings.

Now, when some circumstance such as an inquisitive human brings it to pass that there are no returning ants, it does not seem strange that the routine would be upset. In going to the office mornings I start off alone. I might not think it strange if I passed no one at first but if, in a street where there are ordinarily many acquaintances coming and going, I saw no one, I would be very apt to be at least surprised. What I did next might not be what my own brother would do in a similar case and certainly might be very different from what an ant might do even if an ant could think and was in a similar situation.

I fully realize that, even if one admits that it was the lack of ants returning from the front that demoralized a column thirty feet long, to say nothing of the hundreds of ants waiting in the nest for some signal, one can still avoid the necessity of saying that ants think by saying that these ants were deprived of the stimulus (incoming ants) for continued progression in an outward direction. Perhaps, if this is found by further work to be really what happened, it will be desirable to coin a new work ending in "–tropism" and to say that this word explains the deed. Meanwhile, an *Atta* colony remains a remarkable bit of natural history.