SURVIVAL OF THE PUPAL STAGE OF THE SCREWWORM, *COCHLIOMYIA HOMINIVORAX* (COQUEREL) (DIPTERA: CALLIPHORIDAE) IN SUBTROPICAL MEXICO

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ABSTRACT

Survival of the screwworm pupal stage was studied under different ecological conditions over a 12-month period in southern Mexico. Survival (measured as successful adult eclosion) differed only slightly between the wet and dry seasons, but survival was highest (avg. 75%) in sheltered sites and lowest (avg. 23%) in exposed sites. High soil temperatures at exposed sites were probably responsible for high mortalities. Only during the cool months was there any survival at exposed sites. Moisture levels were of minimal influence, though high mortality from especially heavy rains may occur in sheltered sites.

Key Words: Insecta, Screwworm, Mexico, Pupa, Survival, *Cochliomyia hominivorax*, Calliphoridae.

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INTRODUCTION

Screwworm populations exhibited seasonal fluctuations before they were eradicated from the temperate regions of North America. These fluctuations were attributed to mortality, or at least an inability to increase, during cold winters (Lindquist and Barrett 1945) and hot summers (Krafsur 1987). In tropical southern Mexico the screwworm is also very seasonal, but there the fluctuations are related to the moisture cycle rather than temperature. Spencer et al. (1981) and Mackley (1986) have shown that adult abundance and oviposition rates are highest during the wet season. In southern Mexico the wet season is from June to November; June is the rainiest month with a second peak in September. The dry season is from December to May. The coldest months are January-February, while the hottest months are March-April. Thus the hottest and coldest time of the year occur during the dry season. Southern Mexico has a diverse topography and thus local levels of rain, moisture and temperature vary according to exposure and elevation (Mullerreid 1982). Still over most of the region ambient temperatures seldom exceed 40°C or drops below 15°C.

Spencer et al. (1981) hypothesized that reduced activity of screwworms in the lowland tropics was most likely due to changes in soil moisture. They maintained that mortality to the pupal stage would result from either heavy rains, or from prolonged drought. In support of their hypothesis they cited the laboratory studies of Bruce (1939) and Melvin and Bushland (1938) who demonstrated the inhibition of emergence from water saturated soils; and Baumhover (1963) who demonstrated high mortalities due to desiccation. Other workers have ascribed changes in local screwworm populations to moisture levels. Parman (1945) stated that poor drainage or heavy rains resulting in saturated soils reduce screwworm numbers. Rahn and Barger (1973) conversely, noted that increases in screwworm cases often follow a few weeks after moderate to heavy rains, and added that outbreaks never occurred during a drought. The consensus seems to be that rainfall favors population increase, but extremes of soil moisture cause mortality.

The relative importance of these factors is unresolved, and largely untested. Not surprisingly there is also disagreement. Thomas (1986) demonstrated that screwworm pupae are largely unsusceptible to drowning, although emergence may be delayed under saturated conditions; and Krafsur (1987) could find no relationship between rainfall and population change. Therefore, Spencer et al.'s (1981) hypothesis of mortality due to soil moisture stress as an explanation for seasonality of the screwworm in the warm tropics is conjectural.

The purpose of the present study was to measure survival of screwworm pupae in the tropics during both the dry and wet seasons. Screwworm larvae have little choice in selecting pupation sites. In nature the parasitic larva egresses its host, falls to the ground, and burrows a short way into the soil to pupate. Travis et al. (1940) showed that the majority of larvae pupate within a foot of where they fall. They also reported that penetration into the soil was less than 1 inch, although Laake et al. (1936) found that in sandy soil, penetration averaged 2.25 inches. It was important then, to design an experiment to examine pupal survival under different ecological conditions. The present report describes such an experiment, conducted in Chiapas, Mexico during 1987.

MATERIALS AND METHODS

Experiments were conducted on the grounds of the sterile fly production facility operated by the Comisión México-Americana para la Erradicación del Gusano Barrenador del Ganado, located at Chiapa de Corzo, Chiapas, Mexico. This facility is located in the Central Depression of Chiapas in the valley of the Grijalva River at an elevation of 789 m above sea level. Three sites were selected for study with a distance between sites of ca. 200 m. One site was open away from buildings and vegetation and thus completely exposed to sun, wind and rain. A second site was sheltered within a patch of forest which afforded complete shade most of the year. The natural vegetation in this area is classified by Miranda (1975) as low semi-deciduous forest. This forest is characterized by a canopy of 8-15 m height and the trees shedding their leaves during the dry season. The dominant trees are *Alvaradoa amorphoides* Liebm. and *Acacia* spp. A third site, semi-shaded, was located in the open but at the base of a large guanacaste tree, *Enterolobium cyclocarpum* Gr.

Recording thermographs were located at the open and shaded sites; a rain gauge was located at the open site. During one week of each month from January to December 1987 screwworm pupae were placed at each of these sites and weather recorded during that time. The pupae used during this experiment were from larvae reared in the laboratory using the methods described by Taylor and Mangan (1987). When larvae crawled out of the larval medium they were placed in a 10-liter plastic tub containing clean sand to a depth of 15 cm. at room temperature. Holes were punched in the bottom of the tubs to allow drainage.

The tubs were kept indoors until all larvae had burrowed into the sand to pupate (approx. 2 hrs). At that time replicate tubs (two ea.) were placed at each of the three outdoor sites, while an equal number were kept in the laboratory as controls. Each tub contained 100 pupae and these tubs were placed directly on the ground. After seven days of outdoor exposure all tubs were returned to the laboratory. Pupae sifted out of the sand, counted, and placed in cages where emergence ensued within 1-2 days. Viability of pupae was then determined by the numbers of adults that emerged.

Because the screwworm is a parasite of livestock, wild animals and occasionally humans, the precaution of using a special double mutant strain of flies was used in these experiments to safeguard against early emergence or escape of the adults. The adults of this strain have white eyes and curly wings, rendering them blind and unable to fly. In spite of these disadvantages this strain survives and reproduces normally in the laboratory, and more importantly for this test, the immature stages are functionally normal. Preliminary tests in November 1986 indicated that pupae of this strain exhibit normal, emergence rates (ca. 90%) when exposed out-of-doors, equivalent to that achieved in the laboratory or by wild-type strains.

Statistical comparisons of sites was done by paired t-tests of the monthly survival values among sites and between sites and controls, and by Analysis of Variance to compare seasons. The effects of rainfall and temperature on survival were tested by correlation analysis. Significance of F, t and r values were determined from tables published by Sokal and Rohlf (1973).

RESULTS

The weather data summarized in Tables 1 and 2 demonstrate that 1987 was typical in that rainfall occurred during June to October, and September and June were the wettest months. The warmest daytime temperatures occurred in the dry season, averaging 4.5°C warmer than the wet season. March was the warmest month, daytime temperatures during the experiment for that month averaged 5°C hotter than the average highs for the other dry months. The coldest temperature, 15°C, was recorded during February, but the average overnight low temperatures were uniform year round.

The data in Table 2 show the survival rates of pupae by month and by ecological site. Table 3 summarizes the survival data by season. Overall the differences in survival observed between the wet and dry seasons were not significant by comparison of F-values from the Analysis of Variance. Ecological conditions at the pupation site were much more important in determining survival of the pupae. Survival was uniformly higher in the sheltered site than in the exposed site, with the values for the semi-shaded site falling between the two. These survival differences were significant with a paired t-test (Table 2). The data reveal significant differences between months within a site. For example, the month of September stands out because of the sharp drop in survival that occurred at the sheltered site. These differences reflect important interactions between tempeature and rainfall and the influence, or lack of, sheltering vegetation.

Sheltered Site

Survival at the sheltered site was high (> 75%) every month except March-April, the hottest months, and September, the rainiest month. Mean survival rate

Table 1. Temperature data at exposed (sun) and sheltered (shade) sites, 1987, Chiapa de Corzo, Chiapas.

Month	Max Sun	Max Shade	Mean Max Sun	Mean Max Shade	Mean Min Sun	Mean Min Shade	Min Sun	Min Shade	Mean Flux Sun	Mean Flux Shade
JAN	37.0	34.5	33.9	32.6	19.4	19.8	17.0	18.0	14.5	12.8
FEB	39.0	38.0	34.9	33.6	20.1	23.1	15.0	17.0	14.8	10.5
MAR	42.0	41.0	40.4	39.3	20.0	20.4	17.0	18.0	20.4	18.9
APR	38.0	36.0	34.1	32.2	20.4	21.7	18.0	16.0	13.7	10.5
MAY	37.0	*	35.1	*	22.4	*	20.0	*	12.7	*
JUNE	33.3	35.0	29.9	32.5	20.7	25.0	20.0	24.4	09.2	07.5
JULY	33.3	34.4	31.7	32.8	20.9	24.7	20.0	23.3	10.8	08.1
AUG	33.3	33.3	31.4	32.6	20.3	24.1	19.4	23.3	11.1	08.5
SEPT	33.3	32.2	32.1	31.4	20.5	24.2	20.0	23.3	11.6	07.2
OCT	31.5	30.5	31.3	28.6	19.0	20.0	18.0	17.0	12.3	08.6
NOV	37.0	33.0	34.8	31.3	20.0	21.3	19.0	20.0	14.8	10.0
DEC	38.0	34.0	34.4	31.1	19.1	19.6	17.0	17.0	15.3	11.5

* Due to equipment failure, no data for May at this site.

excluding those three months was 87.8%, approaching that of the controls (91.5%). In fact, a paired t-test shows that survival at the sheltered site was not significantly different from the controls (Table 2). Even during the hottest month of March when there was no survival at the other two sites, there was 41% survival at the sheltered site. The sharpest decline in survival occurred during September and was probably due to the heavy rains (154 mm) during the experiment that month. This result is consistent with the hypothesis that high soil moisture could cause drowning of pupae. The study by Thomas (1986) demonstrated that high mortalities would result if pupae are subjected to more than four days of oxygen depletion. In nature this could happen if there were more than four consecutive days of heavy rains, or if after a heavy rain soils were not able to dry out. Since the exposed sites did not have high mortalities at this time the second hypothesis is the more plausible. Perhaps the shade was a disadvantage, preventing the soil from drying out and resulting in the drowning of the pupae. Despite the September value, overall there was no significant difference between dry season and wet season survival at the sheltered site.

Exposed Site

Survival at the exposed site was very low in seven months of the year (Table 2), significantly lower than at the other two sites. There was no survival of pupae at the exposed site during the hot dry months of February to May. One can suppose that this was due to either the heat or the drought. However, comparing the moist months of July-September, when there was low survival, with November-January

Table 2. Mean survival rate (adult emergence) of pupae by month and by site, and precipitation during week of experimental replicate.

Month	Controls	Exposed	Semi-shade	Sheltered	Rain (mm)
JAN	96.0	51 ± 10	50 ± 20	86 ± 1	0
FEB	97.5	0	25 ± 1	93 ± 5	0
MAR	81.0	0	0	41 ± 9	0
APR	91.5	0	35 ± 2	62 ± 11	0
MAY	89.0	0	73 ± 9	89 ± 4	0
JUNE	94.5	48 ± 0	72 ± 3	74 ± 11	100
JULY	91.0	5 ± 1	66 ± 13	86 ± 6	27
AUG	93.0	6 ± 6	92 ± 2	91 ± 2	20
SEPT	97.0	1 ± 1	35 ± 1	10 ± 0	154
OCT	87.5	78 ± 3	91 ± 2	90 ± 2	1
NOV	87.3	52 ± 23	88 ± 4	82 ± 2	0
DEC	93.0	32 ± 9	87 ± 2	96 ± 1	0
MEAN	91.5	22.9	59.7	75.3	
Paired t-test		4.54	3.60	2.16*	

* Not significant: critical t (11 df, p = .05) = 2.20.

Table 3. Comparison of mean pupal survival in months with rain (June-October) versus dry months (November-May).

	Controls	Exposed	Semi-shade	Sheltered
WET SEASON	92.6	27.7	71.46	70.5
DRY SEASON	90.8	19.4	51.4	78.6
F-value (ANOVA)*		0.23	1.33	0.27

* Critical F (df 1,10; p = .05) = 4.96.

when there was no rain but high survival, suggests that moisture was not a critical factor at the exposed site. Table 5 shows that neither ambient temperature or rainfall were effective predictors of survival at the exposed site. Table 4 compares soil temperatures with ambient temperatures at the exposed and sheltered sites on four consecutive days during January 1988. While ambient temperatures (daily highs) were similar at the two sites, the shade at the sheltered site prevented the build up of what were probably lethal soil temperatures recorded at the exposed site.

Table 4. Daily maximum soil and ambient temperatures at two ecological sites, over four consecutive days in Chiapas, Mexico, 1988.

	Exposed		Sheltered	
Date	Ambient	Soil	Ambient	Soil
JAN 18	36.0	50.1	34.0	31.3
JAN 19	35.0	53.1	34.5	32.5
JAN 20	35.0	48.9	34.0	31.4
JAN 21	30.0	48.1	30.0	28.4

Table 5. Correlation coefficents (r) for the association between temperature, rainfall and survival at three ecological sites.

Site	Temperature	Rainfall
Exposed	−0.45	−0.26
Semi-shaded	−0.79*	−0.37
Sheltered	−0.20	−0.71*
Critical r (df 10, p = .05) = .576		

* = significant at p = .05

Semi-Shaded Site

The survival data in Table 2 show the positive influence of even partial shade. Except during the hottest month of March, there was always at least 25% survival, and during most months more than 50% survival. During the wet season, and especially during the rainiest month of September, this site had the highest survival. This result was probably obtained because the tree blocked much of the insolation, preventing soil temperatures from becoming lethal, yet the soils had a chance to dry out after the saturating rains. Survival at this site was significantly different than at the other two sites (Table 2). Correlation analysis (Table 5) showed that ambient temperature was a strong predictor of survival at this site.

DISCUSSION

The results of this study demonstrate that the effects of temperature and rainfall on pupal survival must be considered within the context of the immediate environment of the pupa. Sheltered sites have very high survival rates most of the year. Temperatures have very little direct influence in this situation, while heavy rains may occassionally cause high mortality because soils are slow in drying out. In exposed situations high soil temperatures cause high mortalities, whether during the wet or dry season. During the winter when temperatures are moderate, or during the wet season when cloud cover prevents soil temperatures from becoming lethal, survival is much higher (50-80%). Moisture is not an important influence in the open sites.

It is interesting that no predation or pupal parasitism was detected. *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae), a parasite of calliphorid pupae, is found on the grounds of the production facility, and is on occassion a serious pest. Apparently *N. vitripennis*, is incapable of parasitizing buried pupae, which is in accord with the observations of Legner (1983).

It is also interesting that weather factors coincided to produce optimal pupal survival during October, which is also the month with the highest incidence of screwworm cases (Thomas 1987). Nevertheless, the seasonal differences in survival in this experiment were small and would not account for the seasonal differences in adult abundance reported from the tropics, unless an unexpectedly high proportion of screwworm pupation occurs in exposed or relatively open sites. Thus land use, especially in regard to host habitat, is a relevant factor. Therefore, the results of this study do not support the supposition by Spencer et al. (1981) that seasonality of the screwworm is a consequence of soil moisture. These results are in accord with those of Krafsur (1987) who concluded that temperatures were more important than moisture in determining population changes, and that the reported influence of rainfall (i.e. Rahn and Barger 1973) was probably due to the coincident moderating of temperatures that accompany rainfall rather than moisture. The survival of the pupal stage is an important parameter in the population dynamics of the screwworm. However the survival and reproductive rate of the adults is also important, and there is a strong probability that there is a seasonal component to these parameters, which are as yet unmeasured.

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