

THE FEEDING RATE OF THE AUSTRALIAN LADY BEETLE, *RODOLIA CARDINALIS*¹

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INTRODUCTION

Although entomological literature contains abundant testimony to the efficiency of the Australian lady beetle (or *Vedalia* beetle), *Rodolia cardinalis* (Muls.), as a predator of the cottony-cushion scale, *Icerya purchasi* Mask., there are few quantitative data on the feeding of this beetle. An article from the Department of Agriculture and Commerce of Japan² gives the average consumption of the male and of the female for short periods, but the size of the scales and the factors which may condition the rate of feeding are not considered. The present paper presents the results of experiments designed to measure the effect of such factors on the adult beetles. These investigations are a part of a larger project which includes detailed studies of the relations between a predator and its host. The work was conducted at New Orleans, La., in the laboratory of the Division of Tropical, Subtropical, and Ornamental Plant Insects of the Bureau of Entomology.

METHODS

The beetles were confined in 18-mesh screen-wire cylinders, approximately $2\frac{1}{4}$ inches in diameter by $3\frac{1}{2}$ inches high, with muslin tops and bottoms. They were fed on *Icerya purchasi* Mask. taken from infested *Pittosporum* bushes. When fresh leaves were used each day practically none of the scales left the screen cylinders. In a study of the movement of the scales it was found that when infested leaves were put in the cages, only 1 scale out of 364 was absent from the screen cylinders after 24 hours. On the basis of average weights (discussed later) this was a loss of less than one-half of 1 per cent. It was therefore possible to use a coarse-mesh screen, assuming that the beetles were actually subjected to the temperatures recorded by an insectary thermograph, which was checked daily against maximum and minimum thermometers.

In the first series of experiments observations were made daily. The records were taken between 8 a. m. and 8.30 a. m., a period when the temperature was near the minimum and when the beetles were eating less than at any time during the following 12 hours. In other series of experiments observations were made every four hours. In each case a record was made of the number of scales put into the cage and the number that remained at the time of the next observation, the difference giving the number eaten during that interval. Since there was a large difference in weight between scales of different ages, they were divided into three classes which were readily

¹ Received for publication Mar. 12, 1930; issued August, 1930.

² KUWANA, S. I. RESEARCHES ON THE COCCINELLID *VEDALIA* AND THE SCALE INSECT *ICERYA*. Japan. Dept. Agr. and Com., Injurious Insects and Pests Bul. 3, 107 p., illus. 1917.

distinguishable. "Small" scales were those of the first instar, "medium" scales included those of the second and third instars and a few of the fourth instar which differed little in size or appearance from the preceding instars, and "large" scales included the rest of the fourth instar and the adults. In order to eliminate one source of variation the large class was always removed from the leaves. Unfortunately an analytical balance was not available until these experiments were nearly completed. Weighings were then made of scales in the first two classes, and the numbers of scales eaten were converted to numbers of milligrams on the basis of average weights. The small scales were weighed in groups of 20, 500 scales giving a mean weight for this group of 1.936 ± 0.039 mgm.; the medium scales were weighed in groups of 4, 200 scales giving a group mean of 3.032 ± 0.093 mgm. The number of small scales, therefore, was multiplied by 0.0968, and the number of medium scales by 0.758 to give the milligrams of food consumed. This method introduces a source of variation, since there still remains a large difference in size of scales within the same class. However, no better method of recording the data was developed. It is not practicable to weigh the leaves at the beginning and end of the period, making determination and allowance for evaporation. Aside from the deposition of dust, eggs, and excrement on the leaves, the weight of the leaves is so great in proportion to the weight of the scales that variations in the evaporation rate would introduce enormous errors in calculating by weight differences the quantity of food eaten. It is believed that errors resulting from the method used have tended to average out because of the following considerations: *Icerya purchasi* produces continuously throughout the year and, consequently, in infestations of any age the scales are in all stages. Scales for all the daily observations and for most of the 4-hour ones were taken from two caged *Pittosporum* bushes which had been infested for over a year. During the course of the experiments no preponderance of any stage or stages was noted. Further evidence of the averaging out of the errors is found in the curves shown in the illustrations. Where each mean is the average of a considerable number of cases, the points fall rather closely into a smooth curve, a condition which would not be likely to exist unless there had been this averaging out of the errors introduced by the variation in size of the scales.

THE DAILY RECORDS

The records extended from September 3, 1925, to September 6, 1926, covering 11 broods of beetles, with a total of 2,152 observations, divided as follows: On pairs, 1,546; on single producing females, 324; on virgin females, 171; on virgin males, 111.

The 1,546 observations mentioned above were made on 75 pairs, the number of pairs to a brood ranging from 3 to 13. With the exception of a few records made on beetles kept under constant temperature, no experiments were conducted especially to obtain results from single females, but data were obtained in such cases, as the male died before the female.

It appeared possible that, in addition to temperature, several factors might affect the feeding rate of the beetles. The rate might vary with the age of the female. In some individuals the vital activities might proceed at a faster tempo than in others, in which case

under similar conditions there should be a difference in the average life span. There might be seasonal changes, as well as a progressive change with rearing in captivity and inbreeding. Accordingly correlations were made between the quantity of food consumed, in milligrams, and temperature, date (seasonal change), age, life span, and brood number (inbreeding), multiple curvilinear correlation methods being used.³ After two residuals has been calculated, the index of multiple correlation for the pair records, which include the majority of the cases, was found to be 0.81. For the single females only one residual was calculated with $R = 0.69$.

The effect of temperature on the rate of feeding is shown in Figure 1. The rate increased more rapidly with higher temperatures, while below 10° C. the feeding, if not completely stopped, was negligible, although the beetles did not go into the dormant condition. In discussing the mechanism of such an effect it should be considered that food in the case of the adult beetles serves ultimately as a source of

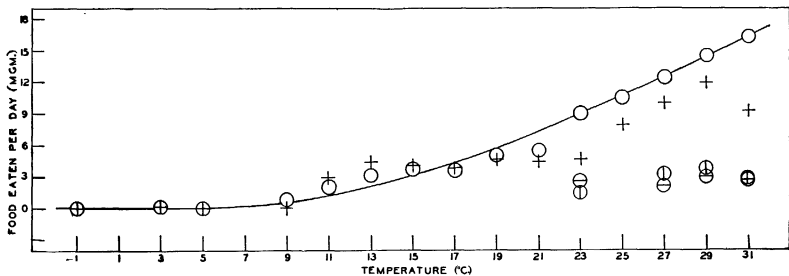


FIGURE 1.—Effect of temperature on quantity of food eaten by *Rodolia cardinalis*. Values for the pairs are represented by circles, values for single producing females by crosses, values for virgin males and for virgin females by circles with horizontal and vertical diameters, respectively. The smoothed curve has been fitted to the pair values. The graph has been fitted free-hand, but between 10° and 30° C. $y = -0.0207 + 0.9105X - 3.9480 \log X$ is an empirical equation giving a close approximation to the curve values

energy for (1) muscular movement, (2) replacement of tissue, and (3) production of eggs. The feeding rate of the beetles, therefore, might be conditioned by the foregoing processes, in which case it would be a resultant of several variables; or it might be directly a function of temperature, and itself the factor governing the rate of movement, egg production, and tissue repair; or the different activities might be independently affected by thermal change.

It is seen that the females ate the larger part of the food consumed by the pairs (the sex ratio was nearly 50 per cent, records on rearing 990 individuals showing 52.04 per cent females), but in contrast to the producing females, the virgin females showed about the same rate as the males. This fact indicates that feeding was dependent upon the rate of oviposition, since the virgin females produced only an occasional egg. If the feeding rate were directly a function of temperature, and the factor conditioning oviposition, no such difference should exist between producing and virgin females. The possibility of both being independently affected is also ruled out. Accordingly there should be a correlation between egg production and food consumption. (This should be true if either activity depended on the other,

³ EZEKIEL, M. A METHOD FOR HANDLING CURVILINEAR CORRELATION FOR ANY NUMBER OF VARIABLES. Jour. Amer. Statist. Assoc. 19: 444. 1924.

not if they were independently influenced by temperature.) In investigating this point the milligrams of food eaten and the number of eggs deposited were totaled for each individual, and correlations made on the basis of daily averages, a method necessary because of periodicities in the oviposition rate. Letting subscript 1 denote food, 2 eggs, 3 temperature, 4 life span, $r_{12.34} = 0.51$, $P = 0.01$.⁴ The effects of temperature and life span have been eliminated statistically, so that there was measured only the association of variations in the individual average feeding, independent of these influences, with variations in average oviposition. The more productive individuals were more effective not only because of their increased progeny, but also because they destroyed more scales during their lifetime.

In the case of vertebrates it is known that the hunger sensations arise from contractions in the empty stomach.⁵ While there is no direct evidence as to the existence of similar reactions in insects, the results presented above do indicate that an internal stimulus, dependent on utilization of food consumed, was involved in the feeding act. However, it was found that feeding did not take place in the absence

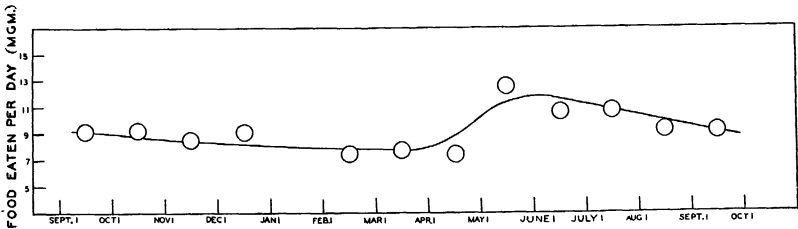


FIGURE 2.—Seasonal changes in daily feeding rate by pairs of *Rodolia cardinalis*

of the proper external stimulus. At the laboratory the beetles could not be induced to feed on any insect other than *Icerya purchasi*, no matter how great the degree of starvation. It appears, therefore, that in these experiments the feeding rate was a resultant of the rate of utilization of food consumed, and that both internal and external stimuli entered into the process. The effect of temperature upon feeding, then, was an indirect one, operating through the response of other activities to thermal change. Investigations not yet reported show temperature to have an important influence on the rate of oviposition. The effect of this factor on rate of movement has been demonstrated for other arthropods.^{6 7}

After temperature, season of the year most affects the rate of feeding, as is shown in Figure 2. The rate changed but little from September to April, but it then increased rapidly to a maximum early in June, declining as the summer progressed. Though the season of maximum feeding was also a season of high temperature, the temperature effect has been eliminated statistically. This was also a period of maximum light intensity.

⁴ FISHER, R. A. STATISTICAL METHODS FOR RESEARCH WORKERS. Ed. 2, rev. and enl., p. 159. Edinburgh and London, 1928.

⁵ CANNON, W. B., and WASHBURN, A. L. AN EXPLANATION OF HUNGER. Amer. Jour. Physiol. 29: 441-454, illus. 1912.

⁶ CROZIER, W. J. ON THE CRITICAL THERMAL INCREMENT FOR THE LOCOMOTION OF A DIPLOPOD. Jour. Gen. Physiol. 7: 123-136, illus. 1924.

⁷ ——— and STIER, T. B. TEMPERATURE CHARACTERISTIC FOR LOCOMOTOR ACTIVITY IN TENT CATERPILLARS. Jour. Gen. Physiol. 7: 123-136, illus.

In analyzing for the effect of age, the life span of each beetle was divided into 10 equal parts, in order to avoid absolute units such as days. The results for the pairs are shown in Figure 3. There was a sharp rise during the first three-tenths, after which the rate fell off slowly with increasing age.

The life span was found to have no significant effect, but the relations between temperature, life span, and food consumption were such that the total quantity of scales eaten per beetle was not a constant under different temperatures. When the total quantity of food was plotted against the mean temperature, the quantity of food eaten was found to be much less at the lower temperatures, although the values are too irregular to permit an exact expression of the relationship.

In estimating the effect of brood on the second residual the means for each brood fell irregularly, showing no significant change in the rate over 11 successive generations reared in the laboratory.

FOUR-HOUR RECORDS

In the second series of experiments the observations were made at shorter intervals. The beetles were caged as before and records

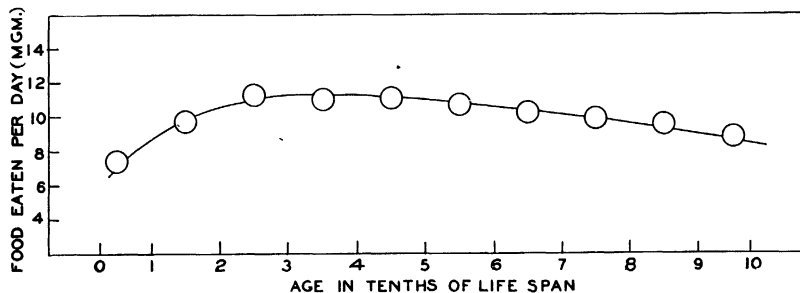


FIGURE 3.—Effect of age on daily feeding rate of pairs of *Rodolia cardinalis*

were taken every four hours. While the daily records were made on individuals bred continuously from the same stock, the 4-hour records were made on two different stocks. The first experiments in this series were made September 20 to 27, 1926, on the line used for daily records. In all, 13 pairs of beetles were used, giving 532 individual values. Beetles for the second set of experiments were taken from an isolated infestation on one bush in the field. Observations were made from March 26 to April 5, 1927, the number of pairs ranging from 9 (first day) to 21, a total of 916 individual records being obtained. Because of the short time covered by these experiments, the only factors considered were temperature and time of day. It was found that the statistical constants for the two sets of tests were quite different, the coefficient for the net regression of food on temperature being 0.171 for the data of 1926 and 0.302 for the data of 1927. Methods of multiple curvilinear correlation were used, and the values for the tests of 1926 were multiplied by the factor 1.32 and added to the data for 1927 to give the curves shown in Figures 4 and 5. The shape of the temperature curve is similar to that for the daily records.

The periodic nature of the feeding is shown in Figure 5. To test the effect of light, experiments were also made under constant light and temperature (25 ± 0.05). The values are shown in Table 1. The

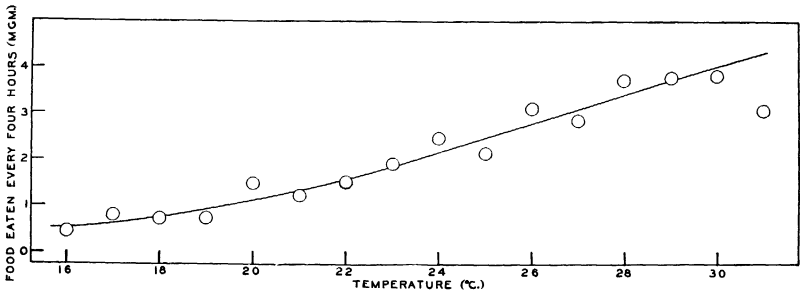


FIGURE 4.—Rate of feeding of *Rodolia cardinalis* as a function of temperature, based on observations of pairs of beetles at 4-hour intervals

probable errors of the means range from 6 to 12 per cent, but the values at 10 a. m. and 2 p. m. may be significantly lower than the rest. In any case it is seen that the curve of Figure 5 was materially altered when light was held constant. The simplest explanation of such an

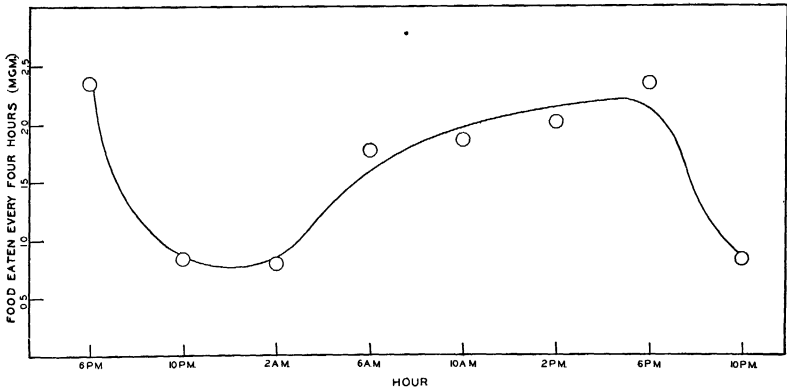


FIGURE 5.—Diurnal fluctuation in the feeding rate of *Rodolia cardinalis*, independent of temperature, based on observations of pairs of beetles at 4-hour intervals

effect would be that in the absence of light the motor activities of the insect were suppressed, resulting in contact with fewer of the external stimuli necessary for feeding. In a qualitative way such an effect on movement has been noted.

TABLE 1.—Diurnal fluctuation in feeding rate of *Rodolia cardinalis* under constant light and temperature

Hour	Average quantity of food eaten
	<i>Mgm.</i>
2 a. m.-----	1.37±0.12
6 a. m.-----	1.49±.12
10 a. m.-----	.88±.10
2 p. m.-----	.93±.11
6 p. m.-----	1.72±.11
10 p. m.-----	1.63±.12

An important point in these records is the difference in values of the regression coefficients. Similar differences were found also in the oviposition and developmental rates of the two stocks. It is evident that mathematical constants describing the rates of biological activities for a species are of doubtful validity. Rather do they represent an average of the particular individuals studied, and they may prove to be true of another population only if that population is composed of the same proportion of the same kinds of individuals. Further investigations are being conducted on this point.

SUMMARY

The daily feeding rate of *Rodolia cardinalis* (Muls.) was found to be a function of temperature, age, seasonal change, and sex. Both external and internal stimuli were involved, the quantity of food consumed varying with the rate of egg production.

The effect of temperature was an indirect one, operating through the response to thermal change of activities which condition feeding.

A pronounced seasonal change was observed, the beetles feeding at an increased rate from May through August, as compared with the rate from September to April.

The effect of age was such that the quantity of food consumed is lowest during the first tenth of the life span, rises to a maximum during the third, then shows a slight decrease.

No systematic change was noted in 11 successive broods reared in the laboratory, but a marked difference was found in a stock taken from the field.

Observations made every four hours showed the periodic nature of the feeding process. These diurnal fluctuations were modified under constant light.

