ON THE AMOUNT OF FOOD EATEN BY INSECTS [1]

GEORGE N. WOLCOTT, Entomologist, Insular Experiment Station.

In the course of another investigation, it became desirable to know how much food insects ate expressed in terms of the weight of the insect itself. A search of literature gave surprisingly little exact data on this point.

The caterpillar of *Telea polyphemus* Cramer, as noted by Trouvelot (I), "when 56 days old—is fully grown and has consumed not less than 120 oak leaves, weighing three-fourths of a pound; besides this it drank not less than ½ oz. of water. So the food taken by a single silkworm in 56 days equal in weight 86,000 times the primitive weight of the worm (1/20th grain). Of this, about ¼th lb. becomes excrementitious matter, 207 grains are assimilated and over 5 oz. have evaporated."

The amount of corn leaves eaten by the armyworm, *Cirphis unipuncta* Haworth, has been measured in square inches (2), and the amount of clover leaves eaten by the weevil, *Hypera punctata* Fabricius (3). None of this data however, was in terms of the weight of the insect, and for the first experiment, the tobacco hornworm, *Phlegethontius sexta jamaicensis* Butler, was chosen because of its large size, rapidity of development, availability in Porto Rico, and incidentally because of its economic importance.

Hornworm eggs weigh .00105 gram each, and the just hatched larva .0004 gram. The caterpillars were kept in small glass dishes with tightfitting covers, the size of the dish being increased as the caterpillar grew and needed more room. The food of the caterpillars in the first instar was not weighed, as the amount eaten was so minute, but the larvae were weighed daily, and their food and excrement in succeeding larval instars. The figures of daily consumption of food and gain in weight of the caterpillars were not comparable, as the larvae might recommence eating after molting at any time of day or night. But in general, they showed enormous consumption of food relative to the weight of the larva in the first, or first two, days of the instar, but actually larger consumption of food the last day previous to the pre-molting period because of the increased size of the larva. The apparent gain in weight was also greater in the first day or days of each instar because of partly digested food with which the alimentary canal was filled, and there was an ap-

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parent loss in weight in the pre-molting period as the digestive tract was emptied. But each instar represents a very definite period of growth, of which the net gain can be readily determined.

The Growth of Hornworm Caterpillars

Instar.	Days	Food consumed		Gain in weight				Excrement (Grams)	% of food
		Weight (Grams)	% of Total	Grams	% of total	% Increase	% of food		
Larva "*A*"									
1st.........	3	.0208 gr.	1 %	.0071	.2 %	1750%	34.2*		
2nd.........	4	.0732 gr.	.4 %	.0285	.9 %	406%	38.9		
3rd.........	5	.4994	2.7	.1448	3 4	508	28.9		
4th.........	5	1.62	8 7	.5948	13.9	411	36.7	.7446 gr.	45.9
5th.........	7	16.0367	86.6	3.4976	81.9	588	21.8	10.0032	62.4
Total....	24	18.2501		4.2732		10733	23.4	10.7478 gr. plus	59.
Larva "*B*"									
1st.........	4	.0187 gr.	.08%	.0064 gr.	.1 %	1600	34.2*		
2nd.........	6	.0788 gr.	.6 %	.0277	.5	432	34 9		
3rd.........	5	.4067	1.7	.1359	2.7	490	33 4	.1176 gr.	28.9%
4th.........	5	2.7756	12.	.8764	17.6	645	31.5	1.5908	57.3
5th.........	7	19.6591	85 6	3.934	78.9	448	20.0	12.5224	63.7
Total....	27	22.9389 gr.		4 9818		12455	21.7	14.2308 gr. plus	61.8
Larva "*C*"									
1st.........	4	.017 gr.	0.7	.0058	.1	1450	34.2*		
2nd.........	4	.0478	.6	.0482	.8	831	32.6	.0232	15 7
3rd.........	4	.3334	1.3	.1146	1.9	238	34.2	.091	27.2
4th.........	5	2.7845	10.9	1 0188	16.7	889	36.5	1.3612	48.8
5th.........	9	22.1636	87.1	4 9203	80.6	483	22.2	12.9584	58.4
Total....	26	25.4461 gr.		6.1077 gr.		15269	24.	14.4338 gr.	56.7

* Computed: average of 2nd, 3d and 4th of all three larvae.
Days of 5th instar are those to attain maximum weight, not to pupation.

Of the food consumed, between a fourth and a fifth becomes caterpillar, and nearly two-thirds excrement. Both fresh tobacco leaves and fresh excrement contain about 86 per cent water—oven-dry leaves are 14.2 per cent of their fresh weight and oven-dry excrement 14.01 per cent—and presumably the caterpillars contained as high a percentage of moisture; thus the figures on fresh leaves, living caterpillars and moist excrement are about the same in relation to each other as those of oven-dry material. The data on excrement appears to show a decreasing digestibility of the food as the caterpillars increase in size, and the last pellets excreted before pupation are lighter in color and possibly not as thoroly digested as the others. But, aside from this, it actually indicates a partial drying-out of the excrement in the earlier instars because of the proportionately larger container used for the caterpillars when they were small. An average of the figures for the excrement for the 4th and 5th instars—54 per cent of the weight of the food consumed—is probably approximately correct for the entire larval period. The smaller net gain of the caterpillar from the food consumed in the last instar is due to the physiologic changes occurring in preparation to pupation and not to a difference in digestibility of the food. These physiologic changes and the ordinary muscular activities of the caterpillar entail the production of urates and other waste products. In addition to the undigested food, the pellets of excrement contain these waste products, which correspond to the urine in higher animals. As these two constituents of the excrement can not be mechanically separated, the presence of the urates adds another factor of error in the data on the excrement. It is however, a relatively constant element for most non-active caterpillars, and will increase considerably in amount in the last instar. The digestibility of, or rather, the net return from, tobacco leaves by hornworm caterpillars is around 40 per cent, most of which becomes caterpillar in the earlier instars, but nearly half of which is used up in internal changes in the final larval instar.

The data on maximum net gain are not so accurate as might be wished, for the weighing should be made as soon as the last pellet of excrement is eliminated, and not at the convenience of the experimenter, as the daily loss in weight after the maximum is reached, at least in the fifth instar, amounts to about a third of the live weight, and as is later shown, the pupa weighs scarcely half the maximum of the larva. The remaining difference between food and caterpillar plus excrement is accounted for as losses of respiration of CO^2 and H^2O from the caterpillar, and from the leaf after weighing before it was consumed. Fresh tobacco leaves lost twenty to twenty-five per cent of their weight the first day kept in tightly-covered glass containers, and the caterpillars never obtained all of the moisture they are credited with. There is also a loss of from one to three per cent at each molt—the weight of the cast skin—and possibly an even greater, but incalculable, loss in the molting fluid.

For comparison with vertebrates which develop rapidly, the pounds of dry matter per day for each one hundred pounds of live weight of chickens and ducks, as given by Mr. Wm. P. Wheeler (4) is:

	Chickens	Ducks	Hornworm Caterpillars
First two weeks	10.1	17.2	20. (first four instars)
Two to four weeks	9.6	17.0	46. (fifth instar)

The large consumption of food in the last instar of the caterpillar is for the internal activities and changes, and maintenance, until the adult can obtain food. It is surprising that a sluggish, cold-blooded insect should consume so much more than active birds which have a high body temperature to maintain, even tho the birds are able to digest, on the average, twice as much of their food.

The caterpillar of *Phlegethontius sexta* attains in 26 days, 12,486 times its original weight (1/2500 gram) and has eaten an amount of food 55,600 times its primitive weight; that is, in half the time required by *Telea polyphemus* it attains more than three times the relative weight of the latter and consumes nearly one-third less food. The difference is due to many factors, the most obvious being the difference in weight of the just-hatched larva, 1/2500 gram for the hornworm and 1/20th gram for the silkworm, which is an unfortunate selection as a basis for comparison. Actually, however, the data carried thus far means practically nothing, as the fully grown caterpillar is not an adult insect—it has merely attained its maximum growth.

Of the three caterpillars, one, "A", escaped when fully grown and lost its life in a battle with a lizard. The other two were reared to adult and from them the following data was obtained:

	"B"	"C"
Weight of pupa, February 2	2.541 gr.	3.0895 gr.
Weight of pupa, February 13	2.3155 gr.	2.8542 gr.
Per cent of daily loss	.842%	.672%
Computed weight of pupa at beginning	2.648 gr.	3.1965 gr.
Computed weight of pupa at end	2.1443 gr.	2.7044 gr.
Weight of pupal skin	.0346 gr.	.0344 gr.
Computed weight of meconium and H_2O loss	1.4105 gr.	1.6518 gr.
Weight of food eaten by larva	23.02 gr.	25.447 gr.
Live weight of adult	.6992 gr.	1.0182 gr.
Per cent of weight of food eaten by larva	3.02%	4.001%
Oven-dry weight of food eaten by larva	3.225 gr.	3.565 gr.
Oven-dry weight of adult	.277 gr.	.399 gr.
Per cent of weight of food eaten by larva	8.6%	11.2%
Ratio: Weight of adult to food eaten by larva	1:11.6	1:8.9
	a *male*	a *female*

The pupæ were not weighed daily as it was feared that the incidental disturbance might prevent the emergence of adults. The loss of H^2O from the pupæ was possibly abnormal, as they were not buried in moist soil, but kept in a closed glass container. The meconium, which consists of the non-gaseous by-products of the activities of the insect since the first day after it, as a fully-grown caterpillar ceased voiding excrement, is excreted by the moth immediately on emergence and was so scattered that it could not be weighed to separate it from the loss of water experienced by the moth in expanding and drying its wings, and the combined weight of these factors is determined by difference between pupa and adult plus pupal skin.

The computed maximum oven-dry weight of the larva is 2.15 times (2.15 for "B", 2.14 for "C") that of the adult; that is, the insect loses over half its dry weight in transforming from larva to adult. The final data showing that the oven-dry weight of the food consumed by the larva is approximately ten times that of the oven-dry weight of the moth, is only an approximation for the species, but even of two insects, gives a basis for comparison with other insects.

Mr. J. J. Davis has very kindly furnished the air-dry weights of adults of *Cirphis unipuncta* (ten museum specimens) as being approximately .048 plus grams. Ten weighed .489 gr., five weighed 235 gr. The air-dry weight of corn leaves from young plants is .02108 gr. per square inch, and .0311 gr. for leaves from mature plants of which the armyworms ate 41.4 square inches to complete their development, or from .872712 gr. to 1.28754 gr. The adult weighs only from 5.5 per cent or 1/18th, to 4.—per cent or 1/26 of this. Its larval period—26½ days—averaged one-sixth less than the hornworm, and obviously corn leaves are less nutritious for armyworms than tobacco leaves are for hornworms.

Indeed the results computed from Mr. Davis' data are so far removed from those on tobacco hornworms that it seemed desirable to determine how great are the variations in the amount of food eaten by caterpillars on different and the same host plants. In most of the feeding experiments which were subsequently conducted, only the last and the next to the last instars were used; the amount of food consumed in the earlier instars, small in any case, being usually computed from that eaten in the next to the last larval instar. The excrement and the portions of uneaten leaf were dried before weighing, to eliminate the error due to partial drying-out which appeared in the hornworm experiment.

Several larvæ of *Feltia annexa* Treitsche, a common cutworm of tobacco in Porto Rico, were used in the first experiment, but only one transformed to adult under the abnormal conditions involved.

	Maximum gross Weight of larvae	Weight of food eaten while under observation		Excrement: Dry weight	Digestibility of food
		Fresh	Dry		
1.....	.807 gr.	3.891 gr.	.551522 gr.	.175 gr.	60%
2.....	.767 gr.	4.517 gr.	.641414 gr.	.253 gr.	60%
3	.643 gr.	5.582 gr.	.792644 gr.	.361 gr.	55%
4.....	.37 gr.	(died)			

Larva number three transformed to an adult which weighed (dry) .064 gr., and its larva had eaten 3.746 gr. of fresh tobacco leaves, or .5244 gr., dry, or 8.2 times as much as the weight of the adult.

A larva of *Prodenia* sp., another less common cutworm of tobacco in Porto Rico, which attained a maximum live weight of 1.7 gr., ate 6.697 gr. (5.6253 gr. weighed and 1.077 gr. computed) of fresh tobacco leaves, or .93758 gr., but died in pupating. Other adults (air-dry) weigh about .1 gr., so its relation to food eaten is probably very much the same as of *Feltia*. Also, an approximately equal portion of the food which it ate was transformed into insect—55 per cent—as of the 5.6253 gr. of food weighed out to it, .36 gr. of dry excrement was obtained. The two cutworms were able to digest and assimilate 55 to 60 per cent of the tobacco leaves and produce adults weighing a little more than one-tenth as much as the food they ate. The hornworm caterpillars, which were able to digest only a little more than 40 per cent of the tobacco leaves, nevertheless produced adults which weighed about one-tenth of that of the food they ate.

A fresh cotton leaf was given to three larvæ of *Alabama argillacea* Hübner which had just molted to the last instar. In three days they had consumed practically all of it and spun cocoons to pupate. The amount actually eaten, after the weight of the stem and the fragments had been subtracted, equalled 4.0488 gr., or dry, .971712 gr. The total net weight of the caterpillars at the beginning of the instar was .2436 gr., and at the end .816 gr., a gain of .5724 gr., or 235 per cent, but this is only 14.1 per cent of the weight of the food eaten. The dry excrement weighed .6448 gr., thus the digestibility of the cotton leaf by these caterpillars is less than that of tobacco, or 34.7 per cent. The hornworms gained approximately 80 per cent of their weight in the last instar, but ate 85 per cent of their food at this time. The *Alabama* caterpillars gained 70 per cent of their weight in the last instar, and may be presumed to have eaten about 75 per cent of their food in this instar. On this basis, the total food eaten amounted to 1.3 gr. (dry weight) to produce three moths whose dry weight was .1025 gr., giving a ratio of moth to food of 1 to 12.6. The lower digestibility of the cotton leaf by the *Alabama* caterpillars necessitated a greater amount of it to produce a proportionate amount of insect.

A larva of *Laphygma frugiperda* S. & A., was able to digest only 25 per cent of tender corn leaves with which it was fed, and the adult (dry) weighed one-twentieth of the dry weight of the food that the larva had eaten. Comparing this data with the results obtained by Mr. Davis with the armyworms, which were also fed on corn, it appears that substantially similar insects feeding on the same host require relatively the same amount of food to produce adults.

More extensive experiments with fifteen larvæ of *Xylomiges eridania* Cramer and ten larvæ of *Bombyx mori* Fabricius, fed on the leaves of mulberry, with food and larvæ weighed after their first instar, give somewhat similar results. The caterpillars of the Noctuid, *Xylomiges,* digested 36 per cent of the somewhat dry and fibrous leaves of *Morus tartarica,* and ate 26.4 times as much food as their adults weighed. The silkworms digested 41 per cent of the tender leaves of *Morus alba,* and ate 23.8 times as much food as their adults weighed. The cocoons produced by ten caterpillars weighed 9.702 gr., of which the silk was 1.1195 gr., or 4.2 per cent of the weight of the food eaten. The weight of the moths (air-dry) was .601 gr., and of 1392 eggs, computed from that of unhatched eggs of previous generations, .599 gr., a total of 1.1 gr., for adults and eggs, or not so much as the weight of the silk. The digestibility of mulberry leaves by these caterpillars was greater than that of cotton and corn, but they ate considerably more of them to produce adults. Apparently it is true in only a rather general way that the amount of food required by insects is inversely proportional to its digestibility.

In the following table, the air-dry weight of the food of some other insects is compared with the weight of the adult, and the ratio between them given. None of this data is as accurate as might be desired, as the weight of all of the insects is plus the weight of food and excrement in the alimentary canal, and is not net as was that of the hornworm and of some of the other caterpillars.

The Amount of Food Needed to Produce an Adult Insect

Insect	Weight of adult in grams	Food or Host	Its weight in grams	Ratio
Hypera punctata Fabr.	.01552	3.09 sq. in. of clover leaves	.10297	1:7
Bruchus dominicanus Jekel	.00312	beans of *Acacia farnesiana*	.02294	1:7.38
Tiphia transversa Say	.024	*Lachnosterna* white grubs	.27325	1:9
Tiphia spp. (females)	.0276			
Campsomeris dorsata Fabr. male	.039	grubs of *Ligyrus tumulosus* Burm.	.28	1:7
Campsomeris dorsata Fabr. female	.046			1:6
Elis haemorrhoidalis Fabr. male	.006	grubs of *Phytalus apicalis* Blanchard	.03562	1:6
Elis haemorrhoidalis Fabr. female	.013			1:3.-
Pyrgota undata Wiedemann	.222	*Lachnosterna dubia* Sm.	.21	1:9
		Lachnosterna fusca Fr.	.17	1:8
Ophion bilineatus Say	.019	Caterpillars of *Feltia venerabilis* Walker	.1178	1:6.2

An additional source of error in the above data is that in the case of the parasitic insects which suck the juices from their prey, the weight of the chinitous exoskeleton of the host, which, strictly speaking, is not eaten, has not been subtracted from the weights given, and this would give an even lower ratio than is indicated. Thus, predaceous insects, which swallow their prey instead of sucking the juice out of it, presumably have about the same ratio as is given for the parasites in the table. The phytophagous insects also have about the same ratio when the food is leguminous, in which case it is a balanced ration, the crude fiber of the plants ingested being the equivalent of the indigestible chitin eaten by the predaceous insects. In the vegetative portion of non-legumes, the amount of protein present is much lower, and greater amounts of such food—roots, stems and leaves—must be consumed by the insect. The cell-sap of plants may form a perfectly balanced ration for some insects, as is indicated by the fact that the excreta of the leafhopper, *Kolla similis* Walker, even when feeding on the young shoots of sugar-cane, is clear, colorless, tasteless and devoid of sugar (5). Such an almost perfect consumption by an insect of the plant juices on which it feeds is due to its active habits. By contrast, the honey-dew excreted by aphids and mealybugs is an excess of carbohydrates which can not be assimilated by these sluggish insects because of their very rapid growth and lack of muscular activity.

Animal and plant juices may be almost entirely completely assimilated by most of the insects feeding on them, and they undoubtedly furnish food in its most digestible form. But the digestive apparatus of animals feeding on crude fibre is adapted to its digestion. The decaying plant tissue eaten by snails, slugs, millipedes and sowbugs, and the cow-dung inhabited by some of these animals and Elaterid and Threviid larvæ can be digested by them. One thinks of wood as being entirely cellulose, and entirely undigestible, yet the termite *Cryptotermes brevis* Walker, due to the protozoa present in its alimentary canal which dissolve the cellulose, can assimilate over half of some kinds of woods eaten by it. Of other, less preferred woods, it assimilates smaller portions (6), but this only further serves to illustrate the point that the digestive apparatus of animals is usually well adapted to digest the foods which they prefer and ordinarily eat.

The consumption of food by an organism has these purposes: (1) maintenance, (2) growth, (3) reproduction and (4) storage for any of the three. Some insects concentrate the consumption of food for all of these purposes into the larval period, while many continue to eat when adult for maintenance and reproduction, but growth for practically all is confined to the larval period. In a general way it is known that of the warm-blooded animals, those maturing most rapidly obtain a greater adult weight for the food consumed than those which mature more slowly, and the smaller animals require more for maintenance in proportion to their size, while cold-blooded animals require food for maintenance only in proportion to thair size and activity, but like the warm-blooded, inversely in proportion to their rate of growth. It is obvious that insects which develop slowly, such as white grubs and wireworms which may require three to five years to become adult in the northern United States, eat less per day in proportion to their size, but certainly consume more for maintenance because they live so long. Active insects with a rapid development, like grasshoppers, eat most per day, but make a less advantageous use of their food for growth than do other insects with about the same rapidity of development that remain quiet and consume less energy in voluntary activity, such as caterpillars. Insects which develop wings and heavy chitinization, and with a complete metamorphosis in their development, require more food for these structures and for the changes and losses involved in passing thru the pupal period, especially when this is protected by an extensive silken cocoon. The cocoons of *Tiphia* and *Bombyx* weigh somewhat more than the air-dry weight of the adults, and that of *Ophion* twice as much.

Two of the factors involved in the most economical use of foods for growth by insects have to do with the food, (1) the closeness with which it approximates being a balanced ration for supplying the needs of the insect, and (2) its digestibility. The others have to do with the insect, its rapidity of development, the amount of its activity, and the production of wings, scales, wax, heavy chitinization and similar structures.

Honey-dew and the nectar of flowers, altho not used for growth, are admirably adapted to the needs of adult insects with a high rate of muscular activity, such as butterflies, moths, flies, bees, wasps and ants. All of these insects in their larval stage, no matter what their food may have been, primarily required from it the proteids which were essential to growth. But as adults, carbohydrates, especially if in solution and readily available for assimilation, much better meet their needs. Insects which are not especially active as adults, such as most phytophagous and scavenger beetles, may continue to eat the same kind of food that was acceptable to them as larvæ, for the usually small proteid content of their food is now essential for reproduction. Most of the predaceous insects, such as dragon flies and the Carabid and Cicindellid beetles, are as active as any of those feeding on pure carbohydrates, but swift motility to capture their prey is essential, and is maintained despite the high proteid content of their food.

Many insects live for a long time as adults, the eggs of the female not maturing for some time after the emergence of the adult from the pupal stage. Such insects consume more food for maintenance as adults and for reproduction than they did as larvæ for growth. The clover-leaf beetle as an adult eats 4.76 square inches of leaves and "at least an equal amount of stem" (3) for maintenance, aestivation and reproduction, as compared with 3.09 square inches of leaves eaten by the larva for growth and maintenance. An Otiorhynchid beetle, *Exophthalmodes roseipes* Chevrolat, feeding on the leaves of sea-grape, *Coccoloba uvifera*, which have a digestibility of 42.6 per cent for this beetle, ate .399 gr. of the fresh leaf in four days, or about the equivalent of its own weight, .0982 gr., per day. However, as its dry weight was only 35.7 per cent of its live weight, and that of the tender sea-grape leaf only 19 per cent of the weight of fresh leaves, in a month the beetle would eat 16.2 times its own dry weight and such beetles in captivity at least, often live two or three months. -- The composition of the food, the length and activity of the life of the adult, the number and size of the eggs laid by the female all affect the amount of food which is consumed by the adult.

The amount of food required by an animal for growth, maintenance and reproduction varies so greatly and depends on such a large number of factors that for exact results it must be determined by direct measurement with individuals of the species concerned. But in a rather general way, it may be considered that the following classes of animals require approximately the amounts of dry weight of food multiplied by their own dry weight as indicated in the following table:

Food Required for Insects

Group of Insects	As larvae or nymphs for GROWTH.	As adults for MAINTENANCE and REPRODUCTION
Lepidoptera feeding on grass or other non-leguminous plants	20	
Coleoptera with same habits	20	30
Lepidoptera feeding on leguminous plant tissue	7	
Coleoptera with same habits	7	10
Grasshoppers, mostly grass feeders	15	15
Crickets, mixed feeders	10	10
Predaceous Insects and Ants	8	15
Aphids and Mealybugs	7	15 (aphids only)
Leafhoppers and other active Homoptera and Hemiptera	5	10
Spiders	5	10
Parasitic Insects	5 (or less)	

For determining the amount of damage caused by an insect pest to a crop, however, even if the amount of food eaten by the individual insect is known and the number of insects present in the field can be calculated, this does not give all the essential factors. In the case of living plants, the host is a growing organism which may increase enormously in size in only a few days. The predators and parasites of the insect are another unknown factor. They may gradually and quite evenly reduce the number of certain kinds of insects so that the product of their abundance by weight may remain constant. Or, the majority of the individuals of a species may be able to obtain full growth before being killed by their enemies. Also, the average abundance of an insect thruout the season seldom indicates its importance during the few weeks of its maximum activity. Each insect is a special case, and these considerations only suggest the numerous difficulties attending the solution of even the simplest individual problem of the absolute importance of one insect that feeds exclusively on a single host.

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