STUDIES ON THE SUCCESSION OF SAPROPHAGOUS DIPTERA ON MAMMAL CARCASSES IN SOUTHERN ARIZONA

by

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ABSTRACT

Observations on carcasses exposed in the field were made from December, 1963 to May, 1964 in the Tucson Mountains of Southern Arizona. Adults and larvae of saprophagous species were collected throughout the study period and identified in the laboratory.

Preliminary results indicate that there is a definite succession of species invading carcasses which is controlled by seasonal changes in temperature and by chance factors which affect invasion by saprophagous species.

During the winter months, carcass decomposition occurs slowly because larvae are active only during the day while in spring decomposition occurs very rapidly and larvae are actively feeding throughout the day and night.

Phormia regina (Meigen) was the dominant blowfly species throughout the winter months, Cochliomyia macellaria (Fabricius) during the summer months, and Phaenicia sericata (Meigen) during the spring. Hystricocnemina plinthopyga (Wiedemann) was the dominant flesh fly throughout the study.

Competition for food and space was the main factor which limited the numbers of adults produced from exposed carcasses. The onset of warm spring weather intensified the competition between

larval species. Carcasses in April produced only one-fourth as many adult flies as the carcass exposed in February.

Predators and parasites played only a minor role in affecting the number of adults produced by a carcass.

I. INTRODUCTION

In the last thirty years, the increasing severity of blowfly depredations in the sheep raising areas of Australia, New Zealand, and South Africa have led to detailed queries into the nature of succession of blowflies on carcasses and the factors controlling blowfly abundance. Much of the work done on blowfly activity in North America has dealt only with certain species. Little work has been done on the blowflies and flesh flies present in Arizona.

The present thesis deals with life cycles, seasonal variation and population dynamics of saprophagous Diptera in Southern Arizona. The present work also deals with the development of methods and techniques, description and keys for species present, effects of larval invasion upon carcass composition, seasonal variation in adult and larval activity and species decomposition. Although the study at present has been of short duration, many interesting facts help to complete a picture of fly activity in Arizona.

This study is not intended to be of particular economic value other than as a compilation of information on species which may be of economic importance to the livestock industry or concerning aspects of determining time of death in cadavers as may be encountered in Forensic Medicine.

Of particular importance is the role of the Sarcophagidae in carcass invasion, an aspect heretofore generally ignored. As pioneer invaders of a fresh carcass, the sarcophagids play an important role in the initial breakdown of carcass tissue and indirectly affect the subsequent invasion by various calliphorids.

Much of the work concentrated on saprophagous Diptera since the turn of the century has emphasized the unraveling of the complex taxonomy of the groups involved. This is particularly true in the families Calliphoridae and Sarcophagidae. Within the last fifteen years works have been published by Roback (1954) on the evolution and taxonomy of adult Sarcophagidae based on aedeagal morphology, Sanjean (1957) on the taxonomy of sarcophagid larvae, and Hall (1947) on the Calliphoridae. Name changes for sarcophagids formerly in the genus Sarcophaga are those proposed by Roback (1954).

Papers dealing with the ecology of the Calliphoridae and Sarcophagidae and including such aspects as competition for food and the gamut of biotic factors affecting fly populations constitute only a small part of all the papers dealing with these groups. The majority of the studies concerned with the ecology of the calliphorids have been carried out in areas where sheep are an important bulwark in the economy, notably South Africa, New Zealand, Australia and, to some extent, the Western United States. These studies have dealt with the

species which cause strike in sheep, rendering great losses to the economy. Three such studies are outstanding for their exhaustive treatment. Fuller (1934) deals with species causing sheep strike in Northern Queensland. Smit (1931) presents extensive data on species in South Africa. Ullyett (1950) summarizes Smit's work and presents valuable information on the nature of interspecific and intraspecific competition for food and space among blowfly populations. Virtually no comparable work has been done on the Sarcophagidae, which are of somewhat less importance economically. Most sarcophagids are not known to be primary invaders of healthy animals, but James (1947) records cases of cutaneous, wound and intestinal myiasis by larvae of this family. Some sarcophagids are parasitic on injurious insects such as grasshoppers and beetles and may therefore be considered beneficial.

II. METHODS AND MATERIALS

In late January, 1964, a dog carcass was placed within a screened enclosure in the field. Daily observations were carried out on this carcass from January 29 to March 15. On April 10 two cat carcasses were placed in the enclosure and observed daily until April 30. After the larvae had left the carcasses, the remains were placed by a nearby Palo Verde tree to allow tertiary invaders such as dermestid beetles to complete development.

The enclosure was constructed of 1/2" mesh rabbit wire. Openings in the screen allowed flies and most beetles to pass through readily but kept out coyotes, dogs, rodents and other animals. Additional screening was laid outside the enclosure and secured by heavy rocks to prevent animals from burrowing under the fencing. The inside diameter of the enclosure was four feet square, allowing ample room for the carcasses and for collection and observation.

It was necessary to build a special container to hold carcasses so that maggots, after leaving the carcass, would not be able to escape to the soil and pupate. A wooden platform was constructed and raised 10 inches off the ground on four legs. Escapage was prevented by two-inch-high plywood sides on the platform. Some of the maggots were able to escape by crawling up the sides of the platform or by

forcing their way through cracks in the wood. This can be remedied by constructing sides out of metal and bending the metal inward so that the larvae cannot gain purchase on the metal.

Carcasses were placed within this container, on a layer of dry, loose soil about two inches deep in which the larvae burrowed following the termination of feeding. Sarcophagid larvae in particular have a tendency to wander for some distance before settling down to pupate. By putting barriers around the edges of the enclosure, many of these larvae were captured. Some maggots, notably those of Phormia regina (Meigen), tended to burrow into the hair of the carcass prior to pupation. As many as possible were picked out and the rest counted in order to estimate the total number of flies produced from a carcass.

The study was conducted in two areas about five miles southwest of Tucson, Arizona. The earliest investigation was carried out on a coyote carcass found in the desert. In February, a freshly-killed dog was used; in April, two cat carcasses were put together in the enclosure. Subsequent investigations were undertaken in an area especially chosen for this study. This area is in the southeastern edge of the Tucson Mountains at an elevation of about 2700 feet. The study area can be classified as Sonoran Desert and supports a stand of Palo Verde trees, various species of cholla cactus, prickly pear and Saguaro Cactus. The pen in which the carcasses were kept is located in a shallow

valley bounded on the north, west and south by steep, low mountains and on the east by a gradual slope which descends to the City of Tucson.

Originally, a recording thermograph was used to record temperatures continuously but due to mechanical troubles and the difficulty of finding a secure place where it would not be damaged, this was discarded in favor of a maximum-minimum thermometer which was placed at a nearby ranch. Temperatures were recorded from mid-February and previous records were obtained from the U. S. Weather Bureau's monthly publication of weather data for Arizona. Wind and general climatic conditions were recorded daily. Humidity was not recorded.

Daytime temperatures increase steadily from March to July, reaching a maximum of about 105°F. Nighttime temperatures are usually cool, around 65-75°F. There is a slight decrease in the mean temperature for the months of July and August during the summer rains and a rise again in September, followed by a steady decline until February. Daytime temperatures in January are generally in the sixties and seventies, while nighttime temperatures sometimes dip below 20°F.

Compared with official readings for Tucson, temperatures in the study area averaged three degrees Fahrenheit cooler at night and four degrees Fahrenheit warmer during the day, because the sun strikes the eastern side of the Tucson Mountains early in the morning and the study area is in the shadow of the mountains some time before sunset. Warming begins very early in the day and cooling begins before sunset.

During the six-month period of the present study, it was cooler and drier than what is considered normal. The month of April was especially cold, dry and windy. In May there was a sharp increase in temperature. The maximum and minimum temperatures and mean maximum and minimum temperatures are presented in Table 1.

TABLE 1.--Maximum and minimum temperatures and mean maximum and minimum temperatures in °F. December 1963 to May 1964 in the Tucson Mountains, Arizona.

Month	Max.	Min.	Mean Max.	Mean Min.
December[a]	-	-	69.9	29.2
January[a]	79	14	64.9	25.2
February	74	24	67.1	28.5
March	88	28	77.0	40.4
April	97	37	84.0	49.9
May	104	38	94.0	56.0

[a]Temperatures obtained from U. S. Weather Bureau Monthly Records for Arizona.

III. SUCCESSION OF CARCASS-BREEDING FLIES IN WINTER

A. Decomposition of the Carcass

Except for occasional observations, little work has been done on the decomposition of carcasses, especially as related to insect attack. Mégnin (1894) gives a detailed account of the progressive decay in cadavers and Evans (1963) discusses chemical events that occur after death under varying conditions.

Organic decomposition is tempered by many factors, including climate and severity of attack by bacteria and insects. In general, under warm, humid conditions with an abundance of attacking insects a carcass is reduced to dry, hard parts within a week. Under cold, dry conditions, bacterial and insect attack is considerably retarded or completely abated and autochemical reactions within carcass tissues are protracted over lengthy periods.

The climate of Southern Arizona greatly influences the rapidity of decay. During the summer, humidity is low except during the summer rains but the temperature is high in the daytime and moderately so during the night. Decomposition occurs extremely rapidly under these conditions,

particularly because the activity of Calliphoridae and Sarcophagidae. Decomposition would be more rapid were the atmosphere not so dry. In the winter, it is cold enough during the night to force the insect fauna of the carcass deep into the tissues, where some heat is maintained from the day. Maggots are extremely sluggish under these conditions and appear to feed very slowly or not at all. During the day, however, temperatures usually rise to 70°F. or more and feeding activity within the carcass increases. Because of these alternate cold and warm periods, the period of maximum maggot activity is extended, and the decomposition is spread over a longer period of time.

Under winter conditions during the month of February, with a mean maximum temperature of 67.1°F. and mean minimum temperature of 28.5°F., transformation of a dog from a freshly killed state to the disappearance of all soft parts took 50 days. Under spring conditions during April, with a mean maximum temperature of 84.0°F. and a mean minimum temperature of 49.9°F., decomposition and destruction of all soft parts took place in 11 days. Abnormally high temperatures, as high as 97°F., produced conditions approaching those of summer and increased the rate of decomposition.

Progressive decomposition follows a predictable pattern and has been described in detail by Mégnin (1894), and mentioned by

Fuller (1934). Here, I will present only the major features of this progressive decay without mention of the maggots which are largely responsible for it.

To follow the movements of larvae within the carcasses, a longitudinal incision was made in the ventral surface, from the chest to the hind quarters. This incision exposed layers of muscle and fatty tissue but did not initially extend into the visceral or pericardial cavities. This incision hastened the desiccation of tissues and invasion of maggots.

The first notable sign of decay other than the rancid odor of fatty tissue was the production of gas within the body cavity. This began on the second day and increased to a maximum on the fourth day, rapidly decreasing to disappearance on the seventh day. Evans (1963) states that this gas is usually present in the intestines and expands after death, causing a bloated appearance. The warm sun during the day hastened the expansion and escape of gaseous products.

The odor of rancid fat was particularly noticeable during the first week but gradually decreased thereafter. After the second week it was persistent but not strong.

By the seventh day, the teeth and gums had begun to separate from the roof of the mouth due to maggot attack; cheek tissue had desiccated and the tongue had decomposed to a jelly-like mass of

tissue. Tissues surrounding the incision in the abdomen showed no sign of desiccation and much fluid exuded from the exposed tissues. The visceral cavity was filled with body fluids.

On the ninth day, maggots had converted the fatty tissue around the incision to a semi-liquid mass. On the twelfth day the skin had so dried that the hair began to peel away in large tufts. By the fourteenth day, the mouth region had thoroughly desiccated except for a greenish viscous fluid which dripped from the throat. The teeth had separated from the skull and tunnels of larvae honeycombed the gums and throat. By the seventeenth day, there was a strong ammoniacal odor in the visceral region of the carcass due to the accumulation of waste products from the feeding maggots.

From the tenth day, maggots progressively invaded larger areas of the carcass. After they liquefied and devoured the carcass tissue, the residue desiccated quickly. When the larvae were mature, they bored through the skin of the carcass and entered the soil to pupate. By the fiftieth day, the carcass was completely desiccated and presented a ragged appearance. In some parts of the carcass a gluey greenish fluid persisted during attack by dermestid beetles. The remains of the carcass consisted mainly of skin, hair, bones and dried portions of organs, which were soon attacked by dermestid beetles.

The decomposition of carcasses thus follows a predictable pattern of chemical and mechanical breakdown of tissues. In colder climates, decomposition may be greatly retarded for long periods, but in a mild climate such as that of Southern Arizona, the initial steps of organic decay progress rapidly. By the time autolysis of tissues and gas production is advanced, the larvae of various carcass-feeding Diptera have invaded necrotic tissues and liquefaction of tissues is greatly accelerated. Maggot attack is followed by an accumulation of ammoniacal waste products, eventual desiccation of tissues and subsequent invasion by dermestid beetles.

B. Activity of Adult Carcass-Breeding Flies

Numerous papers concerned with carcass-breeding flies have discussed various aspects which influence adult activity. Deonier (1940) cites the temperatures at which various fly species in the Southwest become active. These include 50-55°F. for Phaenicia (=Lucilia) sericata (Meigen), 50-60°F. for Sarcophaga spp., 41-50°F. for Phormia regina (Meigen) and 55-60°F. for Cochliomyia macellaria (Fabricius). As maximum daytime temperatures were rarely below 60°F., there was usually some activity throughout the winter months. Cushing and Parish (1938), working in Texas, found that blowfly species follow definite seasonal trends of abundance. These trends, which were borne

out by this study, will be detailed below. Smit (1931), in South Africa, and Fuller (1934), in Northern Queensland, also stress the seasonal nature of blowfly abundance. Most of the observations were made with the use of baited traps. Ullyett (1950) correctly points out that the bait within a trap ages rapidly, especially in a warmer climate. Thus different species are preferentially attracted, giving a distorted view of seasonal abundance. Nicholson (1933) found that temperature governed the presence or absence of a species at a given time of year but that abundance was influenced by availability of food and competition. Fuller (1934) found that the presence or absence of blowfly species was related to soil temperature. The present study does not attempt to analyze species abundance, but rather the presence or absence of various species during different times of the year.

Observations on adult flies on carcasses were initiated in December, 1963. The first observations were on a coyote which had been dead for approximately three weeks. The mean maximum temperature in December was 69.9°F. and the mean minimum 29.2°F. It must be stressed that most species were secondary invaders as these observations were begun at a late stage in carcass decomposition.

Cochliomyia macellaria (Fabricius) was the dominant species present, with small numbers of Paralucilia wheeleri (Hough), Phaenicia sericata (Meigen) and Hystricocnemina plinthopyga (Wiedemann).

During the month of December, adults of Cochliomyia decreased in number and those of Phormia regina (Meigen) increased. Eventually all species disappeared except for Phormia, which remained even after the carcass had thoroughly desiccated.

Complete records of adult activity around a dog carcass were kept during February and March. Figure 1 shows the percentage of Phormia, Calliphora and Sarcophaga adults in the daily catches and ambient temperature. The initial abundance of Sarcophaga spp. was high in relation to Phormia and Calliphora spp. but decreased sharply by the third day, while Phormia increased steadily until about the fifteenth day. Calliphora spp. maintained a fairly steady percentage at a given time but this percentage was usually quite low, rarely being more than 40% of the total number of adults present. Cochliomyia macellaria was totally absent from all samples taken from January through April and presumably does not appear during periods of colder weather. The relative abundance of adults throughout February and March corresponded with the progressive aging of the carcass.

Sarcophaga cessator Aldrich was the first to arrive at a fresh carcass in cooler weather during February and April exposures. It reached peak abundance by the sixth day and gradually declined, disappearing on the eighteenth day. Hystricocnemina plinthopyga (Wiedemann) appeared almost simultaneously with S. cessator and occurred

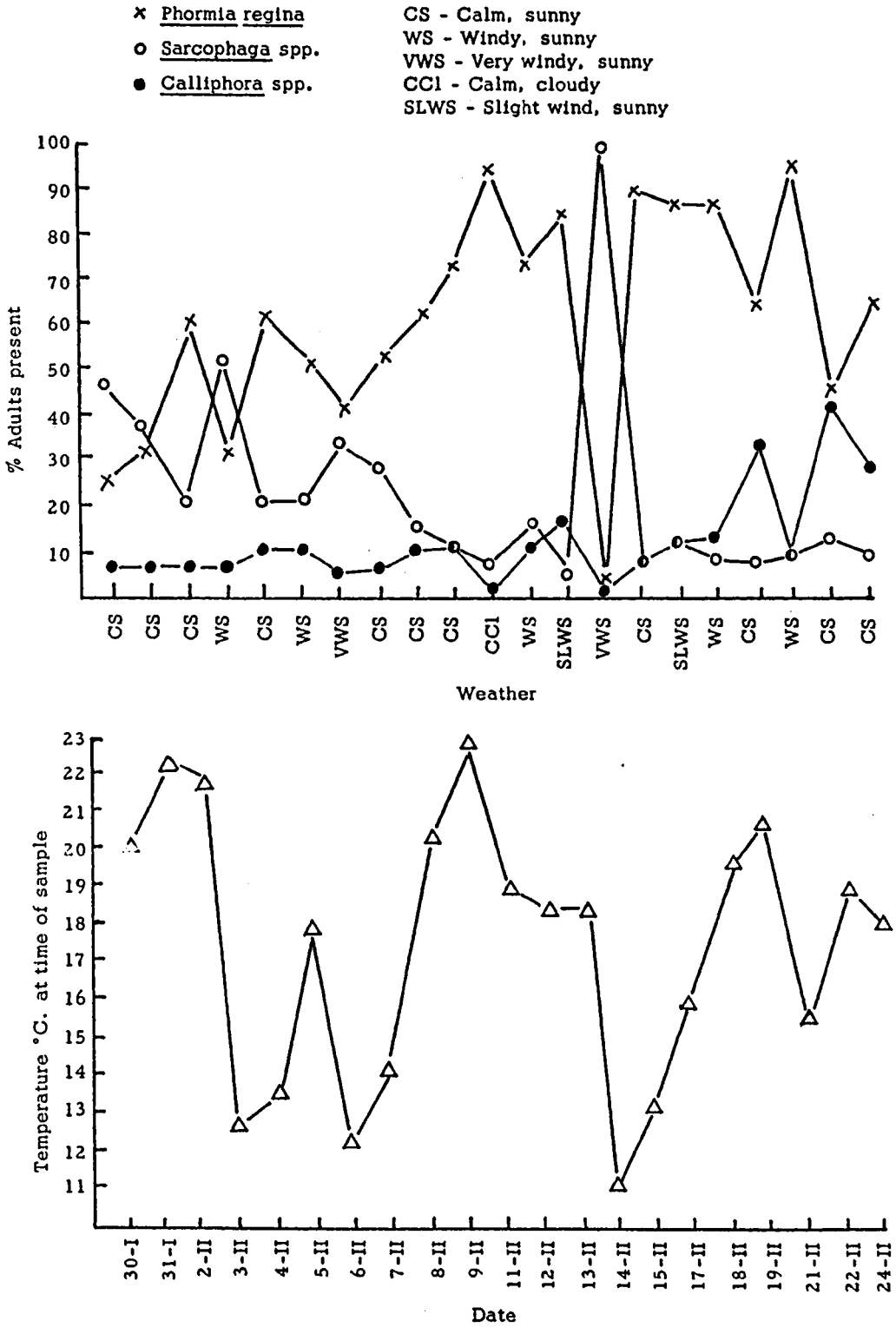


Fig. 1. Weather conditions and adult carcass-breeding fly activity.

more abundantly. It was the most abundant sarcophagid present during the study. Several other sarcophagid species appeared intermittently but not in large numbers and none of these deposited larvae on the carcass. Most commonly seen were Ravinia l'herminieri (Robineau-Desvoidy), a coprophagous form, Sarcophaga misera sarracenioides Aldrich with variable food habits, Metoposarcophaga sulculata (Aldrich), Sarcophaga bishoppi Aldrich, and Oxysarcodexia ochripyga (Van der Wulp), probably coprophagous. These forms probably were attracted by the odors accompanying decomposition of the carcass.

Phormia regina (Meigen) appeared on the second day and increased in numbers until the eighth day. Its numbers remained constant until the twentieth day, except for flucutations due to temperature and weather conditions and then decreased slowly until the carcass was totally desiccated. It was the most abundant species from January through April, comprising about 80% of all adults collected.

Phaenicia sericata (Meigen) appears to be present throughout the year in Southern Arizona, but its numbers are greatly reduced from December through March. Adults appeared on the second day during February, but only during the hottest part of the day. Along with species of sarcophagids, these flies are the earliest to appear, Phormia regina arriving slightly later. During February, when the mean maximum

temperature was 67.1°F., Phaenicia sericata constituted less than 5% of the total adult population.

Species in the genera Calliphora and Eucalliphora were collected from December until March, during a period when mean maximum temperatures varied from 69.5° to 77°F. and mean minimum temperatures from 29.2° to 40.4°F. In this group are Calliphora coloradensis Hough, Eucalliphora lilaea (Walker) and Calliphora livida Hall. Only E. lilaea was abundant. These species appear to be present only during cooler months and can be designated winter species.

Paralucilia wheeleri (Hough) was collected from December to March. This species apparently is never common in Arizona. Only one specimen was collected in February.

One factor which influenced the presence of adults around the carcass was temperature. Note that in Figure 1 there is a decrease in the numbers of Phormia regina and an increase in sarcophagids with decreasing temperature. This was true throughout the study and indicates that the sarcophagids remain active at lower temperatures. Other species of calliphorids appeared to be relatively unaffected by changes in temperature.

The presence or absence of sunlight was also important in determining species activity. Sarcophagids were virtually absent on the rare overcast days, even during the period when they were strongly

attracted to the carcass. On extremely windy, overcast days, few flies of any kind were present. There was usually some wind blowing in the study area but rarely strongly enough to prevent adult activity completely. The combination of a cold, cloudy, windy day usually kept most flies away.

Three factors, temperature, sunlight and wind, were found to influence the presence of adults around the carcass. These three factors must be taken into consideration when determining which species will invade the carcass. Under normal conditions, sarcophagids are the first to invade, but a succession of cloudy days may limit adult sarcophagid activity to such an extent that invasion is prevented or seriously hampered. Under very cold conditions, activity of Phormia regina and other calliphorids may be so limited that a carcass will produce sarcophagids almost exclusively or at least in much greater abundance than normally seen. Thus it is important to consider factors which may prevent or delay normal oviposition on carcasses, by limiting adult activity. This also affects the nature of competition to be discussed in another section (see notes on intraspecific and interspecific competition). Collections in December showed Cochliomyia to be decreasing in numbers while Phormia increased steadily. Species were collected in February and March in accordance with the periods when they were most strongly attracted to the carcass. Sarcophaga spp. were abundant during the first three days of carcass exposure. By the fourth

day, Phormia constituted 50-90% of the adults collected. Calliphora was present throughout the exposure in February and March in low numbers.

C. Invasion of the Carcass by Carcass-Breeding Fly Larvae

There appears to be little information dealing with the progressive invasion of larvae within a carcass and the effects of these larvae upon the state of decomposition. Fuller (1934) mentions progressive decomposition with regard to the effect of maggots on the speed of decomposition. This section deals only with larval invasion and destruction of carcasses.

Penetration of the carcass first occurs through the natural orifices of the body, i.e., mouth, nostrils, auditory canal and anus. Although incisions were made in the carcasses, these were not invaded until after the natural body openings were well populated, possibly due to the preference of certain species for particular parts of the carcass.

Initially, all larvae were the sarcophagids, Sarcophaga cessator and Hystricocnemina plinthopyga. All larval activity was confined to the regions of the mouth and nostrils. During the cool nights, larvae would migrate deep inside the nasal passages and throat, coming to the surface during the day. Periodically, larvae within the nasal cavities would push to the surface and expose their posterior spiracles to the air. The problem of obtaining air is one of the major reasons that crowding is as important

as food in competition of larvae in a carcass. Of the four entrances mentioned above, the mouth and nostrils were invaded earliest, the ears and anus somewhat later.

Under warm conditions, initial penetration occurred so rapidly that within three days the entire carcass was teeming with larvae, making it difficult to follow the path of destruction. Thus, the observations below were taken during February and March.

After five to six days, small scattered egg masses were deposited on the dog carcass. Most of these were found along the edge of the abdominal incision with many scattered, individual eggs. An occasional mass was found beneath the carcass. Some authors have stated that egg masses are laid in the shade beneath carcasses to prevent desiccation and death due to exposure to heat and sunlight, and that young larvae bore their way into carcasses; however, this does not hold true for those exposed during cooler weather. In winter, eggs exposed to direct sunlight hatch faster and are not killed by heat from the sun.

Most of the eggs deposited in February hatched within three days after deposition and the tiny larvae made their way into the subepidermal tissues of the abdominal incision. New batches of eggs were found almost daily until the twelfth day, after which no more were discovered. Several egg masses were deposited around the lips and neck

of the carcass but the young from these eggs migrated to the incision in the chest, rather than to the mouth, which was already filled with larvae of all instars.

During the first five days the larvae were quite small and fed in small groups or pockets in the fatty subepidermal tissue. Fuller (1934) contends that individual larvae are not able to feed alone, as they are not able to produce adequate quantities of digestive juices.

By the tenth day of activity, the pockets of larvae had expanded and some of them merged to form larger pockets. Eventually about ten of these groups merged and larvae were generally distributed throughout the body cavity. The individual groups of larvae constantly widened their spheres of feeding and increased in size. By the nineteenth day, all pockets had merged and larvae were feeding in a general mass throughout the abdominal region.

The earliest arrivals remained in the outer subepidermal tissue and did not readily invade the visceral cavity. This cavity was filled with fluids for about ten days following death, and there was no larval penetration. As this fluid escaped the visceral cavity, adult flies gathered in large numbers to feed. On the twelfth day, some second instar larvae had penetrated the visceral cavity and were wandering over the kidneys and liver. By the fourteenth day many larvae invaded organs and tissues within the visceral cavity. By

the seventeenth day, the cavity was filled with larvae of all instars.

Precisely where larvae begin their attack, other than in natural orifices, depends upon chance, or where the eggs are deposited. In this case, the anterior chest region, the posterior areas of the hindquarters and the limbs and rump were relatively free of larvae, while the mouth and abdominal regions were heavily infested. Eventually, larvae migrated from depleted areas to parts of the carcass not yet invaded. The larvae which had been feeding in the oral cavity moved into the cranium or through the throat into the chest area. In cases where limbs lay near or on top of feeding areas, larvae moved directly to these limbs and invaded sound tissue. Where this was not the case, eggs were usually deposited on the hair of the legs and the young larvae burrowed into the skin. These larvae were discovered when the epithelial layer began peeling away from subcutaneous tissue.

The hindquarters and rump were the last areas to be invaded, after the visceral cavity had been thoroughly excavated. Most of the larvae moved over the surface of the body to uninvaded tissue, burrowed into the skin and commenced feeding. The anal opening was also used as an entrance to this area.

During cool nights, larvae which normally fed actively on the surface of wounds migrated to deep within the body cavity. The importance

of carcass temperatures in relation to blowfly activity has been stressed by Deonier (1940). Saprophagous forms are active throughout the year because of the heat generated by decomposition and the sun. The importance of smaller carcasses in this regard has been questioned by Ullyett (1950), but carcass temperatures are sufficient to allow larval activity even when temperatures are as low as 15°F. at night.

After larvae matured, they crawled out of the main feeding mass, penetrated the skin beneath the carcass and burrowed into the soil. These larvae remained quiescent for several days and then pupated. Many tiny larvae were found beneath the carcass. These larvae presumably were unable to obtain food, having hatched when much of the carcass was already consumed. These forms all die because they are unable to derive any nutriment from the waste products under the carcass.

The invasion of the carcass can be divided into three general stages. The first stage is the invasion of natural orifices, oviposition on wounds and the establishment of small pockets of larvae within exposed tissue. The second stage is the expansion of these small pockets to a large mass of larvae covering the entire feeding surface and the migration of larvae from depleted areas to sources of new food. The third stage consists of remaining small pockets of larvae in isolated parts of the carcass, the death of all larvae which do not obtain sufficient nutriment, the migration of mature larvae to the soil and pupation.

D. Sequence and Activity of Immature Carcass-Breeding Flies

As a carcass ages, there is a sequence in which the larvae of various carcass-breeding Diptera develop. Following initial invasion, there is a pattern which varies with the season. In this study, the species which invaded the carcass were studied with respect to when they arrived, which areas of the carcass they attacked, and how they were affected by the presence of other feeding species. Notes were kept on the movements of each species from the point of initial invasion. Changes in the sequence due to seasonal differences were noted.

The first species to attack the carcass in both the winter and spring seasons were the sarcophagids, Hystricocnemina plinthopyga (Wiedemann) and Sarcophaga cessator Aldrich. These appeared virtually simultaneously, although S. cessator adults were present in greater numbers initially. Both species invaded the oral and nasal cavities. Throughout the present work, these species were the first to appear, both as adults and as larvae. During February, the larvae remained confined to the oral and nasal cavities until these areas were thoroughly consumed. The remaining larvae then migrated to the anterior visceral cavity where there had been little previous activity. One group of larvae invaded sound tissue at the base of the foreleg. In all cases,

groups of H. plinthopyga and S. cessator larvae attacked tissues not previously invaded by other species and only scattered larvae were found in areas where other species were feeding. After much of the carcass had been consumed and the remaining food supply was limited, larvae of all species were found wherever food was available. Ullyett (1950) has suggested that succession in carcasses may be due, in part, to the "conditioning" of the carcasses by one species and that this conditioning may enhance the invasion of the carcass by another species.

After most of the H. plinthopyga and S. cessator larvae had left the oral cavity, a large number of tiny Phormia regina (Meigen) larvae fed on the remaining tissue. Because of their rapid growth and feeding, the larvae of H. plinthopyga and S. cessator crowd out most larvae of other species. As late as the fifteenth day, a female H. plinthopyga was observed larvipositing on the skin between the hind-quarters where no larvae had yet appeared. The next day many tiny sarcophagid larvae were present in this area and had begun to bore through the skin.

Phaenicia sericata (Meigen) was not common during cooler weather and appeared only after the carcass had aged for some time. Adults rarely constituted more than 5% of the flies seen on any day and the number of larvae collected in samples was small. The larvae which

were present were submerged in the large mass of Phormia feeding in the visceral spaces.

Eucalliphora lilaea (Walker) and Calliphora coloradensis Hough made up a minor part of the total larval mass. Specimens collected in samples were taken from the visceral cavity and in regions contiguous with the sarcophagids, H. plinthopyga and S. cessator. E. lilaea and C. coloradensis appear to invade given areas of a carcass slightly earlier than do larvae of Phormia but produce only small numbers of larvae compared to the large numbers of Phormia.

During the cooler months, the sequence of larval invasion was dominated by Phormia regina (Meigen). Deonier (1940) reported that 95 to 99% of the flies active in February were Phormia. The Cochliomyia macellaria (Fabricius) activity reported by Deonier was not noted during this period of the study. Although H. plinthopyga and S. cessator were most obvious during early carcass decomposition, Phormia larvae which hatched from numerous egg masses submerged other calliphorid species so that by the fifteenth day there were two distinct areas on the carcass. One was the mass of H. plinthopyga and S. cessator larvae in areas of newly-invaded tissues and the other was the mass of Phormia larvae with scattered specimens of other species present.

In February there was a diversity of species, most of which produced a small number of adult flies. H. plinthopyga and Phormia constituted 75% of all the larvae collected from the carcass during February. Of all the larvae present in the carcass, those of H. plinthopyga and S. cessator were the most active, readily moving to uninvaded parts of the carcass. The larvae of other species, notably Phormia, tended to move slowly in a mass as the food supply was depleted. The accumulation of waste products may account for migrations of H. plinthopyga and S. cessator, as they often left a part of the carcass where food was still in abundance. Their departure was followed by a rapid accumulation of Phormia and other calliphorids which cleaned up the remains left by the sarcophagids.

During February, it was possible to sample different parts of the carcass periodically to determine what species were present as well as movement of larvae through the carcass. Figure 2 summarizes the results of this sampling and gives the percent composition of the larvae. These percentages fluctuated greatly for each species, as their abundance varied according to where the sample was taken. The species grouped under "other Calliphoridae" include E. lilaea, Paralucilia wheeleri (Hough), and C. coloradensis.

Certain trends are also evident for the abundance of larvae in a given area. The peaks in the curve for H. plinthopyga show a high

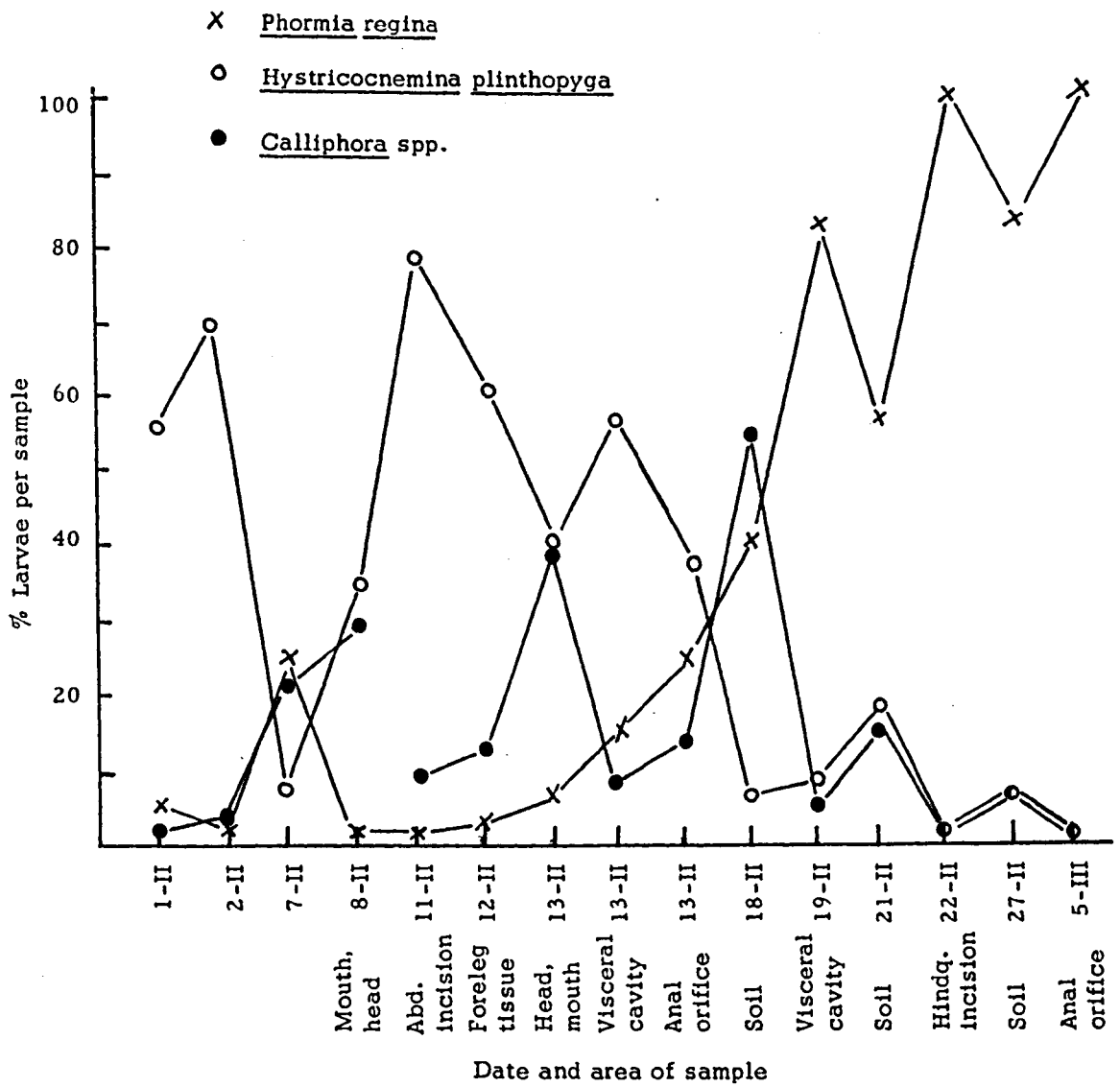


Fig. 2. Percent larval composition of three species of carcass-breeding flies collected from a dog carcass February 1 to March 5, 1964.

percentage of larvae in areas of initial invasion or areas which have not been previously attacked by other species. The only exception was the anal orifice which was invaded almost simultaneously by several species. The curve for "other calliphorids" indicates that these species and the two sarcophagid species were often found together in the same areas, but in all cases the sarcophagids were the initial invaders. The invasion of Phormia occurs in all parts of the carcass but only after the emigration of most sarcophagids. The only fluctuations in the curve for Phormia were for regions where larvae had not previously invaded, and which were occupied, in part, by H. plinthopyga and S. cessator.

In all cases, Phormia larvae were the last to leave the carcass. Stragglers could be found in moist pockets for as long as a week after the carcass had desiccated and could no longer be utilized as food by the larvae.

The sarcophagids Hystricocnemina plinthopyga and Sarcophaga cessator were the first arrivals on the carcass, followed in rapid succession by Phormia, Phaenicia and Calliphora spp. Two species, H. plinthopyga and Phormia, constituted 75% of the entire larval mass. H. plinthopyga was the dominant primary species while Phormia was the dominant secondary species.

IV. SUCCESSION OF CARCASS-BREEDING FLIES IN SPRING

A. Decomposition of the Carcasses

Decomposition of carcasses during April occurs in much the same way as in February, but the phases of decay occupy a period of hours rather than days. Maggot activity was evident within 24 hours and continuous warm weather plus great larval activity reduced the carcasses to skin, bones and hair in ten days. Temperature is most important, governing speed of destruction of carcasses by controlling the activity of insect and bacterial invaders.

B. Activity of Adult Carcass-Breeding Flies

During April, with increasing daytime temperatures, sarcophagids were active only in the early morning and just before sunset. P. regina and P. sericata were active when the sun was hottest from 9 a.m. to 5 p.m.

Several specimens of Paralucilia wheeleri (Hough) were collected at an altitude of 6,000 feet in early June, indicating that this species is found at higher elevations during the summer months.

By mid-April at a mean maximum temperature of 84.0°F., Phaenicia sericata (Meigen) comprised 50% of the total adult flies present. The numbers of H. plinthopyga increased slightly during April but S. cessator dropped almost to zero. During April and May many specimens of S. cessator were taken at elevations of 4,000-5,000 feet. This species occurs chiefly at higher elevations during the hotter months and increases in abundance at lower altitudes with the onset of cold weather in the mountains.

Cochliomyia macellaria (Fabricius) is a summer species and consequently appeared in this present work only in early December when temperatures were moderate. In December, with a mean maximum temperature of 69.9°F. and a mean minimum temperature of 29.2°F., C. macellaria was still active, but it disappeared in January. This species virtually replaced Phormia and Phaenicia during June to November in Texas (Cushing and Parish 1938). Cochliomyia had not appeared by the end of April but was collected abundantly in early June in the mountains of Southeastern Arizona.

No specimens of Calliphora coloradensis Hough, Eucalliphora lilaea (Walker) or Calliphora livida Hall were collected in April.

In April almost all eggs were laid beneath the carcass. Those which were exposed shriveled and died.

C. Invasion of the Carcass by Carcass-Breeding Fly Larvae

The slow progression of larval invasion occurred only during the cooler months. In April, the destruction of a carcass occurred within ten days. Invasion of all tissues took place rapidly and feeding was continuous. Larvae moved deep into the carcass during the day to escape the direct rays of the sun.

D. Sequence, Activity and Abundance of Immature Carcass-Breeding Flies

During the warmer months, decomposition occurred so rapidly that only a few samples were taken. The invasion of tissue by any one species was not well defined and most species were scattered throughout the carcass. From data collected during April at a mean maximum temperature of 90°F., H. plinthopyga and S. cessator were the first to invade the fresh carcasses, concentrating on the nasal and oral passages. Many larvae were also deposited in the abdominal incisions.

H. plinthopyga and S. cessator were rapidly followed by a massive invasion of Phaenicia larvae which completely filled the visceral cavities of the carcasses. Large numbers of Phormia larvae appeared within 48 hours after Phaenicia and these two species made up the bulk of the feeding mass. Larvae and adults of E. lilaea, C. coloradensis and Paralucilia were absent.

E. Effect of Temperature on the Invasion of Carcasses

The controlling effect of temperature upon the invasion of carcasses was illustrated during the spring carcass exposures. In early April, two cat carcasses were exposed side by side in the tray. These carcasses had been treated identically and abdominal incisions were made in both. One of the animals had a black coat while the other was striped.

Samples of larvae were taken from both animals as was done for the dog exposed in February. Within 36 hours after exposure, larvae of H. plinthopyga had invaded the mouth and nasal cavities of the darker animal and there were large egg masses along the edge of the ventral incision. The lighter animal contained neither eggs nor larvae.

After five days, larval activity in the darker animal had reached a maximum and all parts of the carcass were invaded by maggots. In the lighter animal, only the anterior tissue areas had been invaded and there was little invasion or liquefaction of posterior tissues. Throughout the exposure period carcass decomposition of the striped cat was about three days behind that of the darker animal. This immediately pointed to a temperature factor such as the black coat of one carcass absorbing greater quantities of heat, and therefore maintaining a higher body temperature resulting in accelerated larval activity and development.

Temperature readings from the atmosphere and from larval masses within the two carcasses were recorded and differences noted. On April 14, when the atmospheric temperature was 85.1°F., the temperature within the darker animal was 107.6°F., a difference of 22.5°F. The temperature within the lighter animal was 102.2°F. or 5.4°F. cooler than in the darker animal. These readings were taken late in the day so it is likely that the differential might be greater when atmospheric temperature is at a maximum. Temperatures in the carcasses over a period of a week averaged 17-23°F. above atmospheric temperatures. Deonier (1940) discusses the effect of temperature differentials on winter fly populations, but it is evident that temperature differentials observed during the warmer months will also affect the carcass fauna.

In addition to the differences in the rapidity of larval invasion was the difference in the abundance of H. plinthopyga and Phaenicia. Figure 3 shows the percentage of larvae of each species present during carcass exposures. Separate samples were taken daily from each carcass and identified in the laboratory. Note that the curve for Phormia is similar in both carcasses. Phaenicia deposited large egg masses on the darker carcass by the second day and it was teeming with third instar Phaenicia larvae by the fifth day. Phaenicia constituted 70% of all the larvae sampled on April 13. On the same day, for the lighter colored carcass, the number was virtually zero. The greatest number

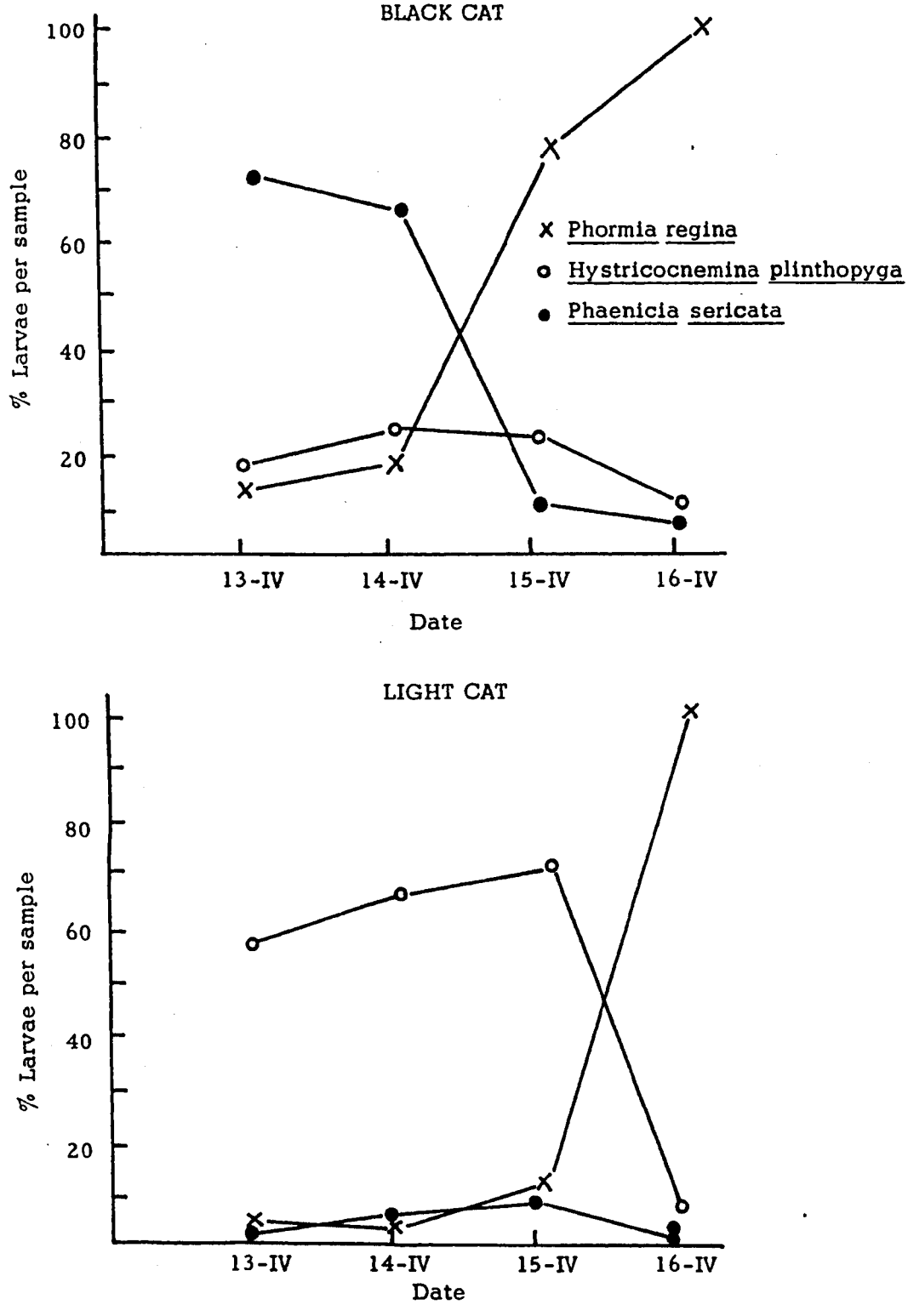


Fig. 3. Percent larval composition of three carcass-breeding fly species in two cat carcasses, April 13 to April 16, 1964.

of Phaenicia larvae taken from this carcass did not exceed 10% of the total larvae taken on any given day.

Exactly the opposite situation occurs in the case of H. plinthopyga larvae. In the darker cat, H. plinthopyga never constituted more than 30% of all larvae taken on a given day and the total was usually lower. In the lighter colored cat, 50-70% of the larvae taken from April 13-15 were H. plinthopyga.

Temperature seems to be the initial controlling factor involved in the establishment of one species over another. After initial invasion, however, factors of competition govern the abundance of species observed. Aspects of competition controlling the abundance of species following establishment will be discussed in the section on competition. Ullyett (1950) discounts the idea that carcass temperatures in small animals differ enough to affect the feeding larvae but the combined heat of absorption of radiant energy by the carcass and heat generated within larval masses should not be discounted as a factor controlling initial invasion of a carcass.

Fly activity in the spring is contrasted with that in winter by the rapidity of larval attack, development of larvae, and destruction of the carcasses. Sampling indicated that Hystricocnemina plinthopyga was first to invade a fresh carcass followed rapidly by Phaenicia. The importance of temperature was emphasized by the differences in the fauna of the two carcasses exposed in April. Phaenicia prevailed in

the carcass with higher temperatures while H. plinthopyga was dominant in the carcass with lower temperatures. A temperature spread of less than 10°F. appears to be critical in determining the fauna present.

V. SEASONAL CHANGES IN SPECIES ABUNDANCE AND ACTIVITY OF ADULTS AND LARVAE

A. Species Diversity

During the cooler months from December to March there is a diversity of species active around and breeding in vertebrate carcasses. This diversity is due to the presence of Eucalliphora lilaea (Walker), Calliphora coloradensis Hough, and Paralucilia wheeleri (Hough) exclusively during cooler periods. These species and Phormia regina (Meigen) are replaced by Cochliomyia macellaria (Fabricius) during the hot summer months. Phaenicia sericata (Meigen) and Hystricocnemina plinthopyga (Wiedemann) appear to be present to some extent throughout the year. Fuller (1934) reports that in Northern Queensland, succession in carcasses is absent in the winter because only one species, Calliphora stygia Fabricius = [Neopollenia laemica (White)], is present abundantly. Smit (1931) states that Chrysomyia marginalis Wiedemann may occur throughout the winter in South Africa, but does not state whether any species are found exclusively during the winter months.

B. Seasonal Changes in the Abundance of Carcass-Breeding Fly Larvae

During the cool winter months, S. cessator constituted about 20% of the total sarcophagid larvae within a carcass. By April, this

number decreased to almost zero, the larvae of H. plinthopyga being the only important flesh fly.

The number of Phaenicia larvae during April increased tremendously. From a total of 1,428 larvae collected from the dog carcass in February, only twelve of these (0.8%) were Phaenicia. From a total of 1,115 larvae collected from the two cat carcasses in April, 340 larvae (30.1%) were Phaenicia. In April, there was a sharp decrease in the number of Phormia larvae collected. The February sample contained 58.8% Phormia larvae while the April sample contained only 20.6%. H. plinthopyga increased from 16.7% in February to 33.5% in April. H. plinthopyga and Phaenicia thus increased at the expense of S. cessator, Phormia and the other Calliphorine and Chrysomyine species. Table 2 shows the totals and percentages for each species for the two samples.

C. Seasonal Changes in the Abundance and Activity of the Carcass-Breeding Sarcophagidae

In Southern Arizona, during the hottest months, C. macellaria flourishes while Phaenicia and Phormia maintain small populations. H. plinthopyga remains abundant throughout the year. These four species make up the summer carcass invaders. During the winter, S. cessator, H. plinthopyga, P. regina, P. sericata, P. wheeleri, E. lilaea and C. coloradensis were all part of the carcass-breeding

TABLE 2.--Totals and percentages of larvae collected from carcasses in February and April 1964.

Species	Total	%
February		
Phormia regina	838	58.8
Hystricocnemina plinthopyga	239	16.7
Sarcophaga spp.	113	7.9
Eucalliphora lilaea	66	4.6
Calliphora spp.	65	4.5
Sarcophaga cessator	48	3.4
Calliphora coloradensis	43	3.0
Phaenicia sericata	12	0.8
Paralucilia wheeleri	4	-
TOTAL	1421	
April		
Hystricocnemina plinthopyga	374	33.5
Phaenicia sericata	346	30.1
Phormia regina	233	20.6
Sarcophaga cessator	103	9.2
TOTAL	1115	

fauna. Thus, Southern Arizona has a varied group of carcass-feeding flies throughout the year.

During the course of a year, most carcass-feeding flies either disappear for a time or fluctuate in numbers. H. plinthopyga is the most versatile of the flesh flies. It was found present throughout the study period, but in greater numbers in the spring with the approach of warmer weather. The fluctuation in the numbers of H. plinthopyga was slight enough to indicate the maintenance of a stable population throughout the year, due to its tolerance of high and low temperatures.

Sarcophaga cessator Ald. is a cool-weather species. Adults and larvae were never as abundant as H. plinthopyga. The latter comprised about 75% of all sarcophagid larvae in February and 98% in April. Although a few S. cessator adults were obtained from larvae in April, most of them died before reaching maturity. S. cessator adults are rare at lower elevations during the summer but were collected abundantly above 5000 feet in June. Many of the specimens taken in Arizona are from mountain localities.

The activity of adult flesh flies changes abruptly as days become hotter. From December to March, both H. plinthopyga and S. cessator were active throughout the day as long as the sun was shining. By April, no sarcophagids were active from 9 a.m. to about

one hour before sunset. Observations made early in the morning and at sunset showed that both species were very active during these periods but disappeared after 9 a.m. or when shadows covered the study area. These periods of activity could determine the presence or absence of larvae found on a carcass. If a carcass is first exposed at mid-day, when the flesh fly activity is at a minimum, this may result in fewer forms being produced from that carcass. If a carcass is first exposed during the night, the activity of sarcophagid adults in the early morning might result in a greater number of larvae produced in the carcass. Thus the fauna of a carcass will be somewhat dependent upon the activity of the adult forms, and the abundance or absence of adults will, in some cases, be due to chance phenomena.

The activity of several other species of flesh flies was noted throughout the study. Some of these were quite common forms. Ravinia l'herminieri (Robineau-Desvoidy) and Oxysarcodexia ochripyga (Van der Wulp), Sarcophaga misera sarracenioides Aldrich, Metoposarcophaga sulculata (Aldrich), and Sarcophaga bishoppi Aldrich were common forms. R. l'herminieri and O. ochripyga are coprophagous forms; S. misera sarracenioides is a scavenger and grasshopper parasite while the habits of M. sulculata and S. bishoppi are unknown. All of these species were present from December to April except for S. bishoppi which appeared only in April. Although many adults of S. bishoppi were captured on the carcass, no larvae were obtained.

The presence of these species of flesh flies can be attributed to the attractive odors emanating from the decomposing carcasses. It is not unlikely that many sarcophagids congregated in the study area and that the concentration of adults probably facilitated mating between the sexes of the species involved. There was much mating activity on the vegetation surrounding the screened area.

D. Seasonal Changes in the Abundance and Activity of the Carcass-Breeding Calliphoridae

Phormia regina is a cool-weather form and was found most abundantly from January to March. During this time, it comprised about 80% of all the Calliphoridae present. By April it had tapered off to about 45%. In December, Phormia gradually replaced C. macellaria as the most abundant species. Adults of Phormia were found soon after the sun warmed the study area and many landed on the cage and rested quietly in the sun. This species was most active during mid-day, large numbers flying around the carcass. Adults were present around the carcass except on the coldest days.

Phaenicia sericata is abundant during the spring and fall. By December, this species was not common, and remained rather rare from December to March. By April, the number of adults had increased greatly and equalled Phormia whose numbers had decreased steadily

from mid-March. Trapping by Cushing and Parish (1938) in Texas showed Phaenicia to be most abundant in the spring from April to July, disappearing from July to January. In this study, Phaenicia was most active during mid-day, and was not present on cloudy or cold days.

Paralucilia is comparatively rare in Southern Arizona and although larvae can be found in most carcasses, they represent only a small fraction of the total larval population. It was active from December to March and can be considered a winter species at lower elevations. A number of specimens was collected in June above 5000 feet and most records from Arizona are from mountain localities.

Eucalliphora lilaea is a winter species and was observed from December to March. It was not present during April. This species was most active on calm, clear, warm days. E. lilaea is the most common of the closely related members of the genus Calliphora, or blue bottle flies. Other species were present but not in large numbers.

Calliphora coloradensis is a winter species. Adults were present from December to March in small but consistent numbers. This species prefers calm, sunny days and was rarely present on windy days.

Cochliomyia macellaria is a hot-weather species, and is completely absent from January to June. By mid-June, many adults were collected at higher altitudes. This species is the dominant

blowfly throughout the hot summer months. Cushing and Parish (1938) trapped adults throughout the year in Texas, but no adults were observed in Southern Arizona until June.

The presence of numerous summer, winter and transitional species assures a diversity of forms throughout the year in Southern Arizona. Ullyett (1950) discusses the effects of overlapping species on competition and also mentions that the presence or absence of a species is due to soil temperatures affecting the developing pupae.

E. Comparison of Larval Sequence in Southern Arizona with South Africa and Northern Queensland

Seasonal variations in species of larvae attacking carcasses correspond with the activities of the adults mentioned above. Seasonal species are either present or absent during certain times of the year, while permanent species exhibit fluctuations according to season.

Ullyett (1950) states that in South Africa, adults of Phaenicia are the first to visit carcasses, followed by various species in the subfamily Chrysomyinae and finally members of the Sarcophagidae. Fuller (1934) found that Phaenicia and Calliphora spp. were the primary flies, but that the importance of sarcophagids in carcass decomposition increased in warmer climates.

In Southern Arizona, from December to March, the sequence which is described by Ullyett (1950) was reversed. The sarcophagids,

H. plinthopyga and S. cessator were the primary attackers. Calliphora spp. followed soon after the sarcophagids and the Chrysomyine species; Phormia and the Calliphorine Phaenicia arrived very late. During April, H. plinthopyga and Phaenicia arrived almost simultaneously. However, each was active at different times of day, as mentioned above. Phormia arrived somewhat later. These events are considerably telescoped by warmer weather and arrival of different species may be only hours apart.

Seasonal abundance was variable for all carcass-breeding species studied. Some species are present in variable numbers throughout the year while others disappear during certain periods. The calliphorids, Eucalliphora lilaea, Calliphora coloradensis, and Paralucilia wheeleri were present only from December to March. Phormia regina was present throughout the year but is most abundant during the spring and fall. Cochliomyia macellaria was present from May to December but was most abundant during the hottest summer months. It was absent during the winter. The sarcophagid, Hystricocnemina plinthopyga, was present throughout the year but was somewhat more abundant in the spring and fall. Sarcophaga cessator was most abundant during the winter and rare during the spring.

Seasonal changes in adult fly activity were most conspicuous for the sarcophagids, H. plinthopyga and S. cessator. During the winter, these species were active throughout the day. In April, they were active from sunrise until 9 a.m. and again from 5 p.m. until sunset. Phaenicia and Phormia were active throughout the day.

Seasonal differences in larval abundance were also noted. In winter, the sarcophagids S. cessator and H. plinthopyga constituted about 20% and 80%, respectively, of the total sarcophagid larvae in the carcass. In spring, S. cessator constituted about 0.5% and H. plinthopyga 95.5%. The number of Phaenicia larvae increased from 0.8% of the total larval mass in the February carcass exposure to 30.1% in April exposures. Phormia decreased from 58.8% in February to 20.6% in April.

VI. INTERSPECIFIC AND INTRASPECIFIC COMPETITION

A. Introduction

Most papers dealing with blowfly problems at least mention the importance of interspecific and intraspecific competition and the effect of competition upon succession within a carcass. Smit (1931) and Fuller (1934) deal with competition generally. Nicholson (1954, 1957) deals with numerous problems arising from the study of blowfly competition and Ullyett (1950) has exhuastively covered the topic for South African blowflies. Since the supply of food furnished by a carcass is always limited and carcasses in most areas are not commonly encountered, competition is usually intense and the authors above adequately discuss the problems arising from a limited food supply and their effect on blowfly populations. Much of the work done also applies to flies in Southern Arizona but there are a few aspects which differ enough from previously encountered situations to warrant discussion.

B. Availability of Carcasses

In Southern Arizona, there is no intensive use of livestock such as in the sheep-raising areas of South Africa and Australia where

blowflies are a constant problem. Most losses arise from screwworm attack or infestation of wounds on cattle, horses and sheep. Carcasses seen commonly on the desert are usually those of smaller mammals, birds and occasionally coyotes and javelina. These are drawn from the wild animal populations upon which the carcass-feeding flies are dependent for their existence. In rare instances, such as for Phaenicia sericata (Meigen) and Sarcophaga misera sarracenioides Aldrich, flies may subsist on material other than carcasses or may invade wounds on animals.

There are many vertebrate scavengers which may deprive carcass-feeding flies of some or all of the food available in a carcass. In one instance, a freshly-killed steer was found near Bells, Arizona. There were many vultures in the area picking at the carcass. Two weeks later only skin and bones remained. There was no evidence that any blowflies developed from this large carcass. Thus the problem of food availability is as acute in the desert as in most areas.

C. Cannibalism

One factor encountered during the studies in South Africa and Australia not seen in Southern Arizona is cannibalism among the fly larvae. Larvae of Chrysomyia albiceps Wiedemann (= rufifacies Macquart) actively devoured larvae of Phaenicia, the so-called

"smooth larvae" of Fuller (1934). According to the present references on calliphorid taxonomy, there are no members of the genus Chrysomyia present in North America. Although Cochliomyia macellaria (Fabricius) is closely related, there is no evidence that this species is cannibalistic.

D. The Work of Ullyett and Nicholson

Based on laboratory work conducted by Nicholson (1957) and Ullyett (1950), with increasing temperature and increased larval activity, intraspecific and interspecific competition becomes keener, resulting in fewer numbers of flies or smaller individuals which are less vigorous than "normal" flies. Nicholson (1957) observed that the basic underlying mechanism involved is that a large number of larvae get too little food to complete development, but, in doing so, waste much of the available food. This is one reason for the drastic fluctuations in blowfly populations.

As many pupae and mature larvae as possible were collected from carcasses during February and April. As expected, the carcass in February produced many more adult flies than those in April. Table 3 gives totals for adults produced from carcasses in February and April.

TABLE 3.--Total adult flies produced from carcasses in February and April 1964.

Species	Total	Percentage
	February	
Phormia regina	3,914	86.9
Hystricocnemina plinthopyga	230	5.1
Eucalliphora lilaea	118	2.4
Phaenicia sericata	107	2.1
Calliphora coloradensis	70	1.5
Sarcophaga cessator	47	1.4
Paralucilia wheeleri	15	0.3
TOTAL	4,504	
	April	
Phaenicia sericata	587	38.8
Phormia regina	576	38.1
Hystricocnemina plinthopyga	347	22.2
Sarcophaga cessator	2	0.9
TOTAL	1,512	

E. Comparison of Adult Flies Produced from Carcasses in Winter and Spring

By thoroughly searching the pen area for stray pupae and sifting through the hair on the carcasses, it was estimated that the number of adults which emerged in the laboratory represented 75% of the total number of emerging adults. If 25% is added to each total, the February carcass produced 5,630 adults and the April carcasses, 1,890.

As shown in Table 3, the total number of adults produced in April was only about one-fourth of that from February. Two species, notably H. plinthopyga and Phaenicia, increased at the expense of Phormia regina (Meigen) which, in April, was no longer dominant. Adults of Phormia tended to be very much smaller than those produced in February. Of a total of 576 P. regina adults produced in April, 50% were undersized, had deformities or were unable to unfold the wings after emergence. The mortality of pupae was higher in April than in February because some undernourished larvae were able to pupate but produced no adults. Mortality never exceeded 10% in any of the samples except in cases where pupae or larvae were parasitized.

F. Competition Between Established Species

Prolonged activity during February permitted observations on the movement of larvae within the carcass. Phormia never succeeded

in becoming established in areas where Hystricocnemina plinthopyga (Wiedemann) or Sarcophaga cessator Aldrich were feeding, while larvae of Calliphora coloradensis Hough and Eucalliphora lilaea (Walker) were most commonly found in such areas. Two factors might possibly be operating here. First, the mechanical aspects of crowding by the large larvae of H. plinthopyga and S. cessator consumed all available space in a given area. This does not account for the presence of C. coloradensis and E. lilaea. Secondly, as discussed by Ullyett (1950), the ability of a species to invade a carcass may be dependent upon chemical conditioning by the presence of previous inhabitants. The rapid invasion of areas deserted by the sarcophagid larvae indicates that in this case Phormia is unable to successfully invade these areas until sarcophagid larvae have departed.

The sequence in which adults larviposit or oviposit also has important bearing on the establishment of a larval population. In the example mentioned above, sarcophagid larvae are the first to become established in carcasses and hence are better able to prevent the invasion by other species. Other larvae which are crowded out and denied access to food move to areas of the carcass which either have not been attacked or which have been occupied and deserted by sarcophagids.

The factors of chance may be important in determining what species may be found inhabiting a carcass. This is best demonstrated by the April carcass exposures. How can the initial preponderance of H. plinthopyga in the dark cat and Phaenicia in the light-colored cat be accounted for? Temperature certainly is part of the answer but whether the difference is due to different temperature preferences is not known. The fact that H. plinthopyga is more active in cooler weather than Phaenicia and that Phaenicia larvae are not common during the winter months may provide a clue. Carcass temperatures in the carcass in which H. plinthopyga predominated were only about 5°F. cooler than in the other. The fact that Phaenicia did not readily oviposit upon the striped cat even though sarcophagid larvae were not well established at the time is puzzling and further work is needed to determine causal factors. On the seventh day after exposure, about 250 dead larvae of H. plinthopyga and S. cessator were discovered scattered around the carcass of the striped cat, in which they had previously abounded. Whether they were killed by the heat within the carcass or by heat from the sun while attempting to migrate to the soil is not known. No such event occurred in the case of the black cat.

Once the larvae of H. plinthopyga or Phaenicia were established in the carcasses, larvae of the other either failed to become

established or did so in very small numbers. This demonstrated that, in the case of primary attacking species, early firm establishment will tend to block the arrival of other potential primary forms, so that one species will develop to the exclusion of another (see Figure 3). Phormia, being a secondary invader, became well-established in both carcasses after many of the primary larvae had completed feeding and migrated to the soil. Chance physical factors, therefore, play a strong role in determining the composition of the initial larval invaders by influencing oviposition and larviposition habits of adults and thereby governing the presence or absence of primary species. Once established, the species present is able to maintain its superiority to the exclusion of other species by utilizing available food and space. Further work on this aspect of competition would prove fruitful.

G. Summary

Factors which influence competition between carcass-breeding fly species include availability of carcasses, cannibalism, and temperature. Because of increased interspecific and intraspecific competition in the spring, only about one-fourth as many adults were produced from carcasses in the spring as in the winter. Many of the adults produced in spring were undersized or possessed other deformities. Calliphorids never became established in parts of a carcass where

sarcophagids were feeding until the sarcophagids migrated to other parts of the carcass. This may be due to mechanical crowding or chemical conditioning of the carcass. April carcass exposures indicated that chance physical factors may determine what primary species will first invade a carcass. Once a given primary species became established on a carcass, it tended to predominate until the arrival of secondary species.

VII. LABORATORY REARING

Mature larvae and pupae collected in the field were taken to a laboratory and placed in gallon jars until emergence occurred. Several artificial diets were tried in an attempt to rear larvae of Hystricocnemina plinthopyga and Sarcophaga cessator, as well as blowfly species. None of these diets was successful. The larvae developed rapidly up to a point but then wandered over the medium and eventually died. The best medium was nutrient agar 5 parts, powder liver extract 4 parts, lyophilized bovine serum 1/2 part, and nutrient salt 1/2 part. Larval development progressed rapidly to small third instar forms but then the larvae died.

Length of pupal period of the carcass-breeding flies was studied in the laboratory, with particular emphasis on seasonal changes in the length of the life cycle.

Phormia is first to emerge in a given sample. Eucalliphora lilaea was usually next to follow. Phaenicia sericata emerged next followed closely by Calliphora coloradensis. S. cessator and H. plinthopyga emerged almost simultaneously. Although periods of emergence overlapped, the periods when the greater part of the emergence of each species took place were well separated. Thus,

one could expect the orderly sequence of adult emergence. Phormia has the shortest life cycle of all the flies studied. Most Phormia, the the last species to leave the carcass, had emerged long before the first, S. cessator, the first species to invade the carcass.

Length of the life cycle for three species in April is given below in Table 4.

TABLE 4.--Length of life cycle in days for three species of carcass-breeding flies in April, 1964.

Species	Egg	Larva	Pupa	Total time
Phormia regina	2	2-6	5-10	9-18
Phaenicia sericata	2	2-6	12-17	16-25
Hystricocnemina plinthopyga	-	3-10	20-26	23-36

Length of the pupal stage seems to account for differences in the life cycle, but further laboratory work will be necessary to determine precisely the changes in life cycle length under varying temperature conditions. Seasonal differences are due mainly to the rapid development of the larvae during warm weather.

Groups of pupae were separated from each sample and placed in individual vials to determine the rate of mortality in the pupal stage. Mortality was low in all samples collected in both February and April.

In all cases, except for the intervention of parasites, mortality was below 10% and did not materially affect the total number of flies which emerged.

VIII. SUMMARY AND CONCLUSIONS

The abundance and variety of carcass-breeding flies seen throughout the year in Southern Arizona can be attributed to the mild, dry climate which prevails most of the year and which therefore provides an excellent opportunity for the study of succession. Though certain species predominate, the presence of at least three or four species throughout the year permits observations on competition.

Preliminary observations on carcasses exposed in the field in Southern Arizona show that there is a definite seasonal succession of species which regularly invade carcasses and that the succession is related to changes in temperature and to chance factors which either limit or enhance the ability of certain species to invade carcasses during certain times of the year.

Competition for food and space is the main factor which will determine the abundance of a carcass-breeding species once it is established upon a carcass but the presence or absence of any species will be related to temperature or other non-biotic phenomena.

Precipitation affects carcass-breeding flies only by adding some moisture to the desiccating carcass and allowing a prolonged

feeding period for the larvae. Although adults are attracted to a moistened carcass, they do not oviposit.

Carcass decomposition occurs rapidly in the warmer months due to greater activity of invading larvae. During the winter, when the larvae are active only during the day and temperatures are low, liquefaction and decomposition occur more slowly.

Invasion of carcasses occurs in a predictable manner. Members of the family Sarcophagidae are always first to invade, followed by members of the genera Calliphora, Eucalliphora and Paralucilia in the winter, and Phaenicia sericata in the spring. The secondary species, Phormia regina in winter and Cochliomyia macellaria in summer, are the last of the blowflies to develop on the aging carcass.

Activity of adults is related to weather phenomena such as temperature, clouds, precipitation and winds. Weather conditions prevailing at the time of carcass exposure sometimes determine which species become established as well as how successful they are in competing with other established species.

In winter, Phormia regina (Meigen) is the dominant species present. In spring, Phaenicia sericata (Meigen) is dominant, but is replaced by Cochliomyia macellaria (Fabricius) in June. Members of the genera Calliphora, Eucalliphora and Paralucilia are present only during the winter months.

Due to differences in length of the life cycle, adults of all species emerge at specific intervals after pupation. Phormia regina, with the shortest life cycle, always emerges first, followed in order by Eucalliphora lilaea, Phaenicia sericata, Calliphora coloradensis, Sarcophaga cessator and Hystricocnemina plinthopyga.

The role of parasites and predators in reducing the number of developing flies appears to be minor, at least during the winter and spring.

Further work on a yearly basis will do much to enhance the knowledge of blowfly activity in the Southwest and to define more precisely the biotic and physical factors which combine to regulate the occurrence and abundance of carcass-breeding flies in Southern Arizona.

IX. APPENDICES

APPENDIX A

TAXONOMY OF DIPTERA ASSOCIATED WITH CARCASSES

1. Introduction

Taxonomy of the Calliphoridae has been well documented due to the economic importance of the group. Hall (1948) adequately covers the problems involved in the description and synonymy of the family. Certain shortcomings in this work are pointed out by James (1953) and concern variation in coloration and the proportions of various structures used by Hall. The problem of variation in this study was noted particularly in the genus Calliphora and the author has attempted to use the characters which are most stable. Shannon (1926) helped to clarify the family as a whole and to determine its boundaries. Townsend (1908) provides an interesting look at the history of the taxonomy of the muscoid Diptera and gives a summary of the morphological characters of the head, thorax, wings, abdomen and legs which are useful in identifying species within the muscoid group. He emphasizes those characters which to him seem most important in identification.

Taxonomy of the Sarcophagidae is somewhat less well known. Recent papers have helped to clarify the evolutionary position and

bionomics of the species. Aldrich (1916), Roback (1954), Sanjean (1957), Downes (1955) and Hallock (1940, 1942) provide good material for the identification of larvae and adults. The family is in a state of flux at present with many name changes being proposed as the family becomes better known.

The keys presented here utilize those characters which present the greatest stability and which are easiest to recognize. In the adult keys, emphasis is placed on field identification. The larvae are separated by means of the morphology of the posterior spiracles and the cephalopharyngeal skeleton. The keys deal only with those flies attracted to carcasses in considerable numbers or those directly associated with carcasses, i.e., those which oviposit and complete larval development on carcasses.

Brief descriptions are given of the flies directly associated with the carcass and include only the characters important in differentiation between species present in the field. Descriptions of calliphorids are based on characters used by Hall (1948) and James (1947); those of the sarcophagids are based on James (1947), Aldrich (1916), and Hallock (1940, 1942).

2. Manipulation of Adults and Larvae

Methods were developed for handling and counting larvae during the course of the work. Larvae collected in the field were immediately

placed in Peterson's KAAD solution consisting of 2.5 ml. kerosene, 70 ml. 95% ethyl alcohol, 10 ml. dioxane, and 17.5 ml. glacial acetic acid per 100 ml. of solution. The purpose of the solution is to expand and harden the maggots so that they can be handled easily. Care must be exercised in the use of kerosene because too little leaves the specimens limp and flaccid and too much explodes them. After submersion in KAAD for about 12 hours, the larvae were transferred to 95% ethyl alcohol for storage.

Samples of larvae were collected from carcasses at intervals of from one to three days to determine species present in the carcass and the movements of maggot species from one area of the carcass to another. These samples from the population reduce the number of larvae present and consequently affect competition to a slight extent.

Larvae were identified and then stored in 95% ethyl alcohol. Slide mounts of the mouth hooks and posterior spiracles were made for all species using Hoyer's medium as a mounting and clearing agent. Drawings of the mouth hooks and spiracles were made directly from these mounts.

Initially, adult flies, beetles and wasps which landed on or near the carcasses were captured by net but since this method of collection tended to mar the specimens, subsequent collections were made by picking the flies off the carcass with small vials. The

flies were taken to the laboratory in these vials, anesthetized with ethyl acetate and killed with hydrogen cyanide gas. The advantage of using such vials in collecting sarcophagids was that the females would often larviposit within the vials and the larvae could thus be easily obtained. Eventually the necessity of obtaining adult samples was obviated by the recognition of the various species as they landed on the carcass.

Larvae which developed on the carcass and then burrowed into the soil directly beneath were collected at ten to fourteen day intervals. The mature larvae and pupae thus collected were taken to the laboratory and put into gallon jars. Initially, vermiculite was used as a substrate to contain the pupae but as adults emerged, a tremendous amount of moisture was generated within the jars. Dry, sandy soil was found to be best for containing these pupae. Muscoid flies are extremely adept at escaping from closed containers, making it necessary to fit a tight lid over the jars to prevent the escape of emerging adults. This situation also created moisture problems within the jars. The best solution was to fit a piece of fine cloth over the top of a jar with two very tight rubber bands. This prevented escape and allowed excess moisture to dissipate.

As adults emerged, they were anesthetized with ethyl acetate, counted, identified and sexed. No attempt was made to propagate adults in the laboratory.

From each group of mature larvae and pupae collected from the carcass, a number was set aside for individual rearing to give an indication of mortality and of the species present in the sample. These larvae and pupae were selected at random and placed in tightly corked vials containing an inch of loose soil. Individual rearing allowed determination of species parasitized by Mormoniella vitripennis (Walker) and Alysia ridibunda (Say).

Mouth hooks and posterior spiracles of third instar larvae were mounted on slides in Hoyer's medium. This medium clears the spiracles and also dissolves any flesh adhering to the mouth hooks. The spiracles were removed with a pair of Dumont No. 5 jeweler's tweezers by gently separating the spiracular plate from the tracheae and posterior cavity. The mouth hooks are easily removed from the anterior end of the maggot and the muscle tissue can be teased from the hooks or dissolved by immersion in potassium hydroxide solution. Hoyer's medium quickly clears any excess tissue clinging to the mouth parts.

APPENDIX B

KEY TO ADULT DIPTERA MOST COMMONLY ASSOCIATED WITH CARCASSES IN SOUTHERN ARIZONA

1. Thorax without a complete transverse dorsal suture anterior to the wings; post-humeral bristle absent; subcostal vein often incomplete; fourth vein usually straight . . . . . ACALYPTRATAE. 2.

   Thorax usually with complete transverse dorsal suture anterior to the wings; post-humeral bristles usually present; subcostal vein complete and ending in the costal vein . . . . . CALYPTRATAE. 3.

2. Body length 3.5-4.0 mm. . . . . F. Piophilidae

   Body length 1.5-2.0 mm. . . . . F. Chloropidae

3. Hypopleuron with weak hair not arranged in rows. Muscoidea 4.

   Hypopleuron with one or more rows of strong bristles . . . . . Sarcophagoidea 5.

4. Fourth longitudinal vein (M 1 and 2) distinctly curved forward; scutellum lacking fine erect hairs on undersurface . . F. Muscidae

Fourth longitudinal (M 1 and 2) vein straight or only slightly curved; scutellum with fine erect hairs on the under-surface . . . . . F. Anthomyiidae

5. Arista long, plumose for about one-half of its length or pubescent; abdomen gray or black tessellated; propleuron and presternum usually bare . . . . . F. Sarcophagidae. 6.

Arista with plumosity extending three-quarters of the length; abdomen usually metallic green, blue, bronze, or black; propleuron and prosternum usually pilose . . . . . F. Calliphoridae. 11.

6. Thorax with three posterior dorsocentral bristles, well defined . . . . . Sarcophaga cessator Aldrich

Thorax with four or five posterior dorsocentral bristles or anterior one reduced 7

7. Hind tibia with distinct villosity 8

Hind tibia without distinct villosity 9

8. Back of head with three rows of post ocular cilia; frontal bristles about ten (in males); hind tibia with dense villosity; length 8-13 mm. . . . . Sarcophaga misera sarracenioides Aldrich

Back of head with four or five rows of post-ocular cilia; frontal bristles about seven (in males); hind tibia with short villosity; length 8-9 mm. . . . . Metoposarcophaga sulculata (Aldrich)

9. Anterior acrostichial bristles large and well-defined; four well-defined posterior dorsocentral bristles present . . . . . Ravinia l'herminieri (Robineau-Desvoidy)

Anterior acrostichial bristles absent or poorly defined; anterior members of the posterior dorsocentral bristles reduced 10

10. Apical scutellar bristles present (in male); female with genital segment red; orifice vertical with stout bristles above . . . . . Sarcophaga bishoppi Aldrich

Apical scutellar bristles absent (in male); female with genital segment yellow; orifice rounded and lacking stout bristles above . . . . . Hystricocnemina plinthopyga Wiedemann

11. Base of radial vein with about seven or eight dorsal setae . . . . . Chrysomyinae 12

Base of radial vein lacking dorsal setae . . . . . Calliphorinae 14

12. Thorax with three dorsal longitudinal stripes extending to the scutellar suture; bucca orange 13

Thorax without dorsal longitudinal stripes; bucca black . . . . . Phormia regina (Meigen)

13. Frontale clothed with dark hairs; squamal lobes dark brown to black; fourth abdominal segment not pollinose laterally . . . . . Paralucila wheeleri (Hough)

Frontale clothed with pale hairs; squamal lobes white or yellowish, rarely light brown; fourth abdominal segment pollinose laterally . . . . . Cochliomyia macellaria (Fabricius)

14. Lower squamal lobe bare above . . . . . Phaenicia sericata (Meigen)

Lower squamal lobe pilose above 15

15. Postintraalar bristles usually two; if three, then the anterior bristle is hair-like and reduced; ascending faciàle bristles strongly developed; frontal bristles usually six . . . . . Eucalliphora lilaea (Walker)

Postintraalar bristles usually three; anterior one usually slightly weaker than the posterior two; ascending faciale bristles weakly developed, frontal bristles eight to ten, some weakly developed 16

16. Bucca black; bristles on faciale extending three-fourths of the way to the antennal base . . . . . Calliphora livida Hall

Bucca orange-red on the anterior half; bristles on faciale extending half way to the antennal base . . . . . Calliphora coloradensis Hough

APPENDIX C

KEY TO THIRD INSTAR LARVAE ASSOCIATED WITH CARCASSES IN SOUTHERN ARIZONA: BASED ON POSTERIOR SPIRACLES AND CEPHALOSKELETON

1. Larvae with dorsal cornua of cephaloskeleton divided; posterior spiracles located in a deep depression . . . . . F. Sarcophagidae. 2.

   Larvae with dorsal cornua of cephaloskeleton not divided; posterior spiracles exposed or in a shallow cavity . . . . . F. Calliphoridae. 3.

2. Peritreme extensions absent or weakly developed; tail of outer arc not enclosing the stigmatic scar; inner slit usually bent slightly inward, or nearly straight throughout its length, rarely sinuous; anterior dental sclerite curved sharply away from the ventral surface of the labial sclerite; hypostomal sclerite roughly quadrate in profile . . . . . Sarcophaga cessator Aldrich

   Peritreme extensions strongly developed; inner extension about one-fourth the length of the middle slit, outer extension about one-third the length of the middle slit; tail of the outer arc enclosing stigmatic scar; inner slit more or less sinuous; dental sclerite only slightly curved, paralleling the ventral surface of

the labial sclerite; hypostomal sclerite narrowed ventrally, roughly triangular in profile . . . . . Hystricocnemina plinthopyga (Wiedemann)

3. Peritreme incomplete; not enclosing the stigmatic scar . . . . . Chrysomyinae 4

Peritreme complete; enclosing the stigmatic scar . . . . . Calliphorinae 6

4. Accessory oral sclerite present . . . . . Paralucilia wheeleri (Hough)

Accessory oral sclerite absent 5

5. Peritreme uniformly broad and darkly pigmented; inner and outer tails of the peritreme ending bluntly; peritreme extension between outer and middle slits poorly developed, bluntly rounded; pharyngeal sclerite lacking window in the ventral extension . . . . . Cochliomyia macellaria (Fabricius)

Peritreme not uniformly broad; darkly pigmented; inner and outer tails of the peritreme narrowed to a point; peritreme extension strongly developed between middle and outer slits, usually tapered to a point; pharyngeal sclerite with narrow well-defined window in the ventral extension . . . . . Phormia regina (Meigen)

6. Accessory oral sclerite absent . . . . . Phaenicia sericata (Meigen)

Accessory oral sclerite present 7

7. Peritreme in the area of the stigmatic scar distinctly lighter in color; peritreme enclosing the stigmatic scar irregularly narrowed; peritreme extensions broadly rounded; outer slit nearly horizontal; middle slit curved outward; labial sclerite broad basally; antero-dorsal process not prolongated . . . . . Eucalliphora lilaea (Walker)

Peritreme in the area of the stigmatic scar uniformly dark; peritreme enclosing the stigmatic scar uniformly broad; peritreme extensions strongly developed, sharply or bluntly pointed; labial sclerite somewhat narrowed basally; anterodorsal process slightly prolongated . . . . . Calliphora coloradensis Hough

APPENDIX D

SPECIES DESCRIPTIONS

Hystricocnemina plinthopyga (Wiedemann)

Recognition characters: Adult - length 9-14 mm. Males easily recognized by their large, bulbous hypopygium; posterior dorsocentral bristles four or five, posterior two of normal size, anterior ones reduced; anterior acrostichial bristles absent or barely differentiated from surrounding hairs; male with hypopygium yellow to orange; first segment very large; hind margin of first segment with a row of heavy bristles; second segment bristly; female with genital segment yellow; orifice rounded with a few heavy bristles above. Larva - as described in the Key.

Habits: Saprophagous, and sometimes a myiasis producer (James, 1947).

Comments: This is the most common sarcophagid associated with carcasses. Larviposition on fresh carcasses usually occurred within one to three days after deposition of the carcass; life cycle was completed in 23 to 42 days depending on the time of year. One female deposited eggs rather than larvae in the laboratory.

Metoposarcophaga sulculata (Aldrich)

Recognition characters: Length 8-9 mm.; males readily separated from other species by extension of the second hypopygial segment far under

the abdomen and median groove in the first segment. Back of head with four or five rows of post ocular bristles; posterior dorsocentral bristles four, well-defined; anterior acrostichial bristles two or three pairs, well-defined; hind tibia with short villosity; female with genital segment red; orifice round; larvipositor absent.

Habits: Unknown

Comments: This species was not taken before mid-February and became increasingly abundant during March and April. Adults were never observed to land on carcasses but did rest and fly in immediately adjacent areas.

Ravinia l'herminieri (Robineau-Desvoidy)

Recognition characters: Length 6.5-12 mm. Usually a small species; posterior dorsocentral bristles four, well-defined; anterior acrostichial bristles large; hind tibia lacking villosity; male with aedeagus slender except at the distal end where it is expanded into two conspicuous knobs separated by a groove; female with genital segment red pollinose; genital orifice oval.

Habits: This species has coprophagous food habits, as Roback (1954) states is common to most well-studied species of Ravinia.

Comments: This species is by far the most common Ravinia in the Tucson area. It did not oviposit on the carcasses.

Sarcophaga bishoppi Aldrich

Recognition characters: Length 10-14 mm. Recognized by yellowish palpi. Back of head with two rows of post ocular bristles; posterior dorsocentral bristles four or five with only the posterior one of normal size; anterior acrostichial bristles absent; apical bristles present in male; male with a long thumb-like structure at the base of the anterior clasper; aedeagus yellow; female with genital segment red; genital orifice vertical with stout bristles above.

Habits: Unknown

Comments: This species was not present before April but became very abundant by mid-April. Many adults were caught on the carcass but no oviposition was noted.

Sarcophaga cessator Aldrich

Recognition characters: Adult - length 9-11 mm. Easily distinguished from other species by the three large posterior dorsocentral bristles. Anterior acrostichial bristles three, well-defined; male with hypopygium reddish brown, often pruinose; second segment not bristly; hind tibia with moderate villosity; female with genital segment orange; orifice rounded with many bristles above. Larva - as described in the Key.

Habits: Saprophagous

Comments: This species was most common from December to March, decreasing in abundance by April. Larviposition on carcasses was extensive from December to March; larviposition was noted in April but few adults emerged from the carcasses.

Sarcophaga misera sarracenioides Aldrich

Recognition characters: Length 8-13 mm. This species is most readily recognized by the extensive reddish-yellow area on the posterior half of the fourth abdominal segment. Posterior dorsocentral bristles four, strongly developed; hind tibia with dense villosity; anterior acrostichial bristles absent; male with aedeagus sharply pointed distally and with four slender processes; female with genital segment reddish-yellow, genital orifice triangular.

Habits: Several authors have commented on the versatility of this species regarding food habits. It has been reared from grasshoppers, decayed meats and garbage and presumably ranges from scavenger to parasite according to the availability of food.

Comments: This species was abundant from December through February and specimens were taken while crawling over the carcass but none were reared from the carcass.

Cochliomyia macellaria (Fabricius) - Secondary screw-worm fly

Recognition characters: Adult - length 6-9 mm., very similar in appearance to Paralucilia wheeleri but can easily be distinguished

by the golden hairs on the frontale and whitish squamal lobes. Palpi narrow, orange; bucca golden with orange hair; thorax metallic blue-green and black, three black longitudinal stripes on dorsal surface of the thorax extending to the scutellar suture; squamal lobes whitish; fourth abdominal segment pollinose laterally. Larva - absence of an accessory oral sclerite distinguishes this species from larvae of Paralucilia wheeleri; peritreme incomplete.

Habits: Saprophagous; very rarely invading old wounds in animals (James, 1947).

Comments: This species was extremely common throughout November and December, but disappeared by the beginning of January. Females laid great masses of eggs on a coyote carcass in early December.

Paralucilia wheeleri (Hough)

Recognition characters: Adult - length 9-11 mm. Distinguished from Cochliomyia macellaria by the brownish-black squamal lobes and black hair on the frontale. Palpi clavate, orange; bucca orange, clothed with yellow hairs; thorax with blue-green metallic lustre; three black stripes on the dorsal surface of the thorax extending to the scutellar suture; squamal lobes brownish-black; fourth abdominal segment not pollinose laterally. Larva - Accessory oral sclerite present; more robust than larvae of Cochliomyia macellaria; peritreme incomplete.

Habits: Saprophagous

Comments: This species was present from December to March but was never abundant.

Phormia regina (Meigen) - Black blow fly

Recognition characters: Adult - 6-11 mm. Distinguished from Paralucilia and Cochliomyia by the absence of the broad dorsal longitudinal stripes. Palpi yellow, clavate; bucca black with black hair; thorax black with greenish or bluish metallic lustre; abdomen shining black to olivaceous; squamal lobes yellowish. Larva - as described in the Key.

Habits: Saprophagous; occasionally associated with wound myiasis. often associated with sheep in the Southwest (James, 1947).

Comments: This species is the most common blow fly present during the winter months, being especially abundant from January to April and tapering off during April.

Calliphora coloradensis Hough

Recognition characters: Adult - length 9-12 mm. Can be recognized by the reddish bucca. Frontal bristles about 10, some occasionally reduced to hairs; bucca reddish for at least the anterior half; short setae on faciale extending one-half the distance to the antennal base; postintraalar bristles three, well-defined but anterior bristles sometimes rather weak; abdomen metallic blue; lower squamae pilose above. Larva - Can be recognized by

the uniform peritreme thickness and pigmentation. Posterior spiracular slits usually rather straight or only slightly bent.

Habits: Saprophagous.

Comments: The abundance of this species coincides with that of E. lilaea from December to March. Adults are most abundant in January and February.

Calliphora livida Hall

Recognition characters: Adult - length 10-12 mm. Similar to C. coloradensis, but bucca is black. Frontal bristles seven or eight; bucca black, clothed with black hair; setae on faciale extending three-quarters of the way to the antennal base; postintraalar bristles three; abdomen metallic blue; lower squamae pilose.

Habits: Saprophagous

Comments: This species was rarely seen and did not oviposit on carcasses.

Eucalliphora lilaea (Walker)

Recognition characters: Adult - length 5-9 mm. Bucca black with grayish pollen; thorax black or bluish-black; most specimens with two postintraalar bristles, occasionally a weak third one; faciale with strong ascending bristles extending from one-half to two-thirds of the distance to the antennal base; abdomen metallic blue; frontal bristles

usually six; lower squamae pilose above. Larva - can be recognized by the irregularly broad peritreme and the area of lighter pigmentation around the stigmatic scar. Other characters as described in the Key.

Habits: Saprophagous

Comments: This species is abundant during the winter months from December to March but disappears by mid-April along with species of Calliphora. Oviposition occurs only during the winter months.

Phaenicia sericata (Meigen)

Recognition characters: Adult - length 6-9.5 mm. This species can be recognized in the field by its bright greenish-bronze metallic lustre. Thorax metallic green but often bluish or purplish in dried specimens; preacrostichial bristles two, strong; postacrostichial bristles three, strong; abdomen metallic green; first segment black; lower squamae whitish, bare above. Larva - Can be distinguished from Chrysomyinae by the closed peritreme and from other Calliphorinae by the absence of the accessory oral sclerite and the thin, lightly pigmented peritreme of the posterior spiracle.

Habits: Saprophagous; workers in Australia, South Africa, England and the Southern United States have described P. sericata as injurious to sheep with wounds or soiled wool. This species also has been used extensively in wound therapy.

Comments: P. sericata is a summer species, being rather rare from December to March but increasing rapidly in numbers during April. It is probably present to a greater or lesser extent throughout the year as is Phormia regina. Oviposition is restricted during the winter months but some adults are produced.

APPENDIX E

PREDATORS AND PARASITES

1. Predators

a. Histeridae

The predators and parasites found during this study probably had little effect on the whole mass of developing flies since they were never present abundantly. Histerid beetles of the genus Saprinus were the most abundant predators from December to April. These could always be found beneath the carcasses devouring larvae. In December, several larvae of Saprinus sp. were discovered in the soil beneath the carcasses. When placed in containers with blowfly pupae, the larvae chewed holes in the pupae and devoured the contents. When ready to pupate, the larvae cemented small soil particles into a spherical case. Adult Saprinus beetles emerged in about 45 days. Xerosaprinus sp., a smaller histerid, was also present, mainly during the cooler months from December to March. Habits are similar to Saprinus sp.

b. Staphylinidae

Staphylinid beetles were quite common, especially during the cooler months. The most conspicuous species was Creophilus villosus (Gravenhorst) a very large and active form. This species was often seen

running actively over a carcass and seizing larvae in its jaws. There were never more than two or three specimens on a carcass at any one time so it is unlikely that they materially reduced the number of larvae. Fuller (1934) states that most of the larvae devoured were those forced away from the carcass and would have starved if not devoured, but in the present study most of those eaten were mature larvae migrating to the soil for pupation. C. villosus usually resided beneath the carcass and seized larvae as they began to burrow into the soil. Numerous other staphylinids of the subfamily Aleocharinae were noted. Beeria punctata Hatch was rarely seen and was never observed feeding on larvae.

c. Formicidae

Two formicids were common throughout the study. Novomessor cockerelli (André) was the most common predator of larvae. These ants were commonly found carrying away larvae in their jaws. Although they could be seen during much of the day, they were most active in the early morning or at dusk. In April, N. cockerelli was seen only at sunrise or after sunset. When the position of the carcass was shifted and a number of larvae crawled away, N. cockerelli individuals darted in and picked off stray larvae. Usually, individuals patrolled around the carcass and snatched individual larvae as they strayed from the carcass.

Another species, the common desert fire ant, Solenopsis xyloni (McCook) was noted during carcass exposures in April. A large number

of workers was present beneath the tray containing the carcass and as larvae escaped and burrowed into the soil, the workers of S. xyloni attacked them and eventually carried them off. A large number of small larvae were destroyed in this manner.

Although ants are sometimes a nuisance, their activities during this study were restricted and they were never present in large enough numbers to materially affect the maggot population. Only rarely did any individuals ascend the carcass tray and seize larvae directly from the carcass.

2. Parasites

Two parasites were found to infest the maggots or pupae, the pteromalid chalcidoid Mormoniella vitripennis (Walker) and the braconid, Alysia ridibunda Say.

a. Mormoniella vitripennis

M. vitripennis is apparently cosmopolitan in distribution and was reported by Fuller (1934). Laing (1937), studying the habits of M. vitripennis, found that it is strongly attracted to carrion by olfaction after nine days, even though no host larvae are developing on the carcass. M. vitripennis oviposits only on exposed pupae, and is unable to penetrate the soil. Most pupae are thus protected and only

under exposed conditions will the pupae be parasitized. Laing found that the female M. vitripennis mounts a pupa and thrusts her ovipositor inside. As a drop of fluid exudes, the female laps up this fluid and then deposits one or more eggs inside the pupa.

During the carcass exposure in February, adults of M. vitripennis were abundant around the carcass by the eleventh day after initial exposure. After all the larvae had left the dried carcass, thirty pupae lying exposed on the surface of the soil were collected. Eight of these were found to be parasitized by M. vitripennis. The number of Chalcids per pupa ranged from three to twenty-five. No other parasites were collected from larvae or pupae in February. Although adults of M. vitripennis were abundant during the April carcass exposures, no parasitism of pupae by this species was found. In all cases, the host pupa was that of P. regina, a secondary species. Fuller (1934) states that only pupae of secondary species are attacked.

b. Alysia ridibunda

The Braconid parasite, Alysia ridibunda, was found during carcass exposures during April. It is not certain from descriptions in the literature whether the parasite encountered here and that described in other papers are the same species, but its range coincides with A. ridibunda as described in the literature. If the parasite involved here is the

same as that described by Roberts (1935), it has a very wide distribution, from New York south to Florida and west to Arizona. In laboratory experiments, Roberts found that the female stands over a host larva and the ovipositor is thrust into the soft body, depositing a single egg. A. ridibunda was reported to be active from March to November but was found during January and February only as mature larvae or hibernating pupae. Lindquist (1940) attempted to introduce A. ridibunda into the Uvalde, Texas area but without success.

Phaenicia sericata (Meigen) is reported to be a host for A. ridibunda but no specimens were obtained from Phaenicia pupae. All the specimens came from pupae of Hystricocnemina plinthopyga (Wiedemann). Sarcophagid larvae are known to be the preferred hosts. A total of 389 H. plinthopyga pupae produced 42 A. ridibunda adults and 347 normal H. plinthopyga adults. The rate of parasitism was about 12%. As the April carcass exposures occurred during the beginning of A. ridibunda activity during the spring, it is not unlikely that this rate of parasitism might increase during the summer months. No A. ridibunda were obtained from pupae collected in December.

Both A. ridibunda and M. vitripennis contribute little to reducing the flies produced from a carcass, although Lindquist (1940) reports up to 80% parasitism of H. plinthopyga by A. ridibunda.

APPENDIX F

OTHER INSECTS ASSOCIATED WITH DECAY

1. Dermestidae

Insects which are associated with carcasses after the maggots have departed were found in abundance. Most conspicuous of these were the large dermestid beetles, Dermestes marmoratus Say and Dermestes maculatus DeGeer. Both species were present at about the same time in the carcass but D. marmoratus was far more abundant. Throughout the course of the study, adults of both species crawled beneath the carcasses and fed on the fluid products of liquefaction. Adults were attracted to carcasses as early as the third day. Larvae of D. marmoratus and D. maculatus did not appear until all flies had left the carcass and body tissues were thoroughly dry. Carcasses exposed in December and February still had numbers of larvae on them in April. The remaining skin and bones were reduced to a fine powder by the feeding of the larvae.

2. Miscellaneous Diptera

Another late member [or tertiary form as defined by Fuller (1934)] was the cheese skipper, Piophila casei Linnaeus. The larvae of the cheese skipper are readily recognized by their curious habit of springing into the

air. These larvae were most abundant while the carcass still retained some moisture and after most of the maggots had departed. This species commonly attacks cured meats in storage (Metcalf, Flint and Metcalf, 1962).

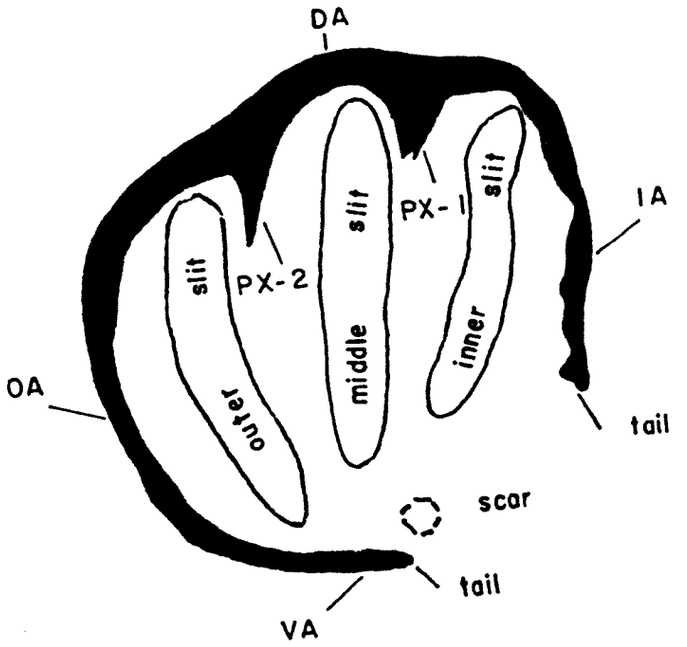
Several other dipterous species were observed flying around carcasses at various times. Many Anthomyiidae were present, including Ophyra aenescens Wiedemann and the striking Ophyra leucostoma Wiedemann. Several tachinid flies were also caught either on the carcass or resting on the cage screening. Musca domestica Linnaeus was occasionally seen during the study and probably came from nearby ranches where it is abundant. During the first week of exposure, Chloropidae were very abundant where there were accumulations of fluids from the carcass. None of these species was observed to breed in carcasses.

Fig. 4. Generalized posterior spiracle of Sarcophaga. Third instar, left, posterior spiracle.

Terminology: OA = outer arc, DA = dorsal arc, IA = inner arc, VA = ventral arc, PX-1 = peritreme extension 1, PX-2 = peritreme extension 2. (After Sanjean, 1957)

Fig. 5. Generalized cephaloskeleton of Calliphora. Lateral view. Third instar.

Terminology: AC = accessory sclerite, DS = dental sclerite, LS = labial sclerite, HS = Hypostomal sclerite, PS = parastomal sclerite, DA = dorsal arch, DC = dorsal cornua, VC = ventral cornua (terminology adapted from Hall, 1947).


DA
IA
PX-1
PX-2
slit
slit
slit
middle
inner
outer
OA
tail
scar
tail
VA

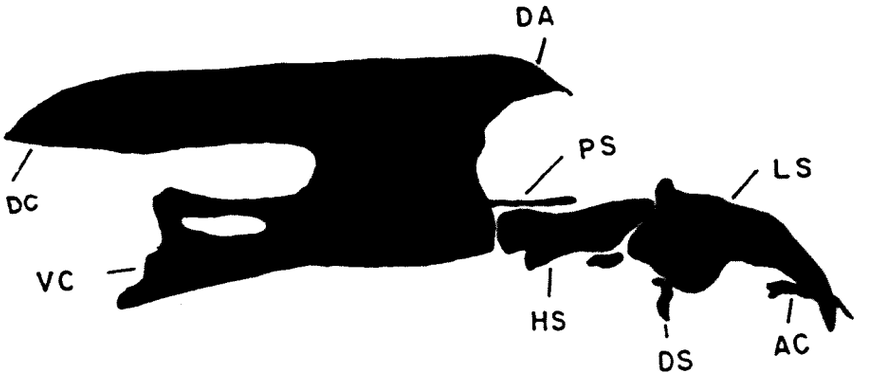
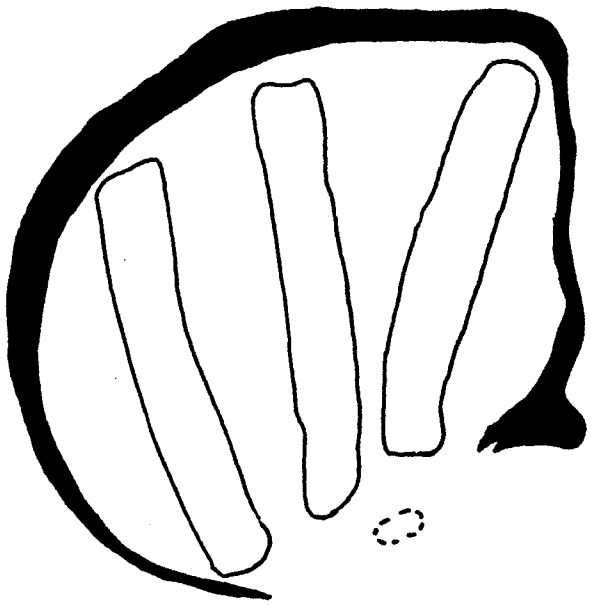

DA
PS
LS
DC
VC
HS
DS
AC

Fig. 6. Sarcophaga cessator Aldrich. Left posterior spiracle. Third instar. x200.

Fig. 7. Sarcophaga cessator Aldrich. Cephaloskeleton. Third instar. x200.



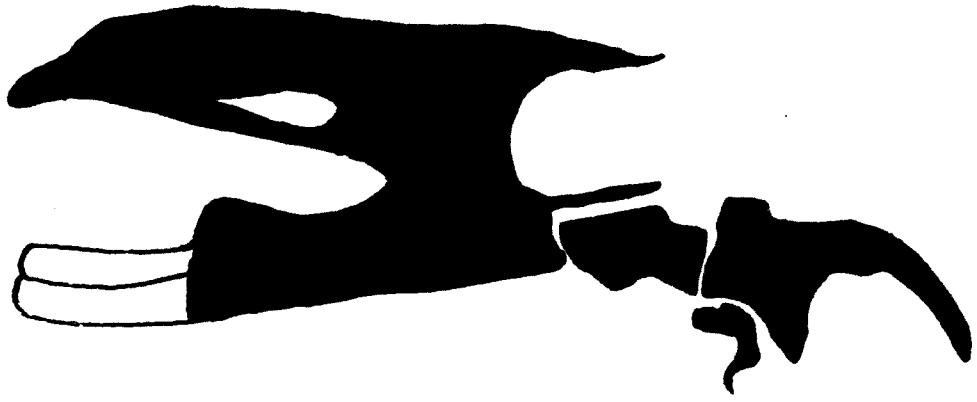


Fig. 8. Hystricocnemina plinthopyga (Wiedemann). Left posterior spiracle. x200. Third instar

Fig. 9. Hystricocnemina plinthopyga (Wiedemann) cephaloskeleton. x200. Third instar.

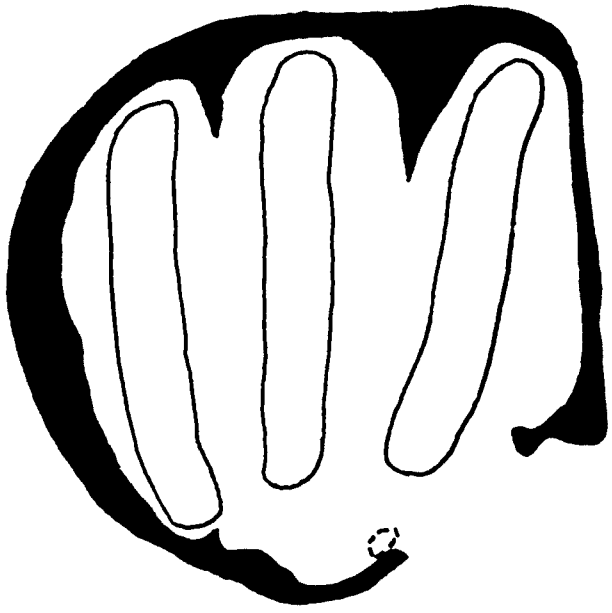


Fig. 10. Cochliomyia macellaria (Fabricius). Left posterior spiracle. Third instar. x200.

Fig. 11. Cochliomyia macellaria (Fabricius) cephaloskeleton. Third instar. x200.

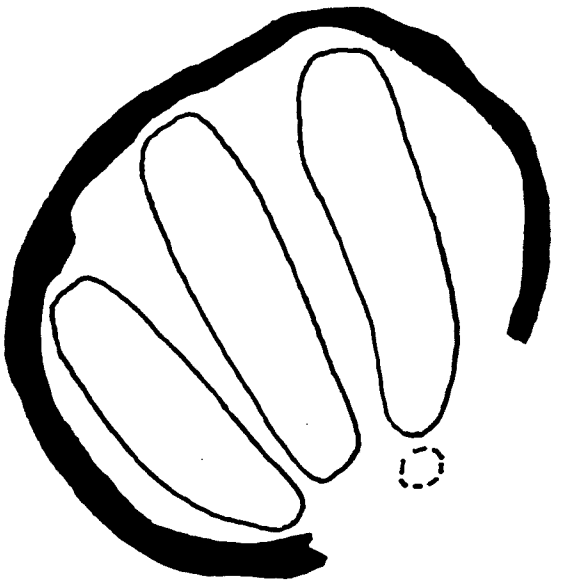


Fig. 12. Paralucilia wheeleri (Hough). Left posterior spiracle. Third instar. x200.

Fig. 13. Paralucilia wheeleri (Hough). Cephaloskeleton. Third instar. x200.

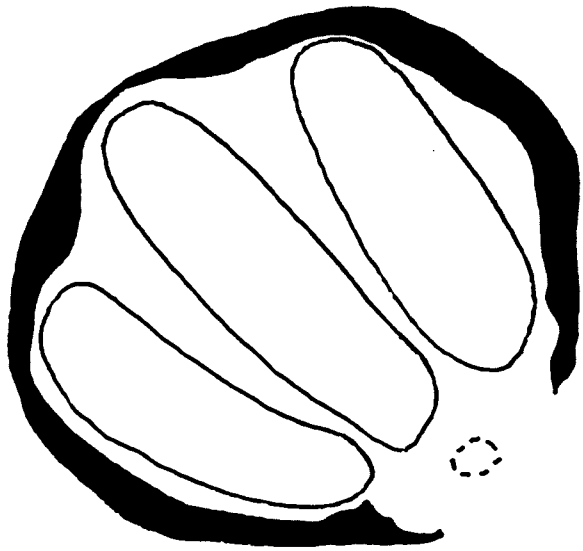


Fig. 14. Phormia regina (Meigen). Left posterior spiracle. Third instar. x200.

Fig. 15. Phormia regina (Meigen). Cephaloskeleton. Third instar. x200.

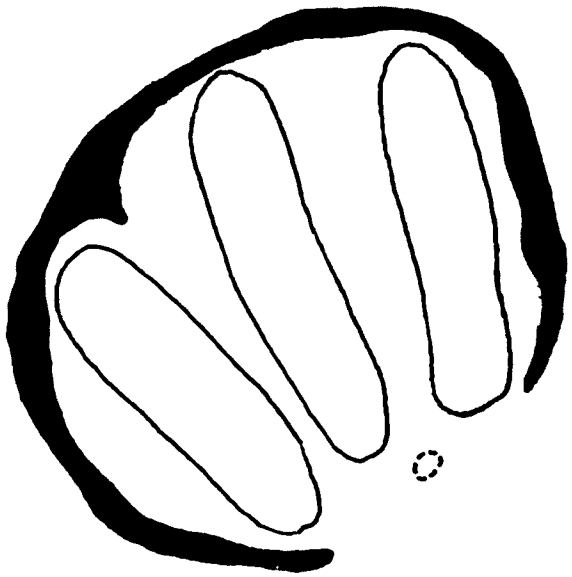
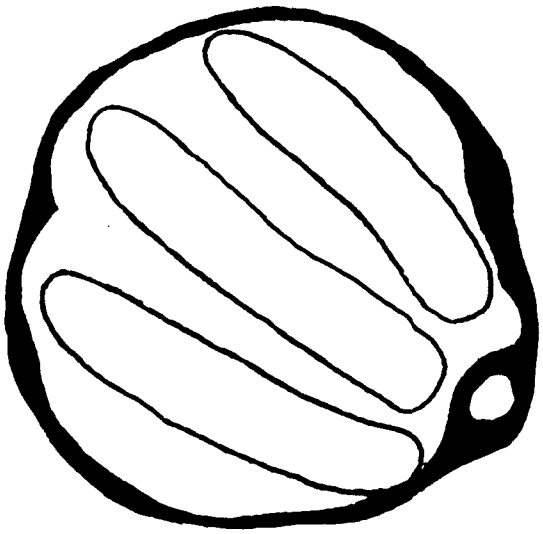


Fig. 16. Phaenicia sericata (Meigen). Left posterior spiracle. Third instar. x200.

Fig. 17. Phaenicia sericata (Meigen). Cephaloskeleton. Third instar. x200.



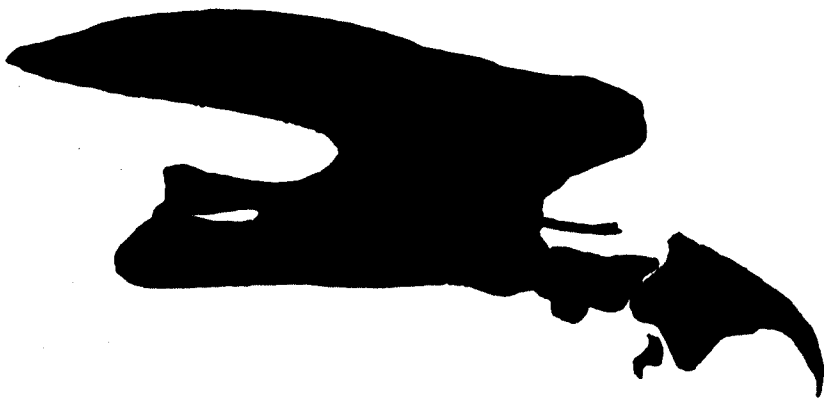


Fig. 18. Eucalliphora lilaea (Walker). Left posterior spiracle. Third instar. x200.

Fig. 19. Eucalliphora lilaea (Walker). Cephaloskeleton. Third instar. x200.

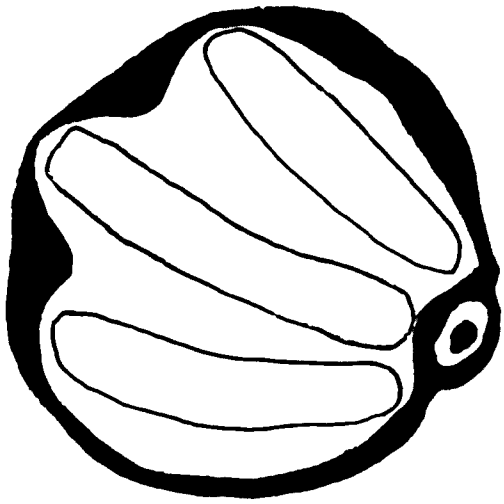
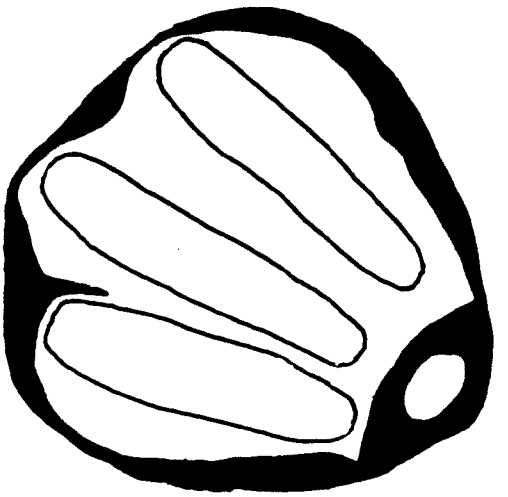


Fig. 20. Calliphora coloradensis Hough. Left posterior spiracle. Third instar. x200.

Fig. 21. Calliphora coloradensis Hough. Cephaloskeleton. Third instar. x200.



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