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Final-instar larvae of Tetragoneuria cynosura collected in Guilford Co., N.C. from October 1974 until March 1975 were subjected to experimental temperatures and photoperiods. These environmental factors were analyzed for their effects on food consumption, weight changes, and certain aspects of starvation in larvae. Animals were maintained at 11-hour and 14-hour photoperiods at temperatures of 15°C and 20°C until emergence. Three additional studies were also undertaken to investigate further the effects of photoperiodic induction on final-instar larvae.

Larvae maintained at either photoperiodic condition at 15°C showed no differences in rates of food consumption; however, differences did occur with larvae on the two daylengths maintained at 20°C. The most significant differences in feeding rates occurred when larvae housed at different temperatures on a constant photoperiod were compared. Larvae maintained at the higher temperature on both photoperiodic conditions had much higher feeding rates over their short-day counterparts. Animals that were used in feeding experiments from October until March responded faster to 14-hour daylengths than to 11-hour photoperiods. Weight changes in larvae of the experimental conditions were correlated with results obtained from the feeding studies.

Larvae collected in March were subjected to different conditions of starvation. When larvae were starved for the first two weeks following collection and then fed, they showed a pronounced increase in the rate of feeding over control fed larvae. Larvae fed for only the first two weeks following collection had similar feeding rates to the controls. Weight changes of all fed larvae corresponded to their feeding rates.

Animals that were starved continuously had a slight decrease in their weights.

Photoperiodic studies were undertaken to determine the minimal number of 14-hour days necessary to produce a long-day response. Animals collected in November, January, and February were maintained on an 11-hour photoperiod at respective temperatures of 20°C, 20°C, and 15°C after being subjected to a varying number of long-day photoperiods. Results at 20°C suggest that more than six but less than 21 long-day photoperiods are necessary for a response similar to that of long-day controls. However, at 15°C results suggest that all groups of larvae responded similarly to long days except animals subjected to only three long days.

SOME PRE-EMERGENCE STUDIES ON FINAL-INSTAR LARVAE OF *TETRAGONEURIA CYNOSURA* (ODONATA)

by

William Jeffrey Mantz III

A Thesis Submitted to
the Faculty of the Graduate School at
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in Partial Fulfillment
of the Requirements for the Degree
Master of Arts

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Approved

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Thesis Adviser

APPROVAL PAGE

This thesis has been approved by the following committee of the Faculty of the Graduate School at the University of North Carolina at Greensboro.

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I wish to express my sincere gratitude to Dr. P.E. Lutz who introduced me to the Order Odonata and to thank him for his guidance and generous time which he made available throughout the preparation of this study. I am also grateful to Jim Cheshire and Alice Holt who assisted in the collections of animals for this study. To the faculty and staff goes my appreciation for their thoughts and advice concerning this thesis.

TABLE OF CONTENTS

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LIST OF TABLES

LIST OF FIGURES

FIGURE Page

INTRODUCTION

In temperate climates larvae of the Order Odonata overwinter in various later instars. Some, like Tetragoneuria cynosura, overwinter in the final instar, and during this time many morphological and physiological changes take place. The larval stage just prior to emergence is extremely important for it is the final growth and developmental stage. Three environmental factors that are probably of most importance in determining the rate of growth and development are temperature, photoperiod, and food. Larvae affected by these factors have varying seasonal responses; thus, the rate of larval growth becomes a complex interaction of these factors.

Lutz and Jenner (1964) studied the life history of Tetragoneuria cynosura and qualified it as a spring species in accordance with the classification given by Corbet et al. (1960). Individuals of a spring species overwinter in the final instar, emerge early in the spring, and have a well-defined emergence period due to the synchronizing diapause stage in the final instar. While the emergence period has been determined in a number of dragonfly species, little is known of the larval activities preceding the period of transformation.

Pre-emergence studies on the rates of food consumption, weight changes, as well as effects of starvation, have received very little attention throughout the Order Odonata. Calvert (1947) made food consumption studies on two species of Aeshna, but rates of feeding on a day-to-day basis were not determined. Lutz (1962) made a preliminary

food consumption study comparing the effects of two daylengths on the rate of consumption in larvae of Tetragoneuria cynosura. Probably the most extensive study was undertaken by Kasimov (1956) in which he determined the daily rate of food consumption in larvae of Anax imperator. He compared the daily weights of the prey ingested to the body weight of the larvae. Kasimov (1956) also determined that oligochaetes were preferred food of dragonfly larvae over other aquatic prey, probably due to their benthic existence.

Through numerous experimental studies, both daylengths and temperature have been found to be instrumental in synchronizing the larval development and emergence of dragonflies. Photoperiodic studies by Corbet (1955, 1956), Jenner (1959), Schaller (1960), Montgomery and Macklin (1962), Lutz and Jenner (1964), and Lutz (1968, 1974a, b) have shown that daylength is an important factor in regulating larval development in several species of Odonata. Jenner (1959), Lutz and Jenner (1964), and Lutz (1974a) determined the effects of varying daylengths in larvae of Tetragoneuria cynosura. Data in which temperature was used as a factor in controlling larval development are quite limited. Corbet (1956, 1957) suggested that the rate of development in various instars of larva may be controlled by temperature. Lutz (1968, 1974a, b) suggested that elevated temperatures would induce rapid developmental responses in larval instars. In addition, Lutz (1974b) and Schaller (1960, 1962, 1965) have studied varying effects of temperature and daylength on larval development, but Lutz (1968) was the first to report both the separate and combined effects of temperature and photoperiod on larval development in Lestes eurinus. The roles of daylength and

temperature in synchronizing larval development are now quite evident, but the effects of these environmental factors on food consumption and body weight are not clearly known.

The present investigation was undertaken to give attention to the rates of food consumption and weight changes, and to explore aspects of starvation in larvae of Tetragoneuria cynosura collected in the final instar. The rates of food consumption and weight changes were followed from collection until emergence. To investigate further the separate and combined effects of temperature and photoperiod, these environmental factors were employed on final-instar larvae of T. cynosura to induce varying rates of food consumption as well as varying changes in weight. In order to investigate these environmental factors, different experimental conditions were used. In this way effects of light could then be determined when the temperature remained constant. In addition, the effects of varying the temperature could also be observed when the daylength remained constant.

Another aspect of this study was to analyze further the photoperiodic induction as reported by Lutz and Jenner (1964) in final-instar larvae of Tetragoneuria cynosura. Experimental studies were undertaken to determine the miminal number of 14-hour daylengths necessary to produce a long-day response.

MATERIALS AND METHODS

Collections of Tetragoneuria cynosura larvae in the final instar were made at a local impoundment in northwest Greensboro, Guilford County, North Carolina (lat. 36°05'N; long. 79°57'W). The pond was located ca. 460 m north of the intersection of N.C. State Road 2179 (New Garden Road) and N.C. State Road 2352 (Lake Jeanette Road); it had a surface area of about .64 ha with an elevation of approximately 250 m (825 ft) above sea level. In addition to an oak-hickory forest encompassing the pond, witch alders (Alnus serrulata) were found along the margins of the pond.

Six collections of final-instar larvae were made from 23 October 1974 until 18 March 1975. Four collections were made to study rates of larval food consumption in relation to photoperiod and temperature. Two other collections were made for inductive experiments.

Larvae were collected with a Cable-Turtox Scraper Net and placed directly into collecting bottles. In the laboratory animals were carefully separated by hand and randomly placed into individual 237 ml glass bottles filled with pond water obtained at time of collection. This procedure enabled larvae to adjust slowly to the higher experimental temperatures. Groups of larvae were maintained at their experimental conditions until emergence. A 12 cm length of dowel 1 cm in diameter was added to each bottle to provide a means for the larvae to leave the water at time of emergence.

Experimental animals were kept in refrigerated boxes containing fluorescent bulbs which were controlled by timers that supplied the photoperiod. Animals at 15°C were maintained in two Precision Scientific Co. (B.O.D.) boxes. Each contained a G.E. automatic time switch which controlled two 15-watt fluorescent bulbs. These timers were carefully regulated for photoperiods of 11 hours (short day) and 14 hours (long day) in a 24-hour period. Larvae at 20°C on both long-day and short-day photoperiods were maintained in Hotpack incubators. Built-in automatic timers regulated both temperature and photoperiod. Six 15-watt fluorescent bulbs delivered light for the different photoperiodic conditions. All units remained at a constant temperature of ± 1°C.

Larvae involved in feeding experiments were exposed to four combinations of temperature and photoperiod as follows: 15°C, 11 hours; 15°C, 14 hours; 20°C, 11 hours; and 20°C, 14 hours. A random assortment placed 11 individuals in each of the conditions. Every animal was initially weighed to the nearest milligram on a Sartorius-Werke balance and then placed at its appropriate condition. Larvae were weighed every four weeks until emergence. Larvae at all conditions were fed a known number of enchytraeid worms obtained from laboratory cultures. The animals were always given more than enough worms so that an accurate accounting could be made of maximum numbers of worms eaten. Numbers of worms eaten by experimental larvae were recorded every 48 hours. Uneaten prey were discarded so that larvae would be resupplied with a fresh number of worms at each feeding.

In another experiment larvae were partially starved to determine the effects of starvation on growth and development. Larvae collected

on 18 March were maintained at 15°C on a 14-hour daylength. Groups of animals were subjected to the following conditions until emergence: (1) starved for the first two weeks, (2) fed for only the first two weeks, and (3) starved throughout the experiment. Another group of animals were fed continuously to act as controls. Animals that were fed in any of the previously mentioned conditions were given food on a daily basis.

Three inductive experiments were conducted with final-instar larvae to determine the minimal number of 14-hour days (i.e., 14 hours of light and 10 hours of darkness in each 24 hours) necessary for a long-day response. Three experiments were run; larvae in one experiment were maintained at 15°C while larvae of the other two experiments were housed at 20°C. All animals except the short-day controls were placed on a 14-hour photoperiod. For a period of 36 days, six larvae were transferred at three-day intervals to an 11-hour photoperiod where they remained until emergence.

Data obtained from the feeding experiments and inductive experiments were statistically analyzed for mean ($\bar{X}$), standard error of the mean (SE), and t-value to determine significant differences between means.

RESULTS

Food consumption studies were conducted on final-instar larvae; data were interpreted as responses to photoperiod and temperature and as weight changes. These studies were undertaken with animals collected on 23 October and 25 November 1974. Eleven animals were used in each experimental condition. Data for animals collected 25 November are not shown because the results of all four experimental conditions were similar to the ones obtained with animals collected on 23 October.

Fig. 1 shows responses of larvae at two different photoperiodic conditions which were maintained at a temperature of 15°C. Animals at both conditions exhibited no statistical differences with respect to total numbers of worms consumed.

With few exceptions, long-day animals exhibited no statistical increase in rate of feedings over their short-day counterparts. Larvae maintained at the different conditions did, however, display a few significant differences in feeding rates on certain days. For example, short-day animals had a statistically higher rate of food consumption early in the experiment, whereas long-day animals had significantly higher rates of consumption at intermediate days of the experiment. A gradual decrease in the rate of food consumption was observed by animals of both conditions for approximately 52 days.

Larvae maintained at the long-day conditions responded statistically faster than did the short-day animals. Short-day animals averaged 34 days longer until emergence than did their long-day counterparts.

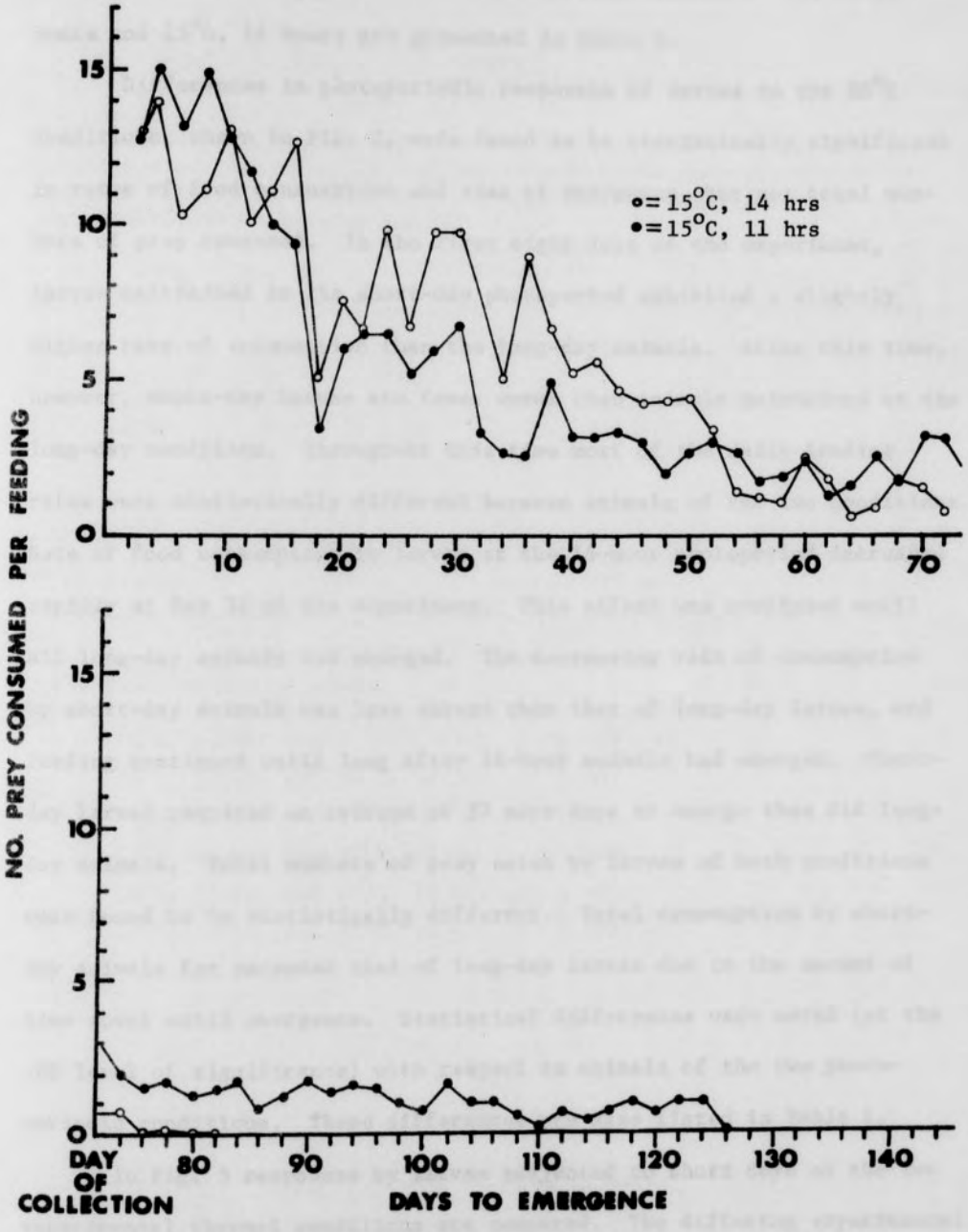

Figure 1. Average rates of food consumption by larvae collected on 23 October 1974, and maintained on photoperiods of 11 and 14 hours at a temperature of 15°C.

Statistical data compiled for food consumption studies for 15°C, 11 hours and 15°C, 14 hours are presented in Table 1.

Differences in photoperiodic responses of larvae to the 20°C conditions, shown in Fig. 2, were found to be statistically significant in rates of food consumption and time of emergence, but not total numbers of prey consumed. In the first eight days of the experiment, larvae maintained at the short-day photoperiod exhibited a slightly higher rate of consumption than the long-day animals. After this time, however, short-day larvae ate fewer worms than animals maintained at the long-day condition. Throughout this time most of the daily feeding rates were statistically different between animals of the two conditions. Rate of food consumption in larvae at the 14-hour photoperiod decreased rapidly at Day 32 of the experiment. This effect was continued until all long-day animals had emerged. The decreasing rate of consumption by short-day animals was less abrupt than that of long-day larvae, and feeding continued until long after 14-hour animals had emerged. Short-day larvae required an average of 57 more days to emerge than did long-day animals. Total numbers of prey eaten by larvae of both conditions were found to be statistically different. Total consumption by short-day animals far exceeded that of long-day larvae due to the amount of time spent until emergence. Statistical differences were noted (at the .05 level of significance) with respect to animals of the two photoperiodic conditions. These differences are also listed in Table 1.

In Fig. 3 responses by larvae subjected to short days at the two experimental thermal conditions are compared. The differing experimental temperatures significantly altered the rates of food consumption and

TABLE 1

Total number of prey eaten by larvae collected on 23 October 1974 and maintained at four experimental conditions; rates were statistically analyzed for the mean ($\overline{X}$), standard error of the mean (SE), and probability values between means.

Condition	n	$\overline{X}$	SE
15°C, 11-hr.	11	214.9	8.49
15°C, 14-hr.	11	222.1	7.79
20°C, 11-hr.	10	332.00	25.38
20°C, 14-hr.	11	283.00	8.74

Probability values between:

15°C, 11-hr. and 15°C, 14-hr. - < .20
15°C, 11-hr. and 20°C, 11-hr. - > .01
15°C, 11-hr. and 20°C, 14-hr. - > .01
15°C, 14-hr. and 20°C, 11-hr. - > .01
15°C, 14-hr. and 20°C, 14 hr. - > .01
20°C, 11-hr. and 20°C, 14 hr. - > .05

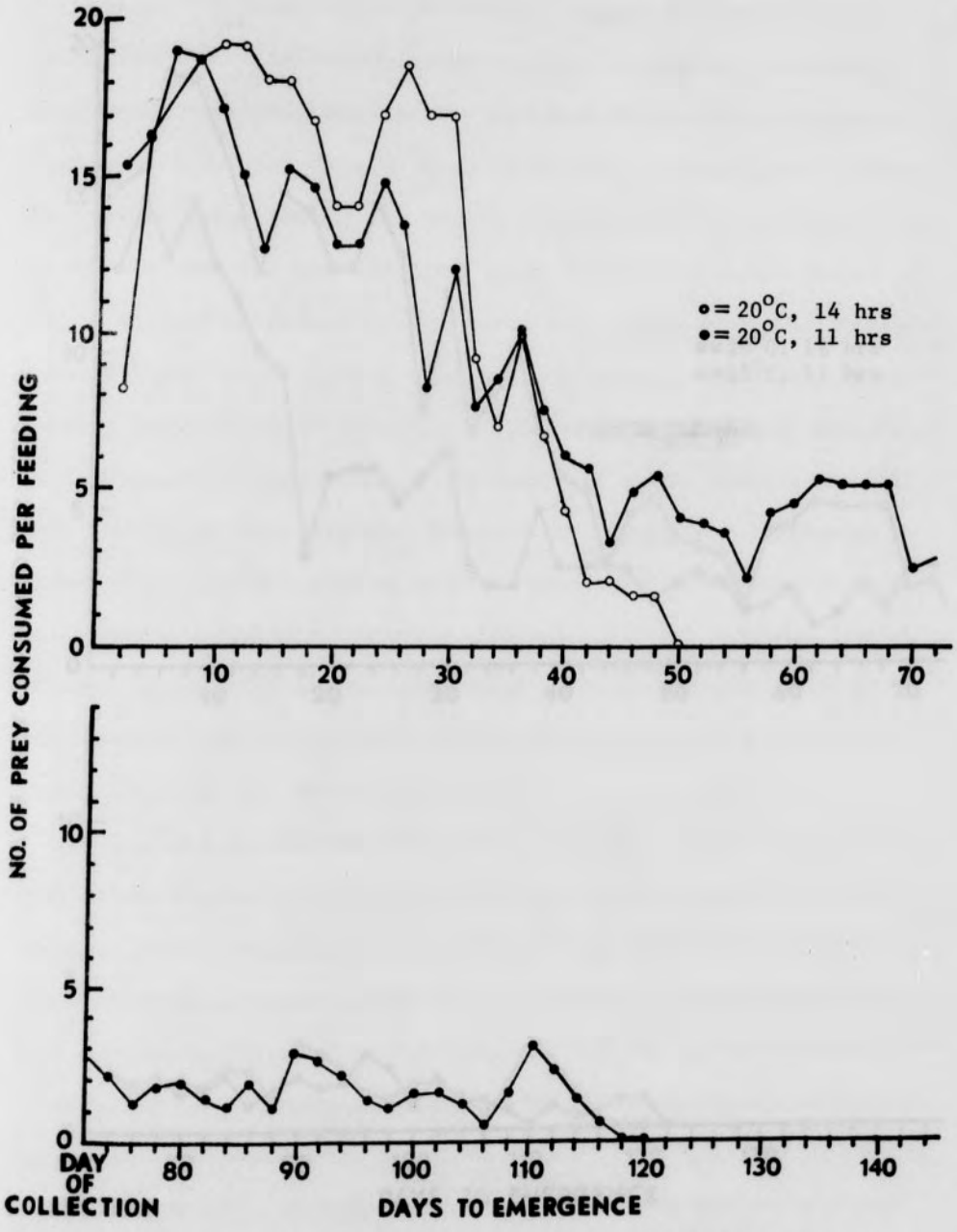

Figure 2. Average rates of food consumption by larvae collected on 23 October 1974, and maintained on 11- and 14-hour photoperiods at a temperature of 20°C.

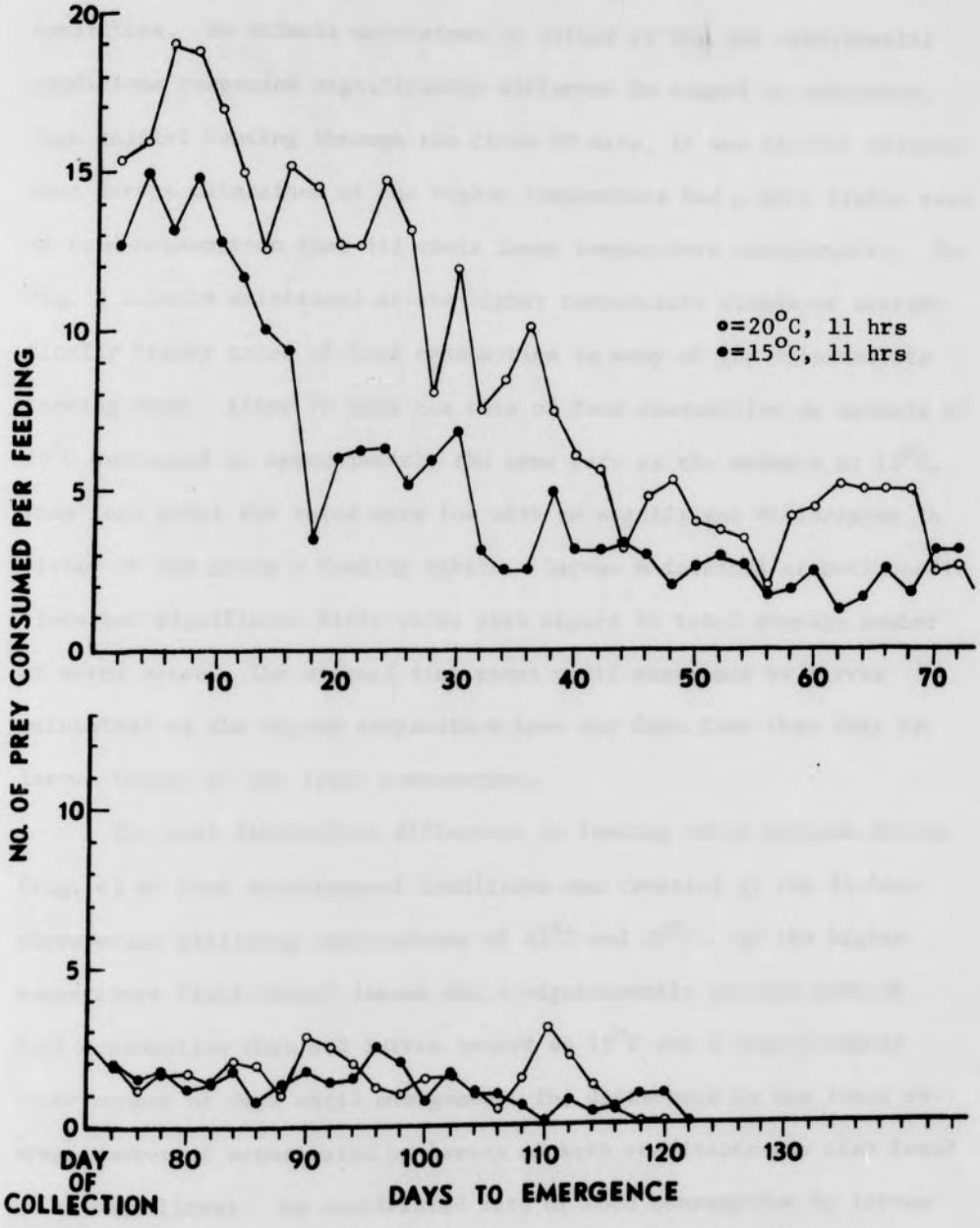

Figure 3. Average rates of food consumption by larvae collected on 23 October 1974, and maintained at temperatures of 15°C and 20°C on a photoperiod of 11 hours.

total number of worms eaten (Table 1) by animals at the two thermal conditions. No animals maintained at either of the two experimental conditions responded significantly different in regard to emergence. From initial feeding through the first 70 days, it was clearly evident that larvae maintained at the higher temperature had a much higher rate of food consumption than did their lower temperature counterparts. In Fig. 3 animals maintained at the higher temperature displayed statistically higher rates of food consumption in many of the intermediate feeding days. After 70 days the rate of food consumption in animals at 20°C decreased to approximately the same rate as the animals at 15°C. From this point the rates were low with no significant differences in either of the group's feeding habits. Larvae maintained at both conditions had significant differences with regard to total average number of worms eaten. The average time spent until emergence by larvae maintained at the higher temperature took six days less than that by larvae housed at the lower temperature.

The most distinctive difference in feeding rates between larvae (Fig. 4) of four experimental conditions was revealed at the 14-hour photoperiod utilizing temperatures of 15°C and 20°C. At the higher temperature final-instar larvae had a significantly greater rate of food consumption than did larvae housed at 15°C and a significantly lower number of days until emergence. The difference in the total average number of worms eaten by larvae of both conditions was also found to be significant. An accelerated rate of food consumption by larvae at 20°C was maintained from the initial feeding until approximately Day 32 of the experiment. The abrupt decrease in rate of consumption

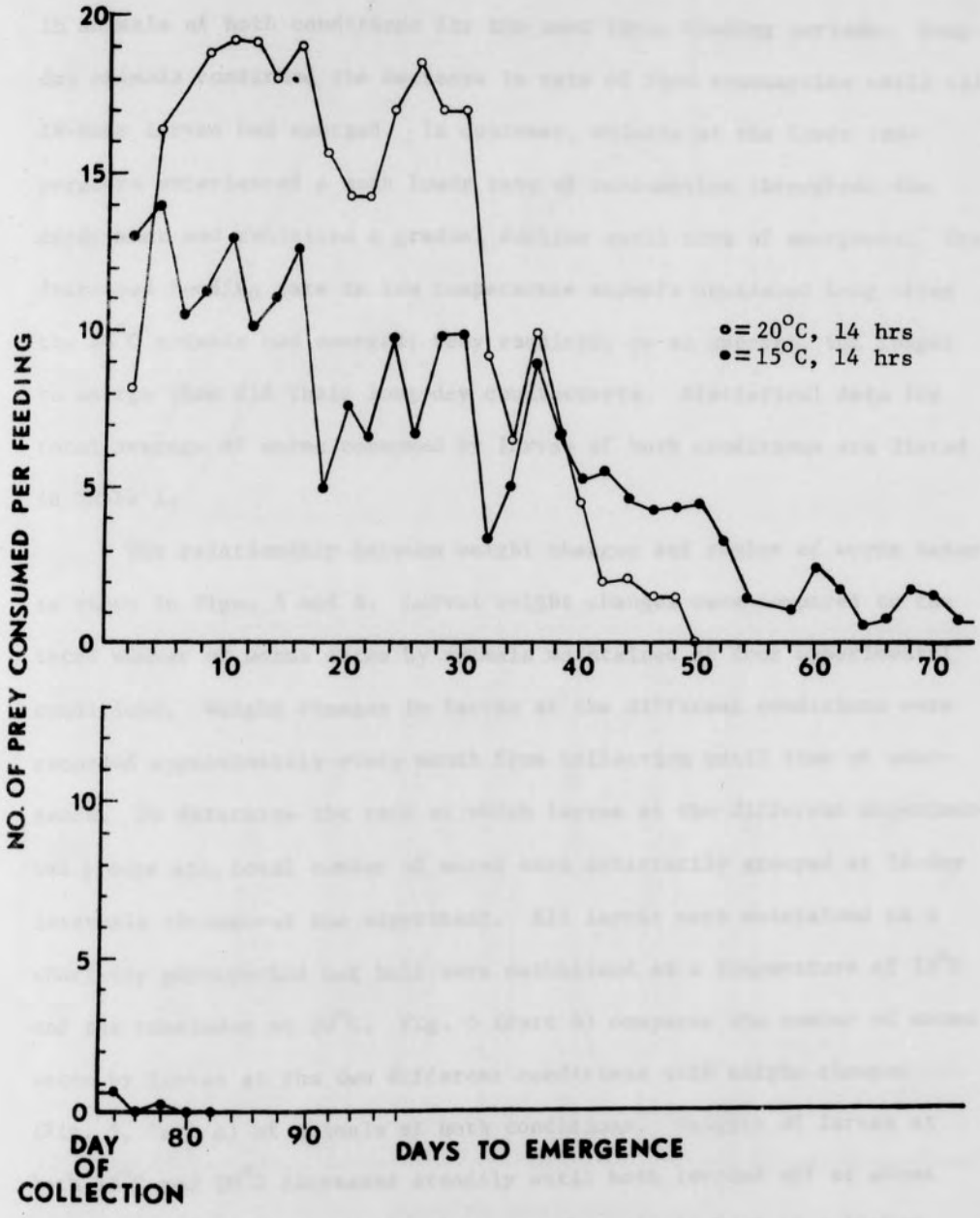

Figure 4. Average rates of food consumption by larvae collected on 23 October 1974, and maintained at temperatures of 15°C and 20°C on a photoperiod of 14 hours.

at this point by long-day larvae produced statistically similar responses in animals of both conditions for the next three feeding periods. Long-day animals continued the decrease in rate of food consumption until all 14-hour larvae had emerged. In contrast, animals at the lower temperature experienced a much lower rate of consumption throughout the experiment and exhibited a gradual decline until time of emergence. The decreased feeding rate in low temperature animals continued long after the 20°C animals had emerged; they required, on an average, 60% longer to emerge than did their long-day counterparts. Statistical data for total average of worms consumed by larvae of both conditions are listed in Table 1.

The relationship between weight changes and number of worms eaten is shown in Figs. 5 and 6. Larval weight changes were compared to the total number of worms eaten by animals maintained at four experimental conditions. Weight changes in larvae at the different conditions were recorded approximately every month from collection until time of emergence. To determine the rate at which larvae at the different experimental groups ate, total number of worms were arbitrarily grouped at 16-day intervals throughout the experiment. All larvae were maintained on a short-day photoperiod but half were maintained at a temperature of 15°C and the remainder at 20°C. Fig. 5 (Part B) compares the number of worms eaten by larvae at the two different conditions with weight changes (Fig. 5, Part A) of animals at both conditions. Weights of larvae at both 15°C and 20°C increased steadily until both leveled off at about Days 100 and 50, respectively; however, the animals kept at a higher temperature increased more rapidly in weight than did that of 15°C

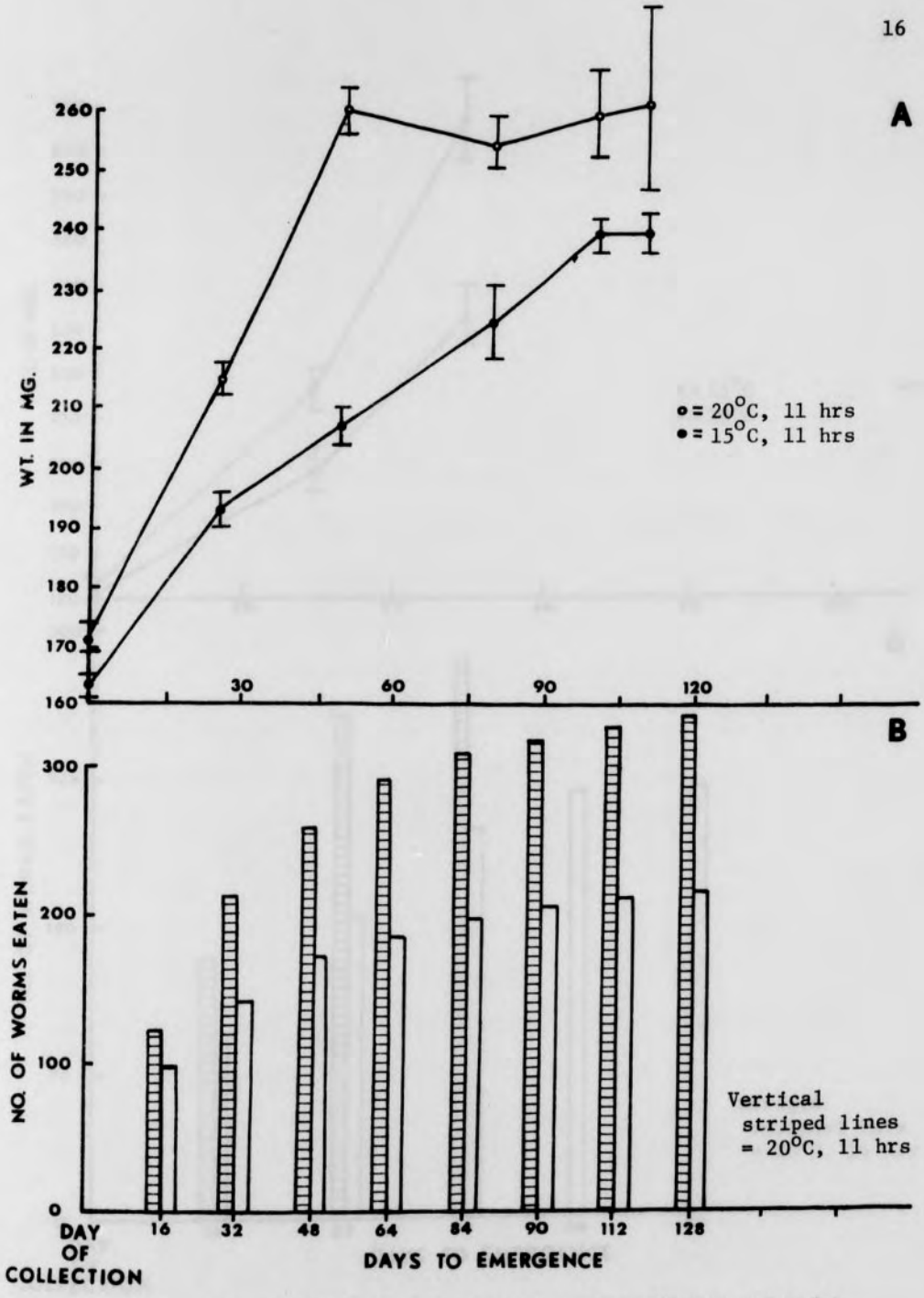

Figure 5. Comparison of weight changes and number of prey eaten by larvae collected on 23 October 1974, and maintained at temperatures of 15°C and 20°C on an 11-hour photoperiod.

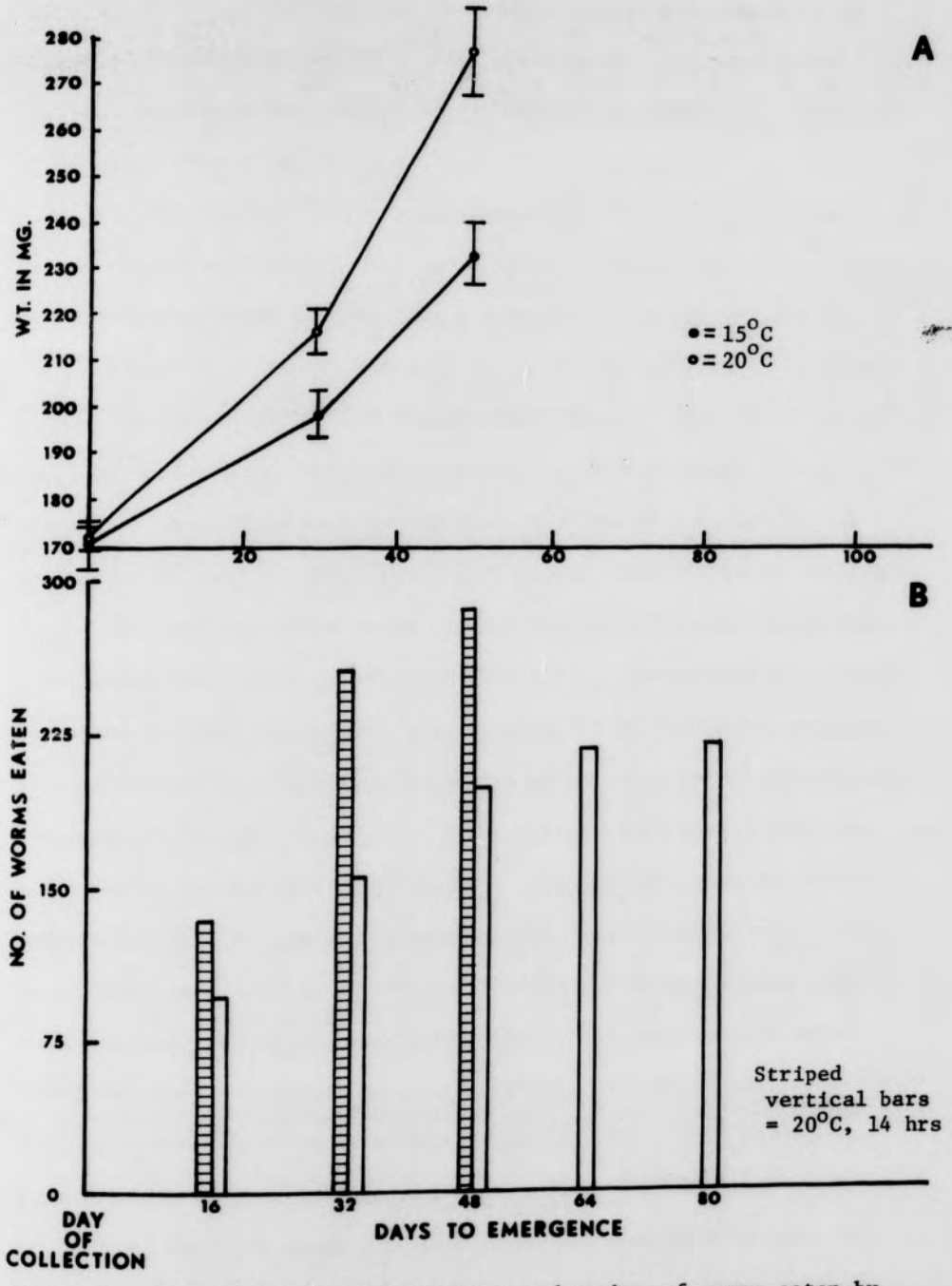

Figure 6. Comparison of weight changes and number of worms eaten by larvae collected 23 October 1974, and maintained at temperatures of 15°C and 20°C on a photoperiod of 14 hours.

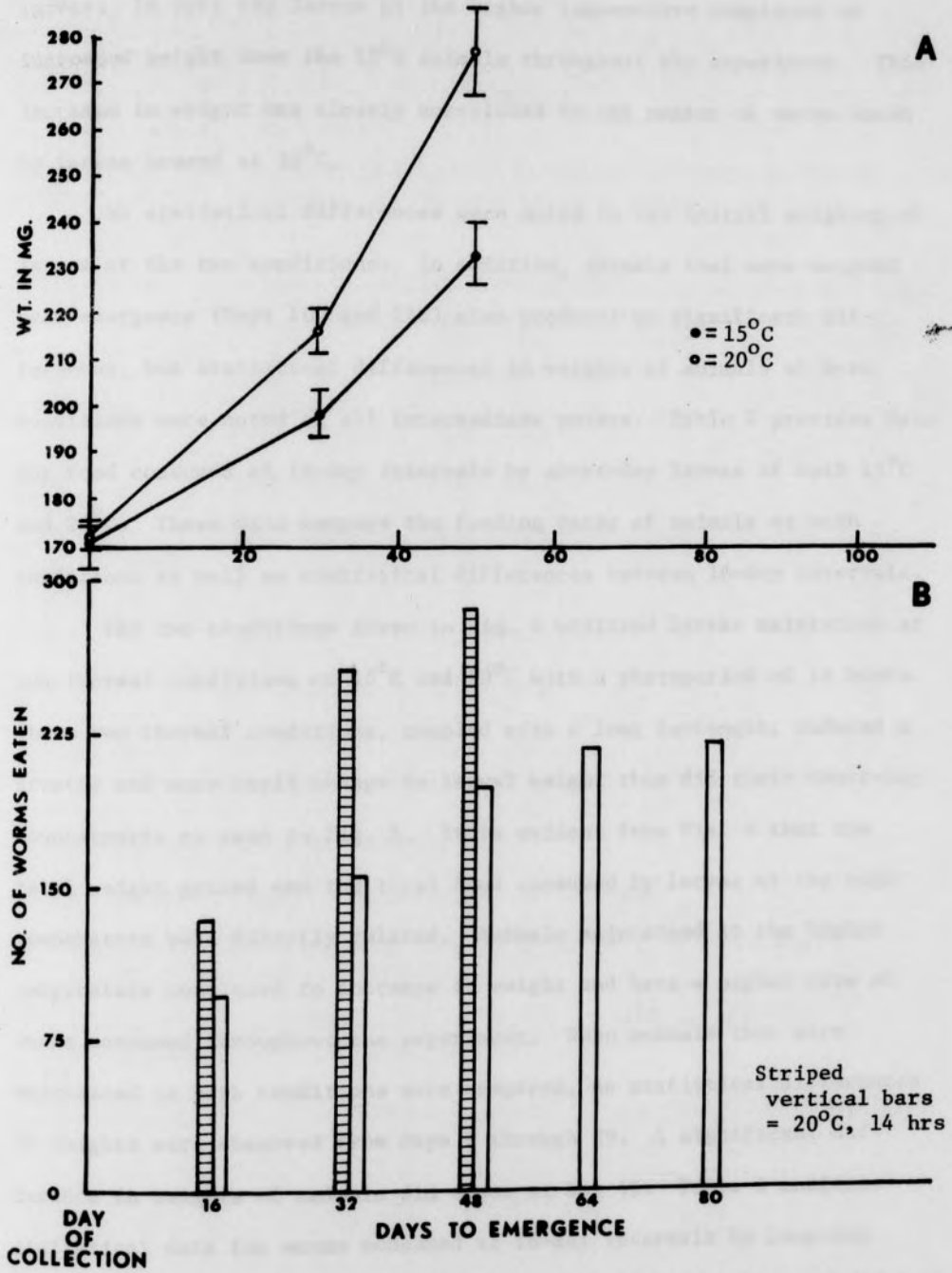

Figure 6. Comparison of weight changes and number of worms eaten by larvae collected 23 October 1974, and maintained at temperatures of 15°C and 20°C on a photoperiod of 14 hours.

larvae. In fact the larvae at the higher temperature displayed an increased weight over the 15°C animals throughout the experiment. This increase in weight was closely correlated to the number of worms eaten by larvae housed at 20°C.

No statistical differences were noted in the initial weighing of larvae at the two conditions. In addition, animals that were weighed near emergence (Days 100 and 110) also produced no significant differences, but statistical differences in weights of animals at both conditions were noted at all intermediate points. Table 2 provides data for food consumed at 16-day intervals by short-day larvae of both 15°C and 20°C. These data compare the feeding rates of animals at both conditions as well as statistical differences between 16-day intervals.

The two conditions shown in Fig. 6 utilized larvae maintained at two thermal conditions of 15°C and 20°C with a photoperiod of 14 hours. These two thermal conditions, coupled with a long daylength, induced a greater and more rapid change in larval weight than did their short-day counterparts as seen in Fig. 5. It is evident from Fig. 6 that the total weight gained and the total food consumed by larvae at the high temperature were directly related. Animals maintained at the higher temperature continued to increase in weight and have a higher rate of worms consumed throughout the experiment. When animals that were maintained in both conditions were compared, no statistical differences in weights were observed from Days 0 through 29. A significant difference in weights of animals did occur at Day 49. Table 3 contains statistical data for worms consumed at 16-day intervals by long-day animals of both high and low temperatures. Feeding rates and statistical differences between 16-day intervals are also noted in this table.

TABLE 2

Statistical data for food consumption at 16-day intervals by larvae maintained on a short-day photoperiod from Day 0 until emergence.

Days	1		2		3	4
	15°C,	20°C	15°C,	20°C		
16	46.3	38.8	46.3	38	+	+
32	78.3	64.4	20.4	25.6	+	+
48	86.5	78.4	11.6	14.0	-	+
64	92.7	87.4	8.2	9.0	-	+
80	97.0	93.3	6.2	5.9	-	+
96	99.2	96.9	4.3	3.6	-	+
112	100	98.3	2.2	2.6	-	+
128	-	100	0.8	0.7	-	+

1 = cumulative % of worms eaten

2 = % increase in nos. of worms eaten per interval

3 = statistical differences between 15°C and 20°C in total nos. of worms consumed per interval

4 = statistical differences between larvae of 15°C and 20°C for total accumulation of worms consumed

TABLE 3

Statistical data for food consumption at 16-day intervals by larvae maintained on a long-day photoperiod from Day 0 until emergence.

Days	1		2		3	4
	15°C,	20°C	15°C,	20°C		
16	57.7	43.0	43.0	57.7	+	+
32	90.6	70.0	27.0	32.9	+	+
48	100	92.1	22.1	9.4	+	+
64	-	98.5	6.4	-		
81	-	100	1.5	-		
97	-	-	-	-		
113	-	-	-	-		
129	-	-	-	-		

1 = cumulative % of worms eaten

2 = % increase in nos. of worms eaten per intervals

3 = statistical differences between 15°C and 20°C in total nos. of worms consumed per interval

4 = statistical differences between larvae of 15°C and 20°C for total accumulation of worms consumed

Weight changes of the four experimental groups were also compared for photoperiodic differences. Fig. 7 indicates weight means and the standard errors for larvae at 15°C and 20°C. The two larval groups in Part A (maintained at 20°C) were statistically similar from initial weighing until Day 29. Average weights in animals of both groups increased significantly until Day 49. At this point the mean weight in long-day animals steadily increased until emergence, but the mean weight in short-day animals leveled off. Larvae of both conditions were weighed on Day 49, and their differences in average weights were statistically significant.

Weights of animals of both groups maintained at 15°C increased significantly as did weights of larvae housed at 20°C; however, weights in short-day larvae leveled off prior to emergence at Day 100. Fig. 7 Part B shows weight changes and standard error ranges for both groups of animals at 15°C. The only statistical difference noted between the animals of the two experimental conditions occurred on Day 49. In contrast to 20°C animals (Part A), the overall increase in weight was approximately the same for both groups maintained at 15°C.

A comparison between groups of fed and starved larvae began with animals collected on 18 March. In contrast to previous feeding experiments, all experimental animals were housed at the same temperature and photoperiod (15°C, 14 hours). The animals were separated into four groups. Two groups of larvae acted as controls; one group was fed ad libitum from time of collection until emergence while the other group was starved throughout the experiment. The third group was fed for a period of two weeks after which time the larvae were starved for the

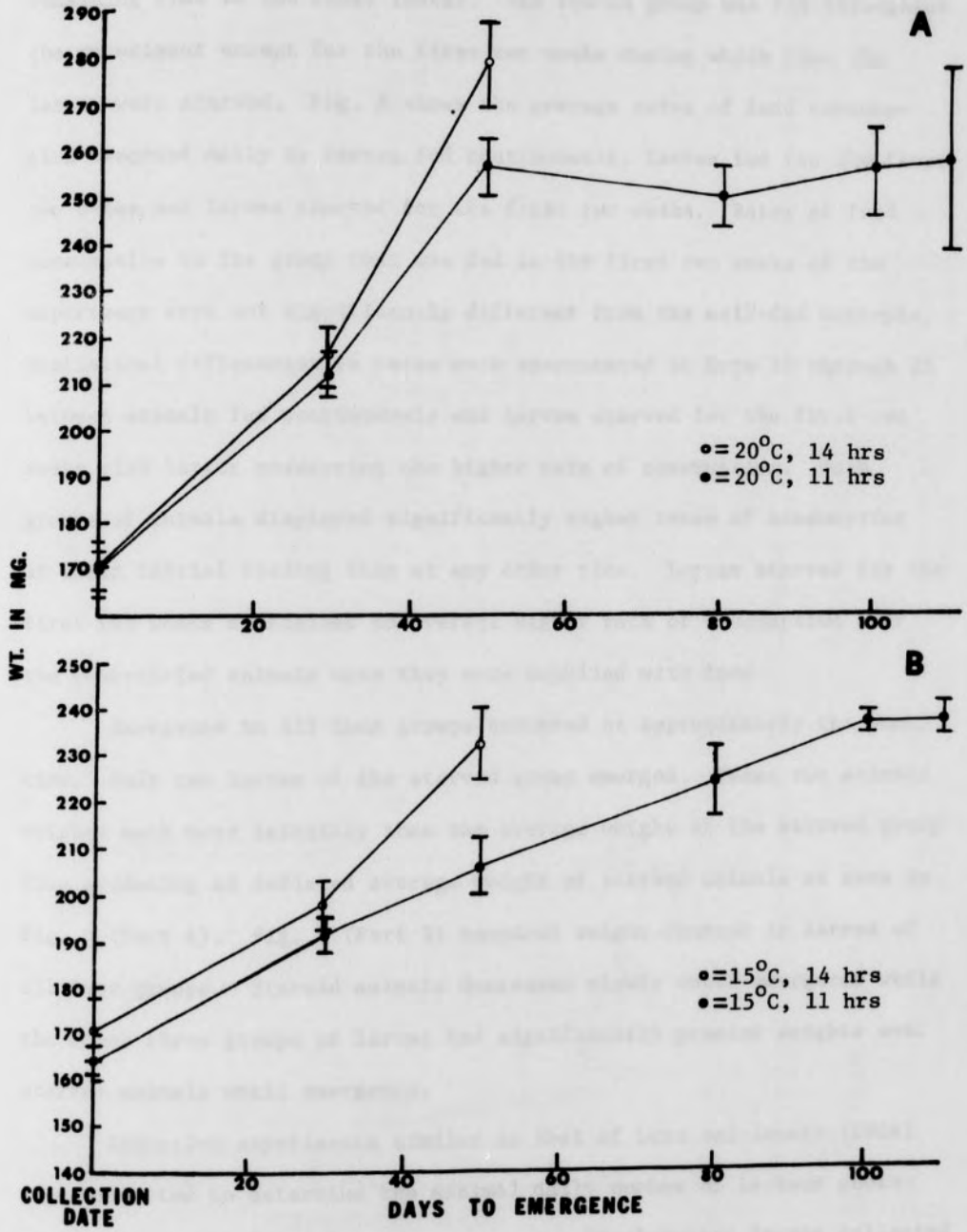

Figure 7. Weight changes of the four experimental feeding groups comparing photoperiodic responses.

remaining time in the final instar. The fourth group was fed throughout the experiment except for the first two weeks during which time the larvae were starved. Fig. 8 shows the average rates of food consumption recorded daily by larvae fed continuously, larvae fed for the first two weeks, and larvae starved for the first two weeks. Rates of food consumption in the group that was fed in the first two weeks of the experiment were not significantly different from the well-fed controls. Statistical differences in rates were encountered at Days 16 through 25 between animals fed continuously and larvae starved for the first two weeks with latter possessing the higher rate of consumption. Both groups of animals displayed significantly higher rates of consumption at their initial feeding than at any other time. Larvae starved for the first two weeks maintained an overall higher rate of consumption over the control-fed animals once they were supplied with food.

Emergence in all four groups occurred at approximately the same time. Only two larvae of the starved group emerged. These two animals weighed much more initially than the average weight of the starved group thus producing an inflated average weight of starved animals as seen in Fig. 9 (Part A). Fig. 9 (Part B) compares weight changes in larvae of all four groups. Starved animals decreased slowly until emergence while the other three groups of larvae had significantly greater weights over starved animals until emergence.

Inductive experiments similar to that of Lutz and Jenner (1964) were conducted to determine the minimal daily number of 14-hour photoperiods essential for a long-day response. Final-instar larvae collected on 25 November were maintained at a constant temperature of 20°C and 15°C,

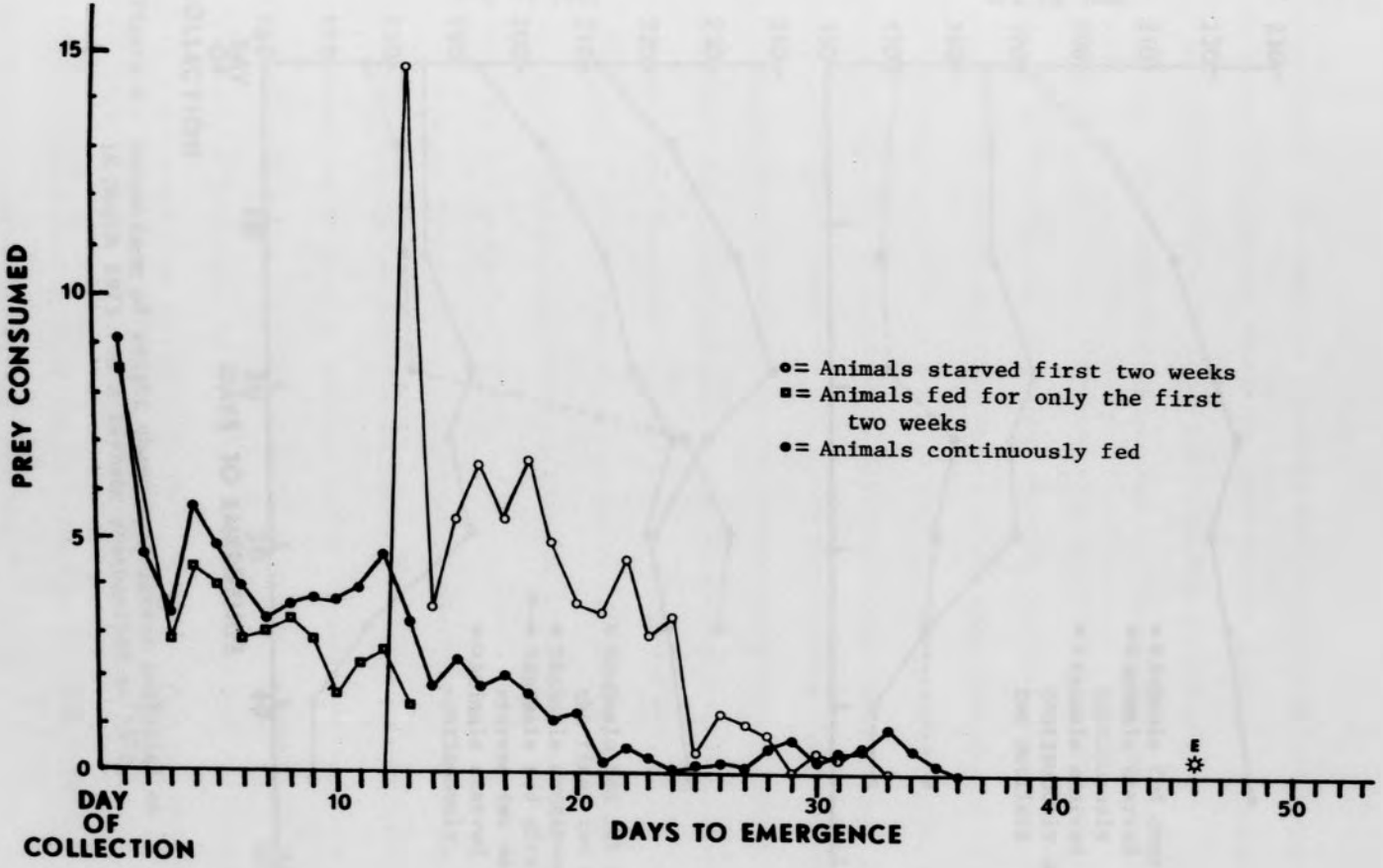

Figure 8. Average rates of food consumption by larvae collected on 18 March 1975 on a 14-hour photoperiod at 15°C. The four categories were: larvae fed continuously, larvae fed for only the first two weeks, larvae starved for only the first two weeks, and larvae continuously starved.

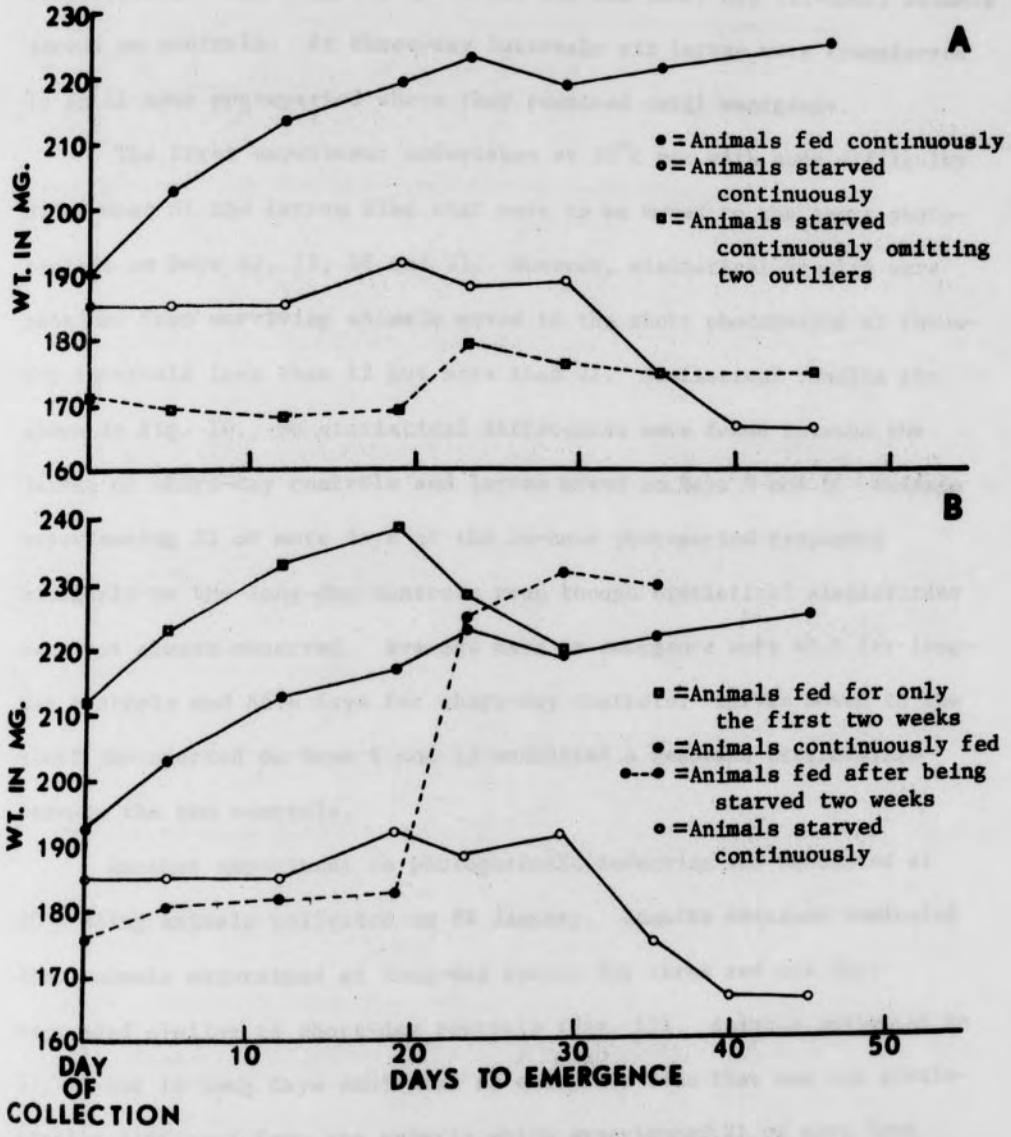

Figure 9. Comparison of weight changes in larvae collected on 18 March 1975 on a 14-hour photoperiod at 15°C.

respectively. Six long-day (14-hour) and six short-day (11-hour) animals served as controls. At three-day intervals six larvae were transferred to an 11-hour photoperiod where they remained until emergence.

The first experiment undertaken at 20°C met with some difficulty since most of the larvae died that were to be moved to the short photoperiods on Days 12, 15, 18 and 21. However, statistical results were obtained from surviving animals moved to the short photoperiod at three-day intervals less than 12 but more than 21. Statistical results are shown in Fig. 10. No statistical differences were found between the larvae of short-day controls and larvae moved on Days 3 and 6. Animals experiencing 21 or more days at the 14-hour photoperiod responded similarly to the long-day controls even though statistical similarities were not always observed. Average days to emergence were 40.5 for long-day controls and 86.6 days for short-day controls. Larvae moved to the short photoperiod on Days 9 and 12 exhibited a response intermediate between the two controls.

Another experiment on photoperiodic induction was conducted at 20°C using animals collected on 24 January. Results obtained indicated that animals maintained at long-day cycles for three and six days responded similar to short-day controls (Fig. 11). Animals subjected to 12, 15 and 18 long days exhibited an emergence time that was not statistically different from the animals which experienced 21 or more long days. Mean days to emergence were 27.6 for long-day controls and 60 days for short-day controls. Only the larvae subjected to nine long days exhibited a response between the two controls.

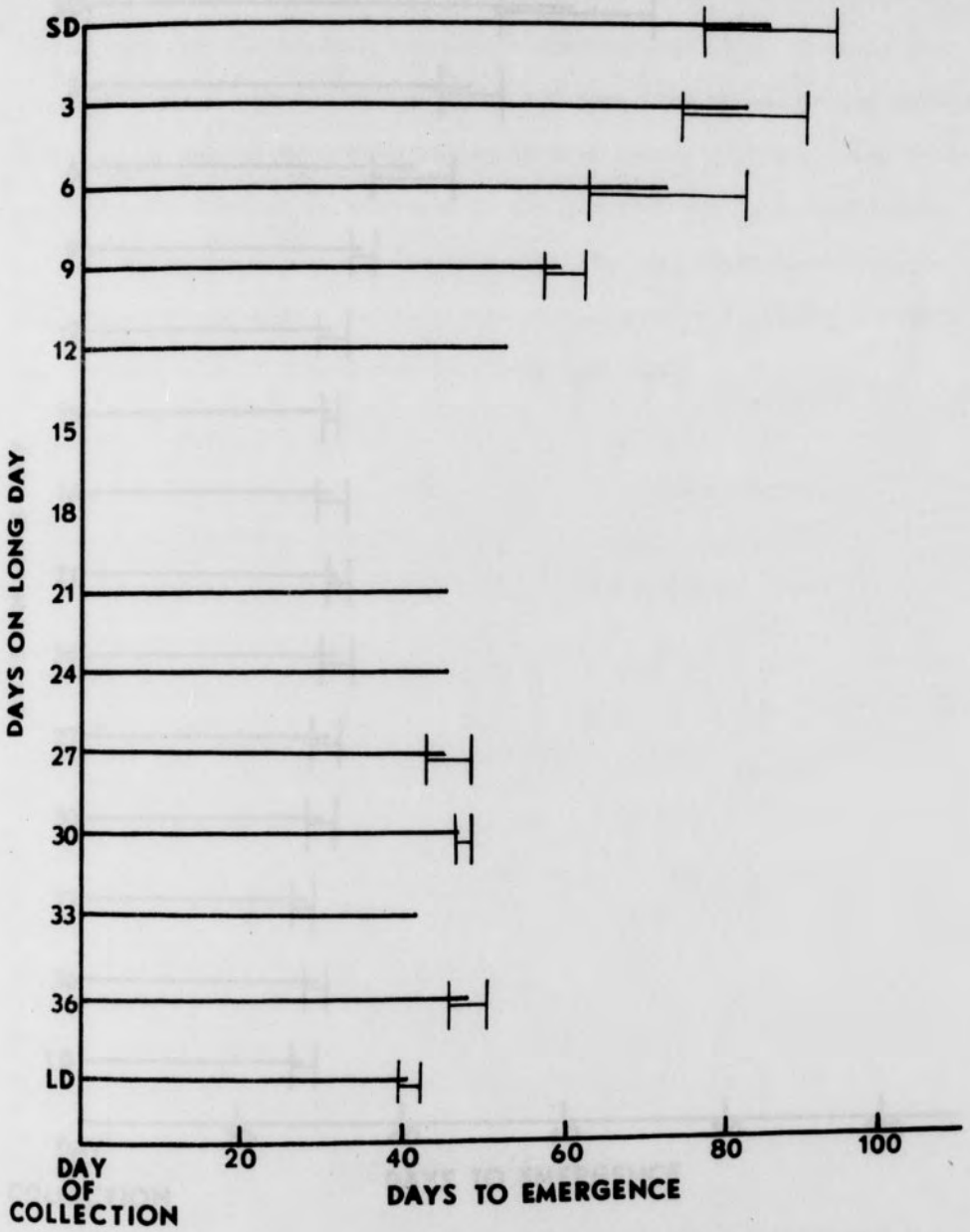

Figure 10. Mean responses by larvae collected on 25 November 1974 on an 11-hour photoperiod at 20°C after being subjected to a varying number of long-day photoperiods.

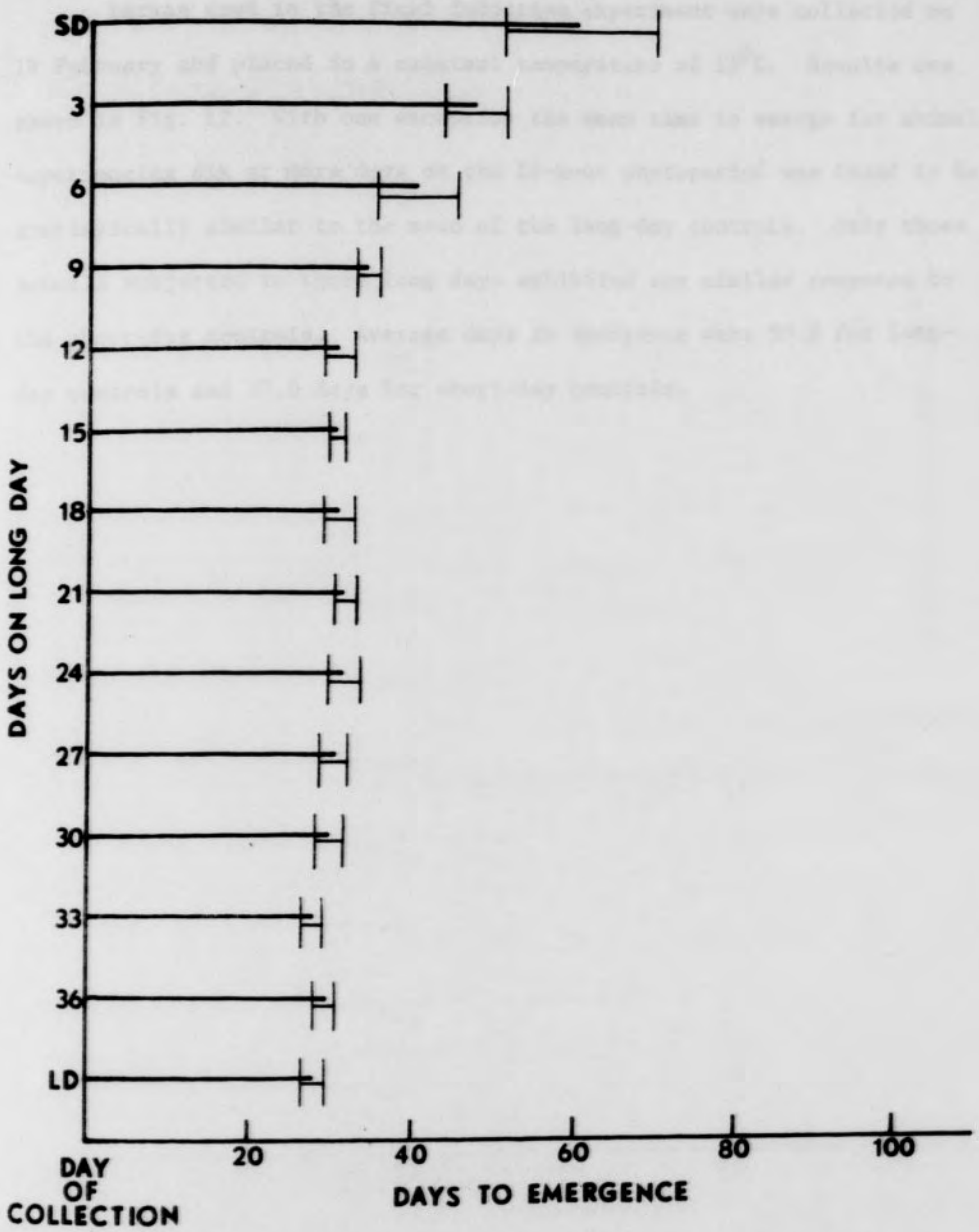

Figure 11. Mean responses by larvae collected on 24 January 1975 on an 11-hour photoperiod at 20°C after being subjected to a varying number of long-day photoperiods.

Larvae used in the final inductive experiment were collected on 18 February and placed in a constant temperature of 15°C. Results are shown in Fig. 12. With one exception the mean time to emerge for animals experiencing six or more days on the 14-hour photoperiod was found to be statistically similar to the mean of the long-day controls. Only those animals subjected to three long days exhibited any similar response to the short-day controls. Average days to emergence were 50.6 for long-day controls and 37.0 days for short-day controls.

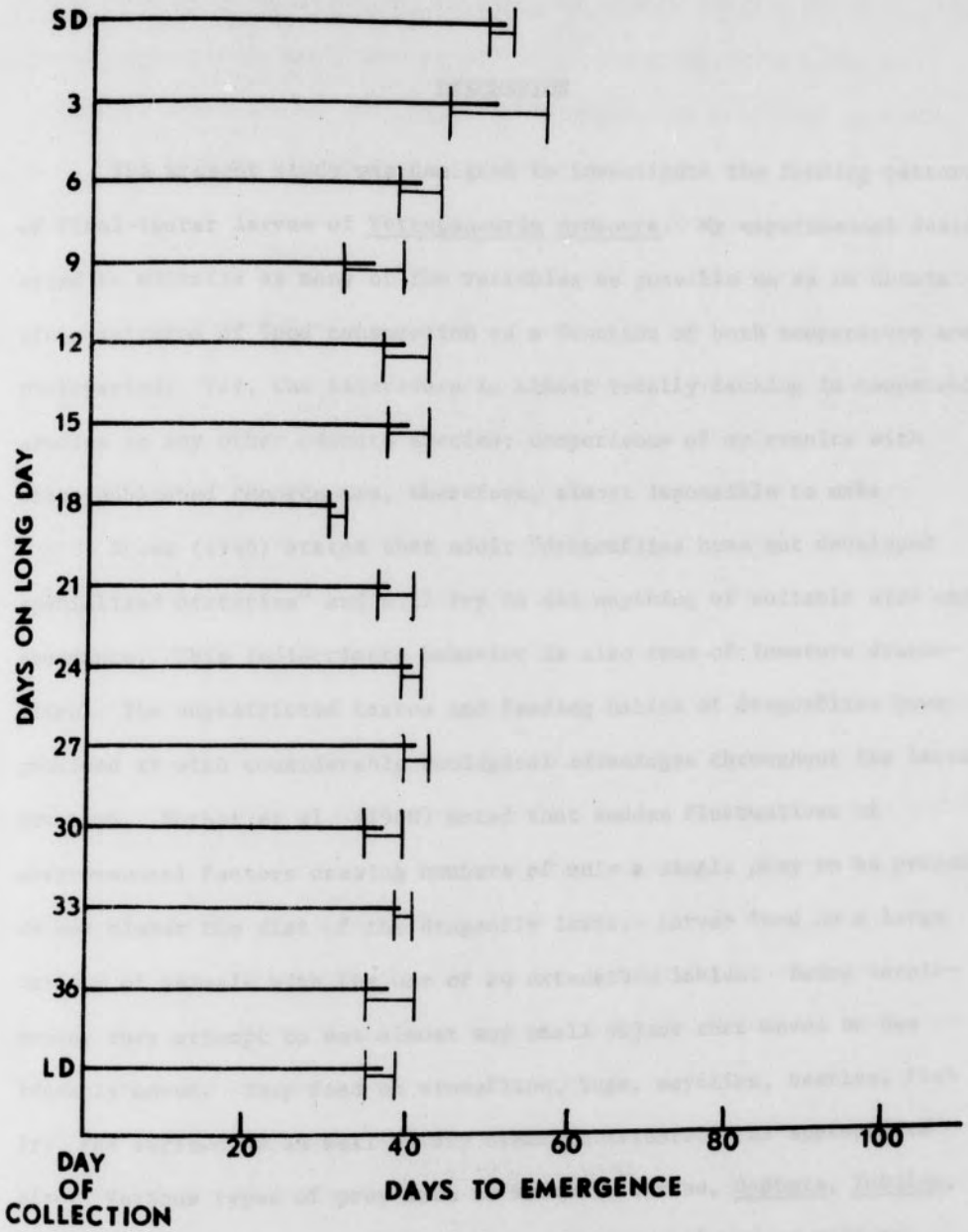

Figure 12. Mean responses by larvae collected on 24 January 1975 on an 11-hour photoperiod at 15°C after being subjected to a varying number of long-day photoperiods.

DISCUSSION

The present study was designed to investigate the feeding patterns of final-instar larvae of Tetragoneuria cynosura. My experimental design tried to minimize as many of the variables as possible so as to obtain clear patterns of food consumption as a function of both temperature and photoperiod. Yet, the literature is almost totally lacking in comparable studies on any other odonate species; comparisons of my results with other published reports are, therefore, almost impossible to make.

Brues (1946) stated that adult "dragonflies have not developed specialized dietaries" and will try to eat anything of suitable size and abundance. This indiscrimate behavior is also true of immature dragonflies. The unrestricted tastes and feeding habits of dragonflies have provided it with considerable ecological advantages throughout its larval duration. Corbet et al. (1960) noted that sudden fluctuations of environmental factors causing numbers of only a single prey to be present do not hinder the diet of the dragonfly larva. Larvae feed on a large variety of animals with the use of an extensible labium. Being carnivorous, they attempt to eat almost any small object that moves or has recently moved. They feed on stoneflies, bugs, mayflies, beetles, fish fry, and earthworms as well as any other invertebrates of appropriate size. Various types of prey such as mosquito larvae, Daphnia, Tubifex, amphipods, mayfly larvae, triclads, ostracods, rotifers, as well as numerous members of the Oligochaeta have been employed in the diet of dragonfly larvae for laboratory studies.

The requirements of an organism to qualify as prey for dragonfly larvae are briefly mentioned by Corbet et al. (1960). In order to stimulate extension of the dragonfly's labium, the prey must be moving, must be within a certain distance of the larva, and must lie between certain limits of size. However, Pritchard (1964) noted "it is not strictly correct to say dragonfly larvae will strike only at moving prey for they will strike at stationary objects that have recently been moving." It is essential, however, that the prey must have been moving just prior to the strike. On the other hand, Lee (1967) reported that predators also had to meet certain qualifications, including the following: the size of the predator in relation to the size of the prey, the state of hunger, and the activity of predators. Pritchard (1964) also mentioned that dragonfly larvae prey upon organisms that fall between certain limits of size. He stated that "the lower limit ensures that energy is not wasted on prey that would yield little food value, and the upper limit ensures that an attack is not released against an animal that is too large to be handled conveniently." In order to keep all of the previously mentioned factors constant, and thus giving more precise rates of food consumption (in all experimental conditions), fluctuations in these factors would have to be minimized. In the present study these factors were minimized by using final-instar larvae with prey being carefully selected for approximate equivalence in size. The state of hunger of the animals was satisfied by giving them an excess of prey (a preliminary experiment indicated the maximum amount of worms a larva would consume in one feeding period).

The predatory behavior of dragonfly larvae has been described by Walker (1953) and Pritchard (1964) as being of two main types, namely the "climbers" and the "sprawlers." Climbers actively pursue their prey among aquatic vegetation. They "perceive the movements of animals much smaller than themselves at a distance of several inches, and stalk their prey with stealthy, cat-like motion, stopping whenever the movement ceases, and thus advancing gradually until within striking distance." "Sprawlers, in contrast, are much more sluggish and even when hungry will make no attempt to strike at their prey until it comes within reach of the extended labium." Pritchard (1964) pointed out that the climbers detect their prey by sight while the sprawlers rely upon tactile stimulation. Numerous observations made during feedings indicate that the larvae of Tetragoneuria cynosura used in the present study fit the "sprawler" category.

Most of the present study was concerned with studying this quantitative rate of food consumed by final-instar larvae of Tetragoneuria cynosura. Quantitative reports on food consumptions of Odonata larvae have been made by Calvert (1947), Kasimov (1956), Corbet (1956), and Lutz (1962). Corbet (1956) observed that feeding in Anax imperator continued during its diapause development. Lutz (1962) studied the effects of varying daylengths on the rates of feeding in final-instar larvae of Tetragoneuria cynosura collected in early spring. The rates of food consumption were recorded up to emergence. These larvae were maintained at 11-hour and 14-hour daylengths at the same temperature. The present study was a more extensive investigation using T. cynosura larvae collected from mid-fall through early spring. As in the study by

Lutz (1962), rates of feeding in larvae were recorded up to emergence. In addition, varying effects of daylengths and temperature on the rates of food consumption in larvae were determined.

With few exceptions the present study has shown that there were no differing rates of food consumption in larvae on either photoperiodic condition at 15°C. However, differences in feeding rates did occur with larvae of the two photoperiodic conditions maintained at 20°C. Animals maintained at the higher temperature on a long daylength had an increased rate of food consumption over their short-day counterparts. The similar study by Lutz (1962) in which larvae were maintained at about 22°C corroborate the present results obtained at 20°C. Since no statistical difference in rates of consumption were induced at 15°C, it suggested that lower temperatures may possibly reduce the effects of light-temperature interaction on the rates of food consumption, as well as slow down their metabolic rate. The effects of a reduced metabolic rate could also hinder the ability of larvae to capture prey by slowing down their reaction time during an attack or increasing the time of the larva's immobility to hunt for food.

Perhaps the most intriguing aspect of this study concerns the observed differences in feeding rates of larvae at the two temperatures. Larvae maintained at the higher temperature (20°C) on the short-day photoperiod had a much higher rate of food consumption than did short-day animals housed at 15°C. In addition, animals maintained at both conditions had significant differences in total prey consumed. Similar responses also occurred between larvae maintained at both thermal conditions on the long daylength. Larvae housed at the higher temperature

again displayed a much higher rate of food consumption over larvae maintained at 15°C. I concluded that temperature had more influence on the rate of food consumption in larvae than did daylength. Even though differences in feeding rates occurred between the two photoperiods at 20°C, these differences were less pronounced than the ones found when responses of larvae to temperatures were compared.

While photoperiod does not play as significant a role as temperature in the feeding of larvae, it does have a definite effect on seasonal response of dragonfly larvae. Lutz and Jenner (1964) studied the life history of Tetragoneuria cynosura and qualified it as a spring species in accordance with the classification given by Corbet et al. (1960). Individuals in a spring species overwinter in the final instar, emerge early in the spring, and have a well-defined emergence period due to the synchronizing diapause stage in the final instar. Corbet (1963) indicated that a diapause stage is a major factor in synchronizing larval development and emergence in spring species. Jenner (1959) has demonstrated conclusively that an absolute photoperiod of 14 hours promotes development in final instar larvae of T. cynosura, whereas, a response to an 11-hour photoperiod was delayed. Lutz and Jenner (1964) were the first to observe seasonal responses of T. cynosura to photoperiods of 11 and 14 hours. They determined that experiments started prior to the autumnal equinox (August and September) showed that the duration of the final instar in larvae maintained on long days was about twice that of short-day animals. However, animals collected following the autumnal equinox period produced an opposite response; the longer photoperiod induced a more rapid development in fall and winter

collections. Additional studies by Lutz (1970; 1974a, b) specified actual months at which these two contrasting responses occurred. In the present study the average time to emergence for animals maintained on a long daylength was greatly reduced over their short-day counterparts. All collections in the present study were made following the autumnal equinox producing similar results to that of Lutz (1962). In comparing short and long-day animals at 15°C, short-day larvae averaged 34 days longer until emergence than did their long-day counterparts. At 20°C, short-day larvae required an average of 57 more days to emerge than did long-day animals.

Investigations of the literature pertaining to weight changes of dragonfly larvae yielded minimal information. Only the study by Lutz (1962) provided information on the weight changes of larvae. The present study has shown that weight changes in larvae of the four experimental conditions increased proportionally with the rate of food consumption. The correlation between the data obtained for weight changes and feeding rates reaffirms the conclusions made on the effects of daylength and temperature on food consumption.

Pritchard (1964) noted that hunger greatly affects the behavior of larvae. He observed that starved larvae would strike floating debris as well as strike at prey while already holding food in its labial palps. In the present study a strong hunger response was clearly evident when larvae, starved for the first two weeks, were initially brought in contact with prey. This initial feeding produced a very significant increase in rate of consumption over animals fed continuously. This elevated rate of food consumption continued for approximately two weeks,

but at this time the hunger stress abated and larvae of both groups responded similarly until emergence.

Weight changes of starved larvae that were fed at one time or another corresponded to their rates of food consumption. Animals fed continuously displayed a gradual increase in weight, whereas animals starved continuously gradually decreased in weight. Animals fed for only the first two weeks increased in weight as in larvae continuously fed, but the weight immediately began decreasing when starvation was introduced. Weights of larvae that were starved for the first two weeks responded similarly to the weights of larvae starved continuously but an abrupt increase in weight occurred after these two weeks due to the interjection of food.

Animals in each individual group emerged at approximately the same time. Kormondy (1959) suggested that last-instar larvae finally cease feeding one to three weeks before emergence. He observed that larvae collected in the spring stop feeding seven to ten days prior to emergence. The present study showed that larvae housed at all four conditions terminated their feeding on an average of about 12 days prior to emergence even though some animals did eat to within 2 days of emergence. Only two larvae of the starved group emerged. All the remaining starved larvae crawled out of their culture bottles and remained perched at the top of their individual dowel. These animals lived many days past the mean emergence time of all groups, but they all died unable to emerge. It was observed, however, that the two starved larvae that did emerge were outliers with respect to the weights of the other starved larvae in the group. Despite the small number of animals in the group,

these observations suggest that larvae must attain enough stored energy as body weight to pass through the period of transformation.

Lutz and Jenner (1964) determined that eight long-day photoperiods were necessary to induce a response similar to that of long-day controls. They suggested that the effect of a long day is initially reversible but measurements of feeding and weight changes indicated some immediate differences in response to the two daylengths. In the present study the results from the first experiment (20°C) suggest that more than six but less than 21 long-day photoperiods were necessary for a response similar to that of long-day controls. The second experimental study conducted one month later (also at 20°C) again suggested that more than six long-day lengths were necessary for similar response to that of long-day controls. However, animals subjected to 12, 15, and 18 long-days produced no differences from animals experiencing 21 or more long days. Results of the present study in animals maintained at 15°C indicated that all groups of larvae responded similarly to long-days except three-day larvae. Lutz (1962) indicated that low temperatures prolong development and reduce differences in response to the two photoperiods. Results from the present study suggest that the lower temperature reduced the incidences of differences between the various photoperiodic groups employed in this study.

My results suggest that the responses by larvae to long days are not immediate nor are they initially permanent. Larvae must experience a number of long days (6-21) before they will respond similarly to the long-day controls. Likewise, it is possible to eradicate the influences of a long day if larvae have not been subjected to it for a time

sufficient enough to elicit a long-day response. Evidence to support this model of gradual attunement to long days is found in both rates of feeding and weight changes. During the early part of my experiments, only gradual deviations in rates of food consumption and weight gains were noted between the long- and short-day groups. This observation supports my position that photoperiodic responses are both gradual and reversible up to a point.

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