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## Life History and Life Process Studies of the Water Scavenger Beetle, *Hydrophilus triangularis* Say

M. D. Hallmark

C. R. Ward

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### Recommended Citation

Hallmark, M.D; Ward, C.R. 1972. Life History and Life Process Studies of the Water Scavenger Beetle, *Hydrophilus triangularis* Say. U.S. International Biological Program, Desert Biome, Logan, UT. RM 72-49.

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RESEARCH MEMORANDUM

RM 72-49

THE LIFE HISTORY AND LIFE PROCESS STUDIES  
OF THE WATER SCAVENGER BEETLE,  
*Hydrophilus triangularis* Say

M.D. Hallmark & C.R. Ward



DESERT BIOME  
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1971 PROGRESS REPORT

THE LIFE HISTORY AND LIFE PROCESS STUDIES  
OF THE WATER SCAVENGER BEETLE,  
*Hydrophilus triangularis* Say

Melinda D. Hallmark  
and  
Charles R. Ward

Texas Tech University  
Lubbock, Texas

MAY 1972

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## ABSTRACT

2.3.6.7.-1

The life cycle of *Hydrophilus triangularis* Say was determined. It is holometabolus with the larval stage consisting of three instars. The first two require from two to three days each and the third instar lasts about twelve to sixteen days, depending on the availability of food. Pupation requires approximately ten days. Laying of the egg mass was described, and from a sample of fifty-three egg masses there were 53 - 170 eggs per case with an average of  $105.1 \pm 7.5$  eggs per case.

Food habits of larvae and adults were studied. The larvae are carnivorous and cannibalistic. Adults meet the standard of their name -- water scavenger beetle -- as they are omnivorous, eating fresh and decaying plants as well as living or dead animals.

Population density studies reflected the varying mortality of different groups of larvae without noticeable effects produced by crowding. From an initial group of 1000 eggs, a life table was formed to determine the age of specific mortality for each immature stage. The highest mortality rate, found in the third instar as shown by the life table, was possibly due to unsuitable conditions for pupation in the laboratory.

Reproduction was found to be affected by environmental factors such as rain in the local playas, while laboratory insects reflected the outside atmospheric conditions. Females layed about every two weeks when there was sufficient incoming water into the playas. A maximum of four egg cases were laid by a single female in a two month period.

Respiration was measured for the larval, pupal, and adult stages. Respiration was not found to be a linear function of weight for all larval instars. Pupal respiration increased towards the end of the stage, but in varying amounts. Regression analyses were performed for each group.

Studies on assimilation, growth and excretion were accomplished using the amount of food ingested and the caloric content of the food and the insect.

#### 2.3.6.7.-2

The amount of food ingested per day increased ten-fold during the larval stages. Growth per day increased through the early second instars and then appeared to level off through the late second instar to late third instar. This increase and leveling off also was observed in rate of respiration per day. Growth and respiration values were combined to give the amounts of assimilation and these values were subtracted from the amounts of food ingested to determine the amount of loss egested. The percentages for these rates were calculated. For percentages of energy converted to growth, the second instar was most efficient with the first instar least efficient. The percentage of assimilated food used in respiration varied with the late second and early third respiring the most, and first instar respiring the least. In studying loss of energy, the early first lost the largest percentage through egestion and likewise had the lowest percentage of assimilated food; the late second instar lost the smallest percentage of ingested food, converting 80% of the food energy into body weight. A study was also conducted on effect of food amounts on growth and it was found that smaller food amounts produced smaller individuals.

The bioenergetics or the energy contained within the biomass was studied, using the bomb calorimeter for each stage along with exuvia, and recorded. Carbon and nitrogen levels were also determined through use of a CHN analyser to provide a basis for IBP studies of turnover rate.

## INTRODUCTION

### Purpose and Scope

*Hydrophilus triangularis* Say is commonly found in intermittent waters throughout Western Texas and New Mexico. Its presence in these waters is of considerable importance as one of the largest predaceous organisms present. Only through study of the major aspects of the life cycle and different aspects of the life processes can the importance of an organism in the overall ecology be understood and used in an energy flow model of these areas. Those aspects studied are: life cycle, ecology, respiration, ingestion, assimilation, growth, and excretion, and a life table and bioenergetic values were determined.

### Review of Literature

Little work has been done in recent years on the water scavenger beetle, *H. triangularis*, but several studies are being done in Europe on a similar beetle, *Hydrophilus piceus* Linnaeus. Many of the early works are difficult to obtain, and later works only mention the species. Authors had many speculations as to function and form of different aspects of *H. triangularis* life cycle. These will be discussed and confirmed or refuted in the following sections.

*H. triangularis* was described by Say (1823). Leng (1920) records the following synonymies: *lugubris* Motschulsky, *tristis* Motschulsky and *subsulcatus* Leconte, including the generic synonym: *Hydrous*. It has been found from New York (Richmond, 1920), to Illinois (Woolridge, 1967) across Wisconsin (Park, 1929), Nebraska (Todd, 1944), Oregon (Brues, 1928), and down to Texas, New Mexico and Louisiana (Todd, 1944). It was often very common and the largest aquatic beetle present (LaRivers, 1954). Their habitat appears to be widely diverse as they are found in shallow ponds with abundant vegetation (Matheson, 1914), ponds and streams (Blatchley, 1910), temporary ponds or playa lakes in the southwest, to hot springs in the west (LaRivers, 1954) and northwest (Brues, 1928, 1932). Brues (1932) took specimens at 36.8°C from a hot spring but noted several dead specimens in springs with higher temperatures. He did not record the presence of larvae at this temperature.

Adults have been collected as early as March 19 in Indiana (Blatchley, 1910) to as late as November 1 in New York (Richmond, 1920). They are often found around lights during spring and summer. Richmond (1920) collected one on November 1 under an arc light. They have been found attracted to electric lights in cities (Blatchley, 1910) and to black lights near ponds where they flew in, then crawled toward the lights.

Several authors described various aspects of the life cycle as follows: egg and case (Garman, 1881; Riley, 1881; Matheson, 1914; Richmond, 1920), larvae (Garman, 1881; Matheson, 1914; Riley, 1881), pupae (Riley, 1881; Richmond, 1920; Matheson, 1914). Papers dealing mainly with adults include studies of an aberrant form (Park, 1929), their habitat (Brues, 1928, 1932), and electrical responses of the adult eye due to the effect of diurnal rhythms. The rhythm was found to be relatively simple for day-type responses while night-type responses were polyphasic containing the slow c-way type (Jahn and Crescitelli, 1940). Other studies have defined the intensity - EMF (electromotive force) relationships of the dark-adapted eyes of *H. triangularis* (Wulff and Jahn, 1943). Other aspects will be discussed in appropriate subsequent sections of this document.

## METHODS & PROCEDURES

### Laboratory Rearing and Maintenance

The major sources of adult *H. triangularis* used in these studies were playa lakes throughout Lubbock County. It was never possible to compare the beetles from Lubbock with those from the Jornada site due to lack of rain at the site and subsequent lack of these organisms.

The adults were collected by nets while sweeping the water and when the beetles surfaced for air. Hand collecting was done as the beetles were eating vegetation near shore or laying egg masses. A few adults were also collected after being attracted to a black light near a playa. They did not fly into the light but landed a few feet away and crawled toward it. Another source was adults reared in the laboratory.

The adults were maintained in five and ten-gallon aquariums and in one gallon jars, used mainly to study reproductive rates. Water temperature was maintained between 70-80°F during the summer and winter by using aquarium heaters when necessary. Aquarium filters were also used to simulate the conditions of clear and aeriated water found in the playa. Daylight hours were provided by overhead fluorescent lights approximately fourteen hours per day. At night the aquariums were covered to prevent the adults from flying or crawling out. Cork floats were provided in most aquariums for the adults to crawl upon and dry. As the adults would also climb the filter hoses, each was equipped with a metal shield curved toward the water, to prevent the adults escaping. The adults were fed a variety of food as discussed in the section on food.

Larvae and eggs were obtained from the playa and the laboratory. Due to the fact that the adults frequently ate the egg masses while in captivity, the eggs were separated in beakers, aquariums or jars until hatching. Upon hatching the larvae were placed in five or ten-gallon aquariums, one-gallon jars or 500-milliliter beakers. The larvae and eggs were maintained under similar conditions to those described for the adults. The section on food habits describes their diet.

#### Procedures For Determining the Different Life Process Rates

The physiological processes of ingestion, assimilation, growth rate, and excretion are interrelated. Ingestion, assimilation and growth were measured. The amount excreted was calculated using the formula by Welch (1968). To determine growth and ingestion rates, larvae were isolated in individual beakers. Measurements of increase in weight and amount of food ingested were taken on each individual, and the dry weight of the food was recorded.

Daily weighing of first instars was detrimental because of the rapid evaporation rate of water from the smaller larvae. The short period needed for weighing was not detrimental to the larger instars. Weighing to the nearest milligram was done on a Mettler balance (Model H16). Each larva was blotted on absorbent paper to remove excess water before weighing.

Respiration studies were conducted to obtain a measure of the basic metabolic rate. Two methods were used in measuring oxygen ( $O_2$ ) consumption. The standard Warburg procedure was used with a Model G. instrument for measuring microliters ( $\mu l$ ) of  $O_2$  consumed during the three larval stages. Each stage was divided into an early and late period allowing for two measurements of each of the three stages after hatching, before and after each molt, and before pupation.

The Scholander respirometer (Scholander, 1950), available from Bellco Glass, Inc., was used for the pupal and adult stages, as it was large enough to accommodate the larger insects. The respirometers were operated using Brodie's Solution as with the Warburg, two grams of potassium hydroxide (KOH) pellets for carbon dioxide ( $CO_2$ ) absorption, and a buffer zone of filter paper for the pupae (Fig. 1). Both flasks of each respirometer were submerged in the same water bath at about  $21^\circ + 1^\circ$  to permit accurate and reproducible readings. In adult studies, the two grams of KOH were placed in little plastic sacks suspended from the top of the vial by a string. The adults were maintained in a dry environment during respiration measurements. The Scholander was used as the Warburg flasks were not large enough to accommodate the adults. As with pupae, measurement were made for several hours with vials submerged in the water bath. Both the Scholander syringe and Warburg flasks were calibrated using the mercury method. Readings on the Warburg were taken for periods of one to four hours. Due to the comparative simplicity and size of the Scholander, readings were taken for several hours at a time. Normally, the live weight and length for each specimen were recorded after each test.

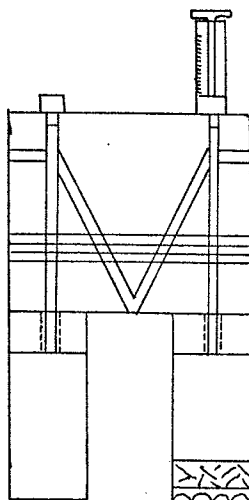


Figure 1. Scholander respirometer as utilized for adult and pupae respiration studies.

A CHN analyser (Hewlett Packard Model 185) was also used to determine the carbon, hydrogen and nitrogen (CHN) levels in the different periods of the larval stages. For these analyses the specimens were frozen alive, desiccated, and ground with mortar and pestle and stored in vials until used.

A Parr oxygen bomb calorimeter (Model 1221) was used to determine the energy equivalents for each stage. As above, specimens were dried, then ground with mortar and pestle and stored in vials until they were used in the analyses. Specimens were never placed in any type of preservative. These data were important in development of energy relationships of this species to be used in the energy flow model of the Jornada playa being studied in the U.S./I.B.P. Desert Biome Program.

## FINDINGS & INTERPRETATION

### Life Cycle

*Hydrophilus triangularis* Say undergoes complete metamorphosis and each stage is described in detail in the following paragraphs.

#### *Egg and Case*

The eggs are laid in a special floating case (Fig. 2). The case was first described by Riley (1881) who was uncertain as to function of the case and process of laying. Matheson (1914) made a more thorough and accurate description of the egg case. Garman (1881) stated the chief object of the peculiar case was to ensure a supply of  $O_2$  to the newly-hatched larvae. More important, this would allow the developing embryos to obtain air.



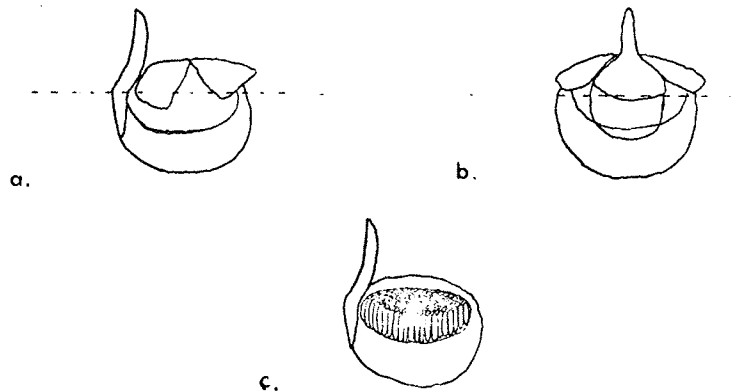


Figure 2. Egg case. a. side view, b. front view, c. position of eggs of *H. triangularis* Say.

In spinning the white outer shell of the case, the female frequently changed positions. The case was spun of silk from the accessory tubes of the genital organs (Wigglesworth, 1965). Often she held to fixed plants and spun the case dorsal side up. The case was attached to any floating debris including dead snail shells, tiny bits of twigs, green grass and other green plants, dead reeds, leaves, and algae. Very seldom was an egg case found still attached to a plant; usually the female severed all connections. Richmond (1920) and Garman (1881) stated that the floating egg cases had never been reported as fastened to living plants, but a few were found still attached to living plants in the local playas. Matheson (1914) also reported none being attached to living plants and also felt that the leaves were attached to serve as floats and to aid in keeping the mast erect and above the surface. This was not found to be true, as cases were spun attached to flimsy bits of algae and served only as attachments for starting the case.

After the female completed the outer case, she spun a thicker inner case (also white) in the top half of the outer case, after which she commenced to lay the eggs. The eggs were a bright golden yellow, 5 mm long [Garman (1881) reported them to be 4 mm long] and were arranged vertically with the posterior end of the developing larvae dorsal. When oviposition was completed, the female closed off the small inner case with a thick triangular shaped closure. This part of the egg case was yellow, broad and flat (while being spun). Upon drying, it changed to a dark gray-brown with the lateral edges curled backward forming a narrow "mast" (Richmond 1920). This was not sealed by a gummy coating as described by Garman (1881), but had the superficial appearance of being gummy.

Early speculation as to functions of the mast included its possible use as a tube for admission of air into the case (Garman, 1881; Matheson, 1914) or as a protection for eggs and newly-hatched larvae (Riley, 1881). Other speculation concerned the possibility that the sternal spine of the adult was used to form the horn (Riley 1881), but this was not found to be true in this study. This mast, or horn, with its spongy webbing at the base on the inside portion of the mast, plus the extra thick webbing on top of the case, kept the case in the correct position to allow the developing embryos to respire. Any egg cases that did not remain afloat or were forced to float upside down failed to hatch.

The eggs were seemingly suspended from the roof (Matheson, 1914) with the portion of sac containing the eggs being laid in the topmost area of the outer case. Matheson (1914) did not find water in the egg portion; however, the eggs did seem to have water moistening them. As the young embryos developed, their increased size caused the inner case to develop cracks in several places, facilitating movement of the hatching larvae into the outer case. There were a few occasions in the laboratory when a female was disturbed while spinning the outer case by movement or by entrance of water into the case. In those instances that she did finish the egg case, she did not use the submerged outer case, but spun the inner case starting at the back and laying the eggs as she increased the size of the case. This case had vegetation above to which the initial strands were attached. These eggs were observed developing normally. Eggs laid in the summer months hatched in three days, but eggs laid in the fall took from five to seven days to hatch, depending on the prevailing temperatures. Warm days produced larvae in five days while a cold spell delayed hatching.

In 53 egg masses studied, there were from 53 - 170 eggs per case with an average of  $105.1 \pm 7.5$  eggs per case. Matheson (1914) recorded two egg cases with 112 and 130 eggs, and Garman (1881) recorded one with 107 eggs.

#### *Larvae*

Upon hatching, larvae remained inside the floating egg case, chewing holes in the sides and crawling out of the front opening onto the ventral and lateral sides of the case. The larvae underwent two molts, with the first molt beginning two days following hatching and the second occurring approximately two to three days subsequently. This essentially agrees with observations by Riley (1881). Matheson (1914) also described hatching of the larvae. He stated that the larvae he observed took eight days to reach the first molt, but this was probably due to inadequate nutrition, as discussed in the section on growth, because it is at least twice as long as normal in studies reported here. He did not observe the second molt and described the larval stadium as thirty days, an interval one and a half times as long as those reported here. Also, the length of the late third instar larvae Matheson (1914) described as 40 mm long was under the average size of those found in the current study. Table 1 gives the average lengths, weights and the 95% confidence intervals for each sample of larvae, plus the number in each sample.

As each larva grew, it turned a light brown color towards the end of the instar. Approximately two to three hours before each ecdysis, the larva appeared to be dark from the pharate larva under the old cuticle. During and after each molt, the new larval skin appeared black and white. The main body of the larva was dark upon molting, but the white head and legs required a longer time to develop, darken and harden. Each ecdysis was accomplished with the larva floating dorsal side up. The thorax split, allowing the larva to slowly extract the thorax and with continued contractions to extract the head, legs and abdomen from the exuvium. With each molt, the head width appeared to double, and each instar could be determined by width of the head capsule. The third instars, as they approached pupation, became restless, then inactive, and ate very little. When placed in a pan with water at one end and three to five inches of soil at the other, the larva crawled to the soil and began to burrow, using its head to dig. Once the larva had found a suitable place, it dug a tunnel almost to the surface and then fashioned an oval pupal cell. However, if the larva pupated quite near the surface, no tunnel was formed. From eclosion to the day the larva entered the soil required from eighteen to twenty-two days. Only four to six days were spent in the first plus the second instars, with the remaining period spent as third instar larvae.

## 2.3.6.7.-8

Table 1. Average live and dry weights and body lengths of reared *Hydrophilus triangularis* larvae. Lubbock, 1971.

Stage	Length (cm)	95% Limit <sup>a</sup>	Wet Weight (g)	95% Limit	Dry weight (g)	95% Limit
Early First	0.86/21 <sup>b</sup>	±0.09	0.0092/21	±0.0008	0.0008/21	±0.00002
Late First	1.59/14	±0.66	0.0349/31	±0.0006	0.040/12	±0.0010
Early Second	2.27/14	±0.21	0.0901/17	±0.0151	0.0094/13	±0.0028
Late Second	3.01/16	±0.13	0.2399/24	±0.0380	0.0357/18	±0.0036
Early Third	3.3/12	±0.17	0.3559/18	±0.0409	0.0348/13	±0.0044
Late Third	5.33/18	±0.29	1.7569/16	±0.0375	0.1094/9	±0.0924

<sup>a</sup>95% confidence interval.

<sup>b</sup>Indicates size group in the sample.

#### *Pupae*

Several larvae were observed in the laboratory as development proceeded from late third to adult. The larva, after entering the soil and fashioning a pupal cell, required two days or more before molting (Matheson, 1914). Pupation usually required ten days before emergence and hardening of the adult (Matheson, 1914). Pupae were white with brown tipped spines and dark eyes. Movement in the pupal cell was facilitated by two spinelike projections located on the tip of the abdomen. Matheson (1914) reported the spines functioning to keep the tender pupa from contacting the soil. Although this might occur in some pupal cells, the pupae studied did contact the surface as they laid dorsal side down on a level plane and in the cells. Before emergence, the head and thorax began to turn brown; after emergence, the head and thorax turned the characteristic dark olive green first, with the wings and body remaining light brown until later, then becoming olive green themselves.

#### *Adult*

From emergence until the adult had hardened sufficiently required one or two days. Matheson (1914) described the hardening of the adult as taking approximately twenty-four hours. After hardening, the adult beetle surfaced through the tunnel which had been started by the larva. The adult male *H. triangularis* could be readily distinguished from the female by enlarged front tarsi which functioned to hold the male on the female's back during mating. This was accomplished by the male clasping the outer edge of the elytra with the enlarged tarsi.

The adult may dig into the moist soil of the drying playa to stay until the next rains. Hibernation occurs in the adult stage (Matheson, 1914; Blatchley, 1910). This was evidenced by the appearance of adults in temporary waters during winter months upon a refilling of the playas that had dried in the previous fall.

### Ecological Aspects

#### *Food Habits*

The larvae were reported to eat several things; fairy shrimp, tadpole shrimp, clam shrimp, tadpoles (Matheson, 1914), snails (Matheson, 1914; Blatchley, 1910), minnows (Matheson, 1914), other small fish as guppies and catfish. They were also found to be cannibalistic when other food was not readily available (Matheson, 1914). Many larvae were observed eating snails in the laboratory. The snail was held between the mandibles with one extending into the snail.

The larva then tilted the head back, placing the snail between the head and back and proceeded to slowly break the shell open like a can opener. Fairy shrimp were also readily eaten by all larval stages. The larger fairy shrimp and tadpoles larger than the larvae in girth were readily consumed by the third instar larvae. The larvae fed by stuffing the food into their mouths with their mandibles. The mandibles encircled the prey and one served to hold it while the other worked in a horizontal plane to move the food little by little into the mouth. Because of cartilage, tadpoles were not completely eaten. This was also true with guppies and catfish, as the larvae consumed only the caudal end.

Food availability had a definite effect upon the length of the larval stages. Larvae fed on natural food, such as fresh or frozen fairy shrimp, tadpole shrimp, tadpoles or snails, developed at a normal rate, while larvae fed on unnatural food such as beef heart took twice as long to complete the instar. Differences in the food sources were also apparent as those fed natural foods were larger, as discussed under life processes. Insufficient amounts of food delayed the completion of larval development. Dixon (1959), in studies of *Adalia decempunctata* (L.), found that a larva had to consume a certain number of aphids in order to complete an instar within a certain time. Their ability to do this depended upon the efficiency of the larvae in capturing food.

The adults definitely met the implied standards of their name, the water scavenger beetle, because they were decidedly omnivorous. They lived and bred quite readily on a diet of algae, *Pithopliora* sp., which grew in modified playas. They readily ate other aquatic plants such as *Marsilea* sp. when these were placed in an aquarium. When the playas were reflooded, the beetles readily ate the decaying plants and roots. Blatchley (1910) stated that adults consumed aquatic vegetation; in this study adults ate living and decomposing vegetation and a variety of organisms in the laboratory. The adults easily found and ate dead or injured tadpoles and devoured any scraps left by the larvae. They ate living animals such as fairy shrimp, small toads, and larvae of their own species that they caught. Adults were observed many times catching small live toads in the aquariums when the adults were crowded and probably hungry. Dead or injured fairy shrimp were readily consumed and were quite prevalent in playa areas.

#### *Population Density*

The effects of population density were measured under two conditions; increased numbers in a standard size container and uniform numbers in containers of different sizes. The results were not clear. One experiment involved growing 106 larvae of one egg mass in a five-gallon aquarium. After ten days, only sixteen individuals survived, comprising one first instar, thirteen second instars, and two third instar larvae. These were then transferred to a ten-gallon aquarium. Of the sixteen, ten reached pupating stage. These trends occurred with other egg masses left in a single aquarium. A few larvae generally reached maturity much quicker than others. In experiments involving different sized containers it appeared that larvae in the largest container grew much quicker than those in smaller containers. One cause of indefinite results might have been the varying mortality rates; for example, only one to five individuals survived in each container. There was varying mortality in the populations not raised with varying population density. In one experiment with fourteen larvae in a five-gallon aquarium, five matured to late third instar; in a ten-gallon aquarium starting with ten larvae only three reached late third instar; and in a 1.75-gallon starting with ten larvae, only four reached late third instar. Dixon (1959) studied effects of prey density on a predatory coccinellid beetle, *Adalia decempunctata* (Linn.), and found that density of prey affected the amount of searching. Under conditions of greater density of prey, less time was required in searching. This may have been a factor for the four larvae in the 1.75-gallon aquarium. The prey had such a restricted area for escape it would be more prone to come in contact with the larvae, thereby requiring less movement of the larvae for searching, and more time for resting. This also lessened contacts among larvae and consequently reduced the probability of cannibalism. This searching was observed to be unorganized and therefore random according to Nicholson (1933). When crossing of paths occurred, the larvae vigorously swam backwards upon contact.

#### 2.3.6.7.-10

In a fourth experiment groups of twenty, ten, or five larvae were placed in one-gallon jars. By the end of the second instar, three larvae of the twenty, four of the ten, and two of the five remained. Food was likely not a limiting factor, as each group was provided more food than they consumed. A fifth experiment replicated the previous one, but added a group of forty of which fourteen remained; here, eleven of twenty and one of both the five and ten groups survived through the second instar.

In the field, the population's density appeared to reach a major peak in August, followed by a few minor peaks as summer progressed. Small showers in June and July began filling the playas, followed by lowering of the water level. The occurrence of major rainstorms, which completely filled the playas, had a drastic effect upon the adult beetle population. Until occurrence of the heavy rains the last of July, only minor oviposition was observed.

Varley and Gradwell (1970) designated density as weather-independent, since weather could neither be detected nor responded to by the population's density. They also suggested how weather effects might appear to be related to density if these acted on a population whose habitat was diversified and where increased density forced part of the population to seek a marginally suitable habitat for survival. This was associated with density-independent mortality which might be caused directly or indirectly by weather through components of temperature, rainfall and humidity. Varley and Gradwell (1970) stated that density-independent mortalities are often the key factors causing population changes and these could also include food supply, parasites, predators and disease.

Parasitism as a factor on population density was neither observed nor studied. However, there have been reports of parasitism. Chillcott and James (1966) noted dipterous larvae infesting a dead larva and a pupa of *Dytiscus fasciventris* Say. These researchers found eggs of the parasite on the thoracic sternum of a larva which had come out of the water to pupate. It is possible that similar parasitism may occur in *H. triangularis* under field conditions. Todd (1944) found two new species of parasitic nematodes in the large intestine of *H. triangularis* adults. In this study, several instances in the laboratory were observed where pupae failed to develop due to diseased conditions. A few adults confined in gallon jars were noticed oozing a milk-like substance from membranous areas of the head, thorax and elytra. Most of these adults died if not transferred to aquariums where water conditions were less stagnant. Predation occurred in the field where smaller instars were eaten by other carnivorous insects or possibly cannibalized by each other; a few predators were present that might affect the adult populations. Although predators were not observed feeding on adults or larvae, the presence of frogs, fish, salamander larvae, and aquatic birds feeding in shore waters, would indicate the possibility of predation since *H. triangularis* was the largest insect present and was quite abundant. McCoy (1969), in a study on bullfrog diets in Oklahoma ponds, found that 73% of those eating invertebrates contained *H. triangularis*, constituting 48% of the total volume of food in the forty-five frogs. Korschgen and Moyle (1955), who studied bullfrog diets, identified insects only to families and found Hydrophilidae occurred in 18.2% of the bullfrog stomachs and constituted 9.2% of the contents by volume.

Food and weather had a definite effect on the life cycle of *H. triangularis*. Both produced density-independent effects as described by Varley and Gradwell (1970), but they also showed the opposite effects. That is, weather and food caused not only a decrease in population levels but also an increase. *H. triangularis* inhabited temporary waters, and the drying of these waters produced a decrease in suitable conditions, with less available food and space for the adults. Adults were observed burrowing into the soil bottom of the receding water or flying off, thus affecting density and causing cessation of oviposition. Evaporation of water also affected the larvae by hindering one major aspect -- availability of suitable habitat. The habitat was marginal, but food sources were at a high, because the declining water level concentrated food sources making them more available for the *H. triangularis* larvae, enabling them to develop more rapidly and requiring less searching time for prey. As the playa water level lowered, adults ceased oviposition, thereby reducing the likelihood of larvae too young to pupate being present as the playa dried.

Very seldom were larvae other than late third instars found in nearly dry playas. This relation of egg-laying to drying of the playas could possibly have been expressed by Cooper (1965) when he found that *Hyalella asteca*, an amphipod inhabiting temporary waters, reflected the effects the level of food had on the expression of individual fecundity. He said that this was common in biological systems. Richardson (1971) noted similar population dynamics in a desert playa.

On the other hand, weather caused an increase in food and suitable habitat. Re-flooding of playas produced more desirable habitat and more available food for the adults because the submerged or partially submerged plants, both green or decaying, were available for consumption. This also produced a marked increase in egg laying as mentioned previously. Increased egg production might have produced a decrease in food shortage for larvae also, but with each rain there was an increase in numbers of prey hatching. Prey such as tadpole shrimp and fairy shrimp began hatching one to two days after the rain, providing quantities of small suitable food for the newly-hatched *H. triangularis* larvae.

Availability of food and prey density effects have been studied for nonaquatic insects. Varley and Gradwell (1970), in studies of field populations of phytophagous insects, showed that the key variable of mortality came at a time when eggs were hatching and the young larvae were seeking to establish themselves and obtain their first meal. Availability of suitable foods was found to profoundly affect survival at this stage. Dixon (1959), in a thorough study of the predator *Adalia decempunctata*, found that the most important feature in the establishment of the larvae was the ease with which the first meal was obtained. Larvae at this stage were the least efficient in capturing prey, requiring a prey density at least twelve times greater than the fourth instars for 50% survival. Mann (1957), studying *Helobdella stagnalis* (L.), an aquatic leech, found 90% mortality early in life; those surviving this critical period had a relatively high expectation of life.

This critical period also appeared to affect *H. triangularis*, but not to as extensive a degree as in the examples cited. This could be due to the wide variety of food suitable for the larvae. The degree of searching observed was directly related to ease that food was found. When food was scarce, there was much searching and commotion caused by the larvae running into each other. Once food was located, the larvae would usually float or swim to the surface, holding the food in the mandibles to enjoy a leisurely meal.

Data from group mortality and individual mortality were combined to form a life table (Table 2) for use at the Jornada site in an attempt to predict cycles observable there. The life table was patterned after tables formed by D.M. Arnold, unpublished thesis. Values from laboratory studies are not exactly convertible to field situations, but they are of great value where there is no previous knowledge. Slobodkin (1960) felt that the laboratory suffers from a lack of reality and the field from a lack of respectability in studying ecological energy relations. The life table is composed of several larval groups, each with varying mortality. Varying mortality has been recorded for other aquatics, as Cooper (1965) found for *Hyalella asteca*.

Table 2. Horizontal life table of laboratory-reared *H. triangularis* to distribution of death according to stage. Lubbock, 1971.

Stage	Number dying during stage out of 1000 initial eggs	Number surviving at beginning of stage out of 1000 eggs	Mortality rate per 1000 alive at beginning of age interval
Egg	20	1000	20.0
First Instar	331	980	337.8
Second Instar	334	649	530.1
Third Instar	198	305	649.2
Pupa	35	107	327.1

### Reproduction

There was more than one generation produced per year depending on availability of water from June through September. Each time the playas refilled, the adults reappeared and laid eggs. Inducement to lay seemed to be a composite of several factors. The atmospheric conditions produced by rainstorms and consequent refilling or adding to a playa always induced mating and production of egg masses. Matheson (1914) gave time of laying as early June; however, in the local playas the peak was observed to be in early August. This delayed peak was caused by weather conditions as discussed earlier. Mating was also affected by temperature, available plant food and fresh water. As stated before, each egg mass contained an average of  $105.1 \pm 7.5$  eggs per case in fifty-three egg cases sampled. Of those cases that hatched, 0 to 5% of the eggs failed to hatch. Of a total of seventy-five egg cases, only six failed to hatch. Where eggs failed to hatch, the egg case sank or did not float high enough to keep the developing embryos from drowning. This was tested by turning a group of egg masses upside down and forcing them to remain in that position. None of these hatched, even though the bottom floated above water. It became apparent that the egg case must be buoyant enough to keep the topmost end of the eggs, which was the posterior end of the developing larvae, above the water line.

The adults were observed mating before and following oviposition. Most ovipositing females had a male hanging on or near her during the process. Upon completion of the egg case, both would swim off with the male riding and attempting copulation with the female. Mating behavior was also observed prior to egg laying; this may have been carried on only among those females who did not have a male in attendance at the last egg laying. Females appeared to signal readiness by a quivering of the body, which would attract one or more males. Females were observed having two males mounting one female. If conditions were conducive to laying, the females would lay about every two weeks. It is not known exactly how many egg masses a female could lay in a single season, but one female was observed to lay as many as four egg masses in a two month period. Females continued to lay approximately every two weeks through the winter months in the laboratory when sufficient plant food, light duration, and water temperature near 70°F were obtained.

Of the mating pairs kept in the one-gallon breeding jars, there appeared to be a cyclic rhythm to laying of eggs. This occurred approximately every two weeks as evidenced by the females observed to lay four masses in two months. As a result, the overlap of larvae of different sizes was minimal. At the time of repeated oviposition the majority of the third instar larvae were about ready to enter the soil for pupation. After the three day period between laying and hatching, most of the third instars were in the soil. This cycling produced an ecological protection of the species as the later instars readily ate earlier instars.

### Life Processes

#### *Respiration*

Ideally respiration is measured at a time when the insect is at a resting stage with minimum movement (Keister and Buck, 1964). Respiration is affected by many variables. These include internal and external variables such as activity, temperature, nutrition, body size, stage in life cycle, season, time of day, previous oxygen experience, genetic background, and habitat (Knight and Gaufin, 1966; Prosser and Brown, 1961; Keister and Buck, 1964; Thorpe and Crisp, 1947; Fox, Simmonds and Washbourn, 1935).

Metabolic rates for homeotherms have been shown to decrease with increasing weight (Kleiber, 1947). For non-insecta poikilotherms there have been examples of decreasing oxygen consumption with increased weight, as in the crayfish (Wiens and Armitage, 1961). Exactly how insects fit into the scheme of oxygen rate as compared to body weight remains to be seen. Knight and Gaufin (1966) found the relationship of oxygen to weight in two species to vary according to the weight group. The rate of oxygen to weight changed decidedly once the larvae reached a certain weight, producing large differences in the coefficient of regression. They stated that it was difficult to distinguish between changes due to metabolic correlates of the life cycle. Petitpren and Knight (1970), in comparing

oxygen rate to weight, found that temperatures produce varying correlation coefficients. They concluded that coefficients of -0.5919 at 13°C and -0.7259 at 20°C were significant, but that coefficient values of 0.1245 at 27°C and 0.0504 at 34°C exemplified a weight-independent metabolism. They stated that differences in oxygen consumption could possibly be due to the different sizes of the individuals and that sensitivity to temperature caused lower response in the larger individuals. Keister and Buck (1964) gave examples of variations in oxygen rate, concluding that much of the efforts of curve-fitting and derivations of exponents and constants have been more descriptive than analytical in value. They further suggested that some insects have shown an impressive and useful correlation of respiratory rate to body weight, as with some estimations of tracheal surface area, but the necessity exists to resist the temptation to relate respiratory rate causally to body dimensions in accordance with contemporary thought to locate metabolic control at a subcellular or enzymic level.

In the experiments reported here, measurements were made of wet weight and length following each determination of respiratory rate, then the insects were dried and weighed. The averages for weight and length and 95% confidence limits are given in Table 1. Linear regression analysis were performed on these factors to determine their relationship to oxygen consumption per hour (Table 3). The correlations and F-tests of weight (both dry and wet) and length were significant, agreeing with other work done on constancy of tissue hydration (Von Brand, McMahon and Nolan, 1957; Keister and Buck, 1964). Even though the F-tests on the relations of oxygen to length, wet and dry weights were significant at the 99% confidence level; the highest correlation coefficient was 0.71 for oxygen to length. When this was broken down into the different stages and the beginning and end of each stage, there was a large variation in correlation (Table 4). A scatter diagram and regression line for oxygen consumption and wet weights are given in Figure 3.

Table 3. Linear regression analyses of body weights, length and oxygen consumption (O<sub>2</sub>) of *H. triangularis* larvae. Lubbock, 1971.

Y	X	Correlation Coefficient	r <sup>2</sup>	F-test	Y-Intercept	b (slope)
Dry Weight	Length	0.906	0.8214	331.062**	- 0.02784	0.02229
Wet Weight	Length	0.917	0.8411	492.281**	- 0.55601	0.36927
Wet Weight	Dry Weight	0.955	0.9126	752.227**	- 0.04260	13.67765
O <sub>2</sub>	Length	0.708	0.5006	93.242**	-34.98030	59.50633
O <sub>2</sub>	Wet Weight	0.552	0.3051	40.825**	76.96173	115.36397
O <sub>2</sub>	Dry Weight	0.494	0.2441	23.246**	65.52057	1700.14673

\*\* Significant at the 99% level.



Table 4. Analyses of different stages: Oxygen consumption per hour to wet weight for *H. triangularis* larvae. Lubbock, 1971.

Stage (Instar)	Correlation Coefficient	r <sup>2</sup>	F-test	Y-Intercept	b (slope)
Early First	-0.334	0.1118	2.140 <sup>NS</sup>	9.92659	-276.98047
Late First	0.332	0.1103	1.487 <sup>NS</sup>	1.96231	475.33740
Early Second	0.683	0.4666	6.999*	9.46660	376.10034
Late Second	0.563	0.3172	6.505*	-106.18114	1034.03833
Early Third	0.721	0.5193	10.803**	-138.10950	984.67725
Late Third	0.098	0.0097	0.215 <sup>NS</sup>	189.88531	26.79724
Pupa	0.483	0.2337	17.685**	- 1.49912	3.11113

\* Significant to the 95% level.

\*\* Significant to the 99% level.

<sup>NS</sup> Nonsignificant.

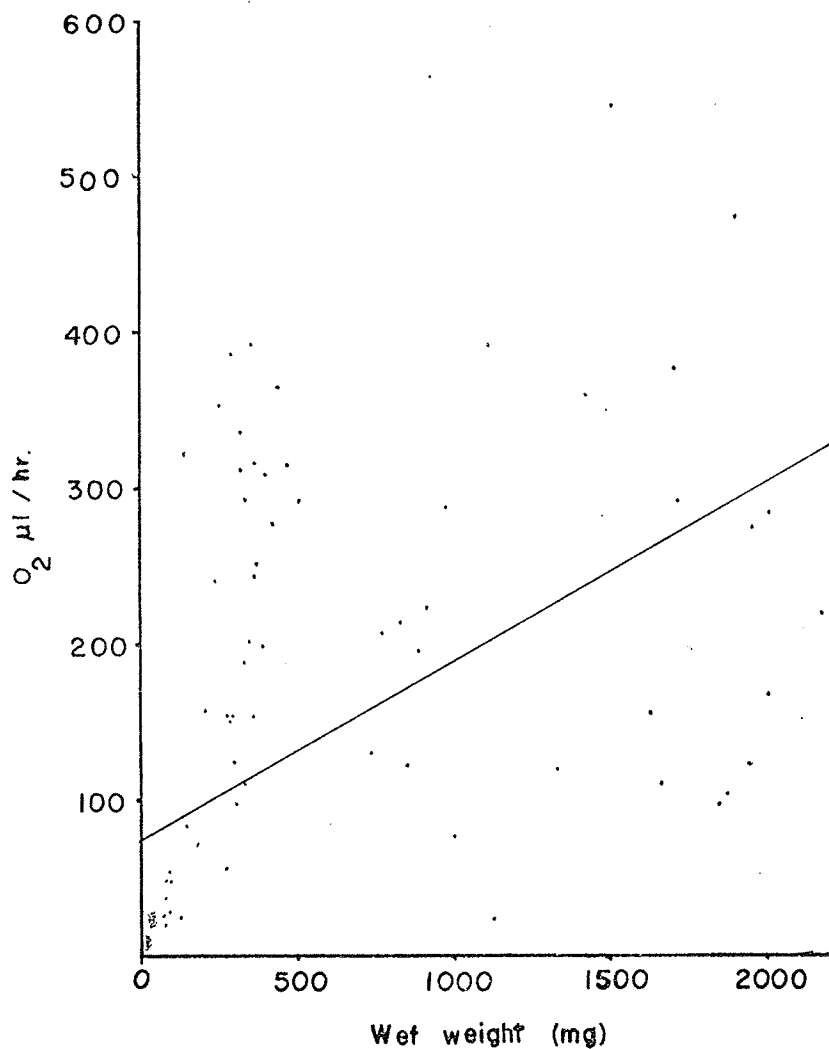


Figure 3. Linear regression analyses of O<sub>2</sub> consumption per hour to wet weight for all instars of laboratory-reared *H. triangularis* larvae. Regression line: Y-intercept = 76.96173, slope = 115.36397.

This variation between and within each group and for the pooled data could be caused by many variables, as mentioned previously. The lack of decrease in oxygen with weight could be due to the difference in type of respiration as carried on by *H. triangularis*. The great majority of water-dwelling insects obtain their oxygen directly from the water, while terrestrial insects have no hindrance for breathing. However, with semi-aquatic insects such as *H. triangularis*, they are required to live, eat and reproduce in the water but periodically must come to the surface to respire. This presents a difficulty when comparing an insect which respire without interruption with one whose respiration is irregularly cyclic. From the first instar through adults (except for pupae) *H. triangularis* makes irregularly-timed trips to the surface, depending on activity or lack of it and feeding state. *H. triangularis* respire from contact with air and also by underwater means. Thorpe (1950) described the adult Hydrophilidae as having combined the requirements for success in being truly aquatic by developing two sets of hairs, macroplastron and microplastron, and keeping them well-groomed. Thorpe and Crisp (1949) discussed the *Hydrophilus* plastron as being of considerable volume and acting as much as an air store as a gill, necessitating surface visits and increasing the buoyancy so that they have to swim down and cling to the substratum. This was not always observed to be true, since both larvae and adult could rest on the bottom surface without aid; they did have great buoyancy and usually had little trouble in getting to the top. Thorpe and Crisp (1949) also noted an observation as to the grooming done by *Hydrophilus*, which they felt was necessary to prevent water-logging. Such grooming as noted by them was also observed every few days in the lab. The adults required a floating object on which to climb out of the water to dry and groom for an hour or more. Thorpe and Crisp (1947) also found the oxygen rate could vary several cubic millimeters depending on the degree of activity and condition of the insect; this might have been an outstanding source of variation in this study. They found definite evidence that the respiration rate was higher in freshly collected insects, possibly due to the slow starvation under laboratory conditions where the normal food was not provided in sufficient quantity. This could be another source of major variation as the quantity and quality of the larval food varied with the availability of fresh food from the field. Starvation has been found to produce a steady decrease in respiration which in the desert locust was about five times that expected on the basis of decrease in weight and of respiring temperature (Clarke, 1957; Keister and Buck, 1964). Sayle (1928) found starvation produced a decrease in carbon dioxide output in *Aeshna umbrosa* nymphs, except during the second week when the metabolic rate was higher than normal.

Sources of variation such as amount of light, temperature, oxygen content and others were eliminated as much as possible; amount of light and temperature and time of day were duplicated as much as possible during each experiment. The three main sources of variation for the larvae have already been discussed. The late third instars, as mentioned previously, appeared to decline in activity as they reached the pupating stage, possibly causing the low correlation of oxygen uptake to weight. Keister and Buck (1964) mentioned that the changes in respiration rate of the first instars and in the last instar, where changes for pupation occur, could be explained by factors such as activation of imaginal disks, water content changes and cessation of ingestion. They suggested that a part of the larval growth, which is mainly cell enlargement, would be the best area for study. Table 4 shows that the time study groups from the early second through the early third, typically involving growth through cell enlargement, show significant correlation between oxygen consumption and weight.

Respiration studies carried on the last five days of pupation showed the rate increased. This has been reported by others also (Keister and Buck, 1964; Bodine and Orr, 1925). As the regression analysis showed, there appeared to be a definite relationship of oxygen per hour to weight. Cyclic releases of carbon dioxide and intake of oxygen were observed during this study. The length and amount of respiration varied with individuals and with time of day. Some appeared to be constantly cyclic and others had a few hours of high respiration followed by hours of low respiration. Keister and Buck (1964) cautioned about reviewing respiration data from pupae since there could be as great as ten-fold differences in respiration rates at different times during the stage with essentially no change in weight. This caution is well taken since half of the pupae showed nearly two-fold increases in the last few days while others increased only slightly.

2.3.6.7.-16

Adult respiration also varied with amount of activity. Even though the vials allowed for minimum movement, some of the adults would struggle as much as possible, while others remained still. Thorpe and Crisp (1947) found the increase in oxygen uptake with activity for adults to be possibly six or seven times the basal oxygen uptake.

*Assimilation, Growth, Ingestion, and Egestion*

Studies in the laboratory were hampered by the availability of different types of food in the field. Studies on ingestion and growth were conducted with natural food. Fairy shrimp were used as their size and weight varied little, and they were easily collected and counted. It is possible that other food such as tadpoles would be preferred by the third instars, but the use of tadpoles for food would have produced more waste while fairy shrimp were clean and easily eaten. Some possible variation was due to food source; for example, Young (1967) found the preferred food varied with age in *Dytiscus marginalis* L. larvae. He felt that this was possibly due to the difference in size of prey as the medium and large larvae ate tadpoles. He did not distinguish between the stages.

Growth rate and ingestion were studied by placing one larva per beaker and feeding a known amount of food. Ingestion was accomplished by holding the prey by one mandible and pushing it in the mouth with the other. Richmond (1920) stated in a general comment that the mandibles macerated the prey, then predigestion occurred prior to the dissolved food being sucked in by the pharynx. This was not found to be true because many larvae were observed eating food such as snails and fairy shrimp without predigestion, as discussed under food habits. Late third instars that have been starved about five hours will eat about 0.0135 g dry weight of fairy shrimp in an hour. Ingestion decreased prior to each larval molt or pupation. The larvae alternately ate and rested. The amount of food ingested by first instars was around 12 to 22% of their wet weight in dry food weight each day with an increase in wet weight of 28 to 50% a day; these values decreased gradually until the late third instars ate only 6 to 10% of their wet weight in dry food with a corresponding increase in wet weight of 15 to 30%. Table 5 gives the amount ingested according to age and the caloric value of the food.

Table 5. Food ingestion for laboratory-reared larval stages of *H. triangularis*. Lubbock, 1971.

Instar	Fairy Shrimp in Period	Days in Period	Fairy Shrimp per day	Calories Consumed Per Day
Early First	8	1.5	5.3	10.76
Late First	20	1.5	13.3	26.91
Early Second	35	1.5	23.3	47.10
Late Second	55	1.5	36.7	74.03
Early Third	275	6.0	45.8	92.53
Late Third	335	6.0	55.8	112.72

Kasting and McGinnis (1965) found the quantity of food consumed by the larvae of the pale western cutworm ranged from 1.4 micrograms ( $\mu\text{g}$ ) to 24  $\mu\text{g}$  in a six-hour feeding period, and that the amount also varied with the type of food. Hanna (1957) studied the rate of growth of four species of caddisfly larvae and found the rate varied with food supply and temperature. He found that increased amounts of food caused increased rates of growth, while a decrease in food caused decreased growth rates. This probably produced some error in studies of *H. triangularis* growth rates as larvae at times may not have been fed all they wanted. Overall growth within a stage was about 32% increase in first instar, 60% in the second instar and 72% in the third. Increase in weight by molting was around 45% increase for first instars and 18% increase for third instars. Table 6 gives the growth and caloric value according to growth stage.

Table 6. Growth during larval stages of laboratory-reared *H. triangularis* larvae. Lubbock, 1971.

Stage	Growth during period. dry weight	Days in period	Growth per day (g)	Calories of growth per day
Early First	0.00002	1	0.00002	0.10
Late First	0.00177	2	0.00089	4.03
Early Second	0.00449	1	0.00449	22.40
Late Second	0.01578	2	0.00769	35.01
Early Third	0.00545	1	0.00545	24.81
Late Third	0.07908	11	0.00719	32.73

Adults in the field were relatively constant in size, but adults reared in the laboratory varied in size depending on the amount of food given the larvae. This was noted in those grown in aquariums and in those from the study using beakers where three different amounts of food were given the larvae. Out of an original group of sixty, six were reared to the adult stage. Their weights corresponded to the amount of food they received. They were divided into three groups as follows: all the food that could be eaten, three-fourths of that amount and half of the full amount (Table 7).

The measurements (Table 8) were recorded for the remaining third instar insects before these were placed in the soil for pupation. A similar effect was also noted by Dixon (1959), who commented that the higher the rate of feeding, the greater the rate of development and the greater proportion of larvae reaching adulthood among predatory coccinellids. This was observable for *H. triangularis* also, and the type of food appeared to have a similar effect, as discussed under food habits.

Assimilation and egestion were studied indirectly. Wastes were always enclosed within a peritrophic membrane, which is thought to be a chitin-containing sheath enclosing the food in the midgut to protect the midgut epithelium from mechanical damage (Waterhouse, 1957). Passage of food took several hours and any liquid wastes quickly diffused in the water.

Table 7. Average food requirements at the beginning and end of each stage per day for growth experiment. Lubbock, 1971.

Instar	Amount of food	Number of fairy shrimp.		Dry weight grams (g).	
		Beginning	End	Beginning	End
First	Full	4	16	0.0023	0.0092
	3/4	3	12	0.0017	0.0069
	1/2	2	8	0.0011	0.0046
Second	Full	16	40	0.0092	0.0226
	3/4	12	30	0.0069	0.0169
	1/2	8	20	0.0046	0.0113
Third	Full	40	60	0.0226	0.0339
	3/4	30	45	0.0169	0.0253
	1/2	20	30	0.0113	0.0169

Table 8. Results of varying food amounts in growth experiment from the six remaining late third instars. Lubbock, 1971

Amount	Wet weight (g)	Length (cm)
Full	1.1170	5.0
3/4	0.9845	4.5
1/2	0.8800	3.5
1/2	0.9133	3.5
1/2	0.7755	3.5
1/2	0.8325	3.7

Teal (1957) gave the formula of Energy  $(E)_{\text{Food}}$  minus  $(E_{\text{Growth}} \text{ plus } E_{\text{Respiration}})$  equals  $E_{\text{Loss}}$ , which was used in formulating the flow chart to be discussed. Respiration values were converted to calories with the average oxycaloric coefficient of 3.38 calories per milligram of oxygen (Ivlev, 1934; Teal, 1957). These values are listed in Table 9.

Welch (1968) formulated a similar energy budget where ingestion (I) equals growth (G) plus respiration (R) plus egestion (E). Assimilation (A) would equal G plus R and the assimilation efficiency is calculated as  $A/I$ . This compares favorably with the equation used by Richman (1958) and Mukerji and Le Roux (1969), where ingestion was equal to growth plus respiration plus egestion and computed by converting all values into calories as shown in Table 10. These values were then converted to percentages to show relationships between the processes in Table 11.

Welch (1968) also gives the formulas of  $G/I$  equals gross growth efficiency and  $G/A$  equals net growth efficiency. Table 12 gives the assimilation efficiency, gross growth efficiency and net growth efficiency for each age group in calories per day.

Table 9. Respiration energy values for *H. triangularis*. Lubbock, 1971.

Instar	$\mu\text{l}/\text{hour}$	$\mu\text{l}/\text{day}$	$\mu\text{g}/\text{day}$	Calories <sup>a</sup> respired per day
Early First	7.4600	179.02	255.85	0.86
Late First	17.7163	425.19	607.60	2.05
First Second	45.0420	1081.01	1544.76	5.22
Late Second	214.2212	5141.31	7346.93	24.83
Early Third	241.0072	5784.14	8265.58	27.94
Late Third	229.1864	5500.47	7860.18	26.56

<sup>a</sup>Calculated from an average oxycaloric value of 3.38 calories per milligram of oxygen (Ivlev, 1934; Teal, 1957).

Table 10. Energy values<sup>a</sup> of life processes for *H. triangularis*. Lubbock, 1971.

Stage	Energy <sup>b</sup> food	Energy growth	Energy respired	Energy loss	Energy assimilated
Early First	10.76	0.10	0.86	9.79	0.97
Late First	26.91	4.03	2.05	20.82	6.09
Early Second	47.10	22.40	5.22	19.48	27.62
Late Second	74.03	35.01	24.83	14.19	59.84
Early Third	92.53	24.81	27.94	39.77	52.75
Late Third	112.72	32.73	26.56	53.41	59.30

<sup>a</sup>Calculated using the formulas of Teal (1957)

<sup>b</sup>Energy expressed as calories/day.

Table 11. Percentage energy involved in each life process for *H. triangularis*. Lubbock, 1971.

Stage of growth	Percent of Energy			
	Growth	Respired	Lost	Assimilated
Early First	0.97	8.04	90.99	9.01
Late First	14.99	7.63	77.38	22.62
Early Second	47.56	11.08	41.36	58.64
Late Second	47.29	33.54	19.17	80.83
Early Third	26.82	30.20	42.98	57.02
Late Third	29.03	23.57	47.39	52.61

Table 12. Efficiencies<sup>a</sup> of *H. triangularis* larvae. Lubbock, 1971.

Instar	Assimilation efficiency	Gross growth efficiency	Net growth efficiency
Early First	0.09	0.0097	0.108
Late First	0.226	0.150	0.663
Early Second	0.586	0.476	0.811
Late Second	0.808	0.473	0.585
Early Third	0.570	0.268	0.470
Late Third	0.526	0.290	0.535

<sup>a</sup>Calculated from formula developed by Welch (1968).

Assimilation appeared to vary with the stage of the insect, as seen in Table 11. Assimilated efficiencies in growth varied from 1% to almost 50%. Guthrie and Brust (1969) concluded that the giant water bug probably assimilated less than 10% of the food ingested. Mukerji and Le Roux (1969) found varying efficiencies for the predator *Podisus maculiventris* Say. This information about consumer species taken in the laboratory can be extrapolated for some idea of the field situation.

#### *Bioenergetics*

There is increasing interest in the energy relationship of the ecosystem, which requires a better understanding of the energy dynamics of individual populations. This has been hampered by incomplete knowledge of both plant and animal energy content. In energy flow studies, it is often necessary to convert biomass to energy or calories (cal) from determinations in the oxygen bomb calorimeter.

The purpose of this study was to provide estimates of a primary carnivore, *H. triangularis*, to be applied to the energy content of the biomass at the Jornada playa. All samples collected in the laboratory were combined in each group analyzed.

Golley (1961) emphasized the caloric value of animal tissue averaged about 5000 cal/g dry weight except under starvation or storage conditions. He stated that the caloric value of an animal is a function of its nutritive condition, life history, and genetic makeup. Slobodkin and Richman (1961) studied cal/g using a bomb calorimeter and found the majority of the organisms tested fell in the 5,400 - 6,100 cal/g bracket. This indicated a skewed distribution with the modal frequency at or near the lower range. A flow chart was formed using the caloric values from bomb calorimetry data plus growth and respiration studies. The flow chart (Figure 4) was patterned after bioenergetic studies done by P.W. Riegert (personal communication). All energy values obtained from bomb calorimetry analyses were placed in Table 13, giving an average of all samples in the group.

Table 13. Bioenergetic values for laboratory-reared *H. triangularis*. Lubbock, 1971.

Material	Caloric Value (cal/g)
Egg	5102.14
Egg Case	4677.64
First Instar	4310.42
Second Instar	4473.48
Third Instar	4875.10
Pupa	4622.51
Exuvium	3176.89
Adult	5761.76

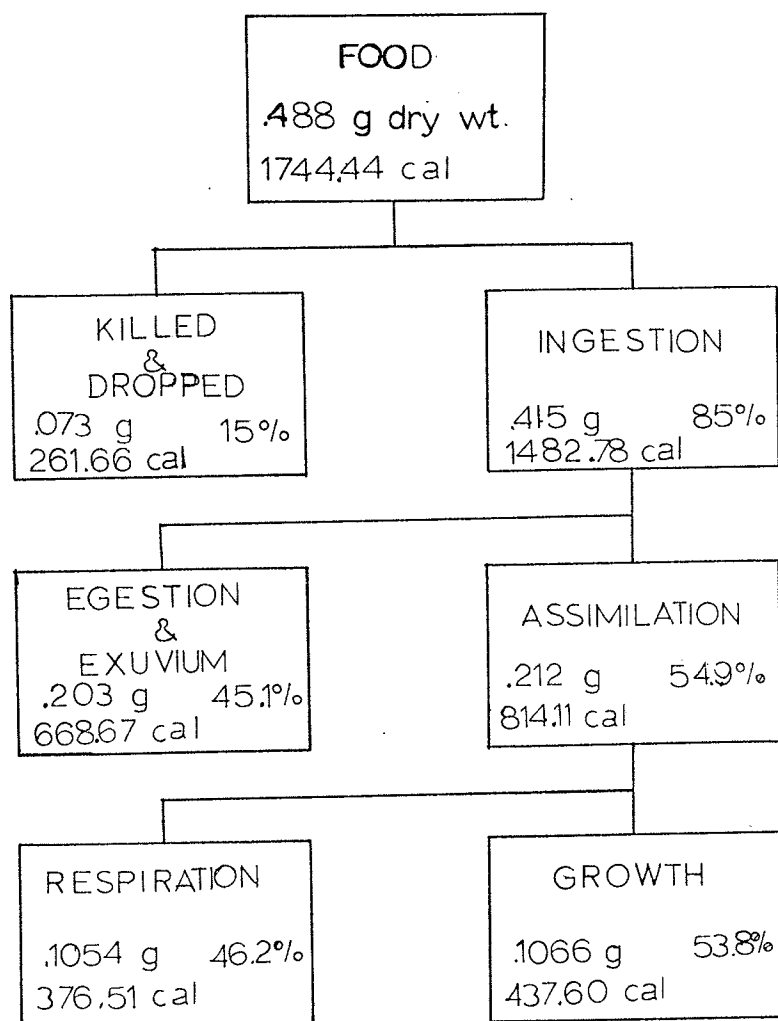


Figure 4. Total energy flow of an average laboratory-reared *H. triangularis* during the period from hatching to pupation.

Studies on carbon and nitrogen levels were also undertaken to obtain some information on the amount of carbon and nitrogen cycled in the playa. Table 14 gives the values obtained as to amount of each according to weight and their ratio to each other. Each sample contained three replicates and all samples in a group were averaged to obtain the values given in Table 14.

Table 14. Average carbon and nitrogen levels in five stages by percentage of weight of *H. triangularis*. Lubbock, 1971.

Stage of growth	% Carbon <sup>a</sup>	% Nitrogen	C to N Ratio
Early First	43.1945	11.2970	3.80082
Late First	37.7790	8.8281	4.30326
Early Second	40.4835	9.2468	4.43198
Late Second	51.7385	12.1260	4.23618
Early Third	58.7450	15.3260	3.83622
Late Third	52.359	12.0118	4.39861
Pupa	14.0608	41.3317	2.93950
Adult	10.3700	59.1600	5.70491

<sup>a</sup>CHN analyses by Hewlett Packard Model 185.



## ACKNOWLEDGEMENTS

Appreciation is expressed to Utah State University for funding of the research project through a NSF grant for the support of the International Biological Program. Desert Biome Project for studies of desert ecosystem.

Appreciation is extended to Charles T. Gaskins for aid in the statistical analyses of the the data presented, and to Dr. Donald Ashdown for his helpful criticisms of this manuscript.

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